Linking climate, distribution and growth in forest research: can dendrochronology improve species distribution modelling?

Tese de Doutoramento

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Linking climate, distribution and growth in forest research: can dendrochronology improve species distribution modelling?

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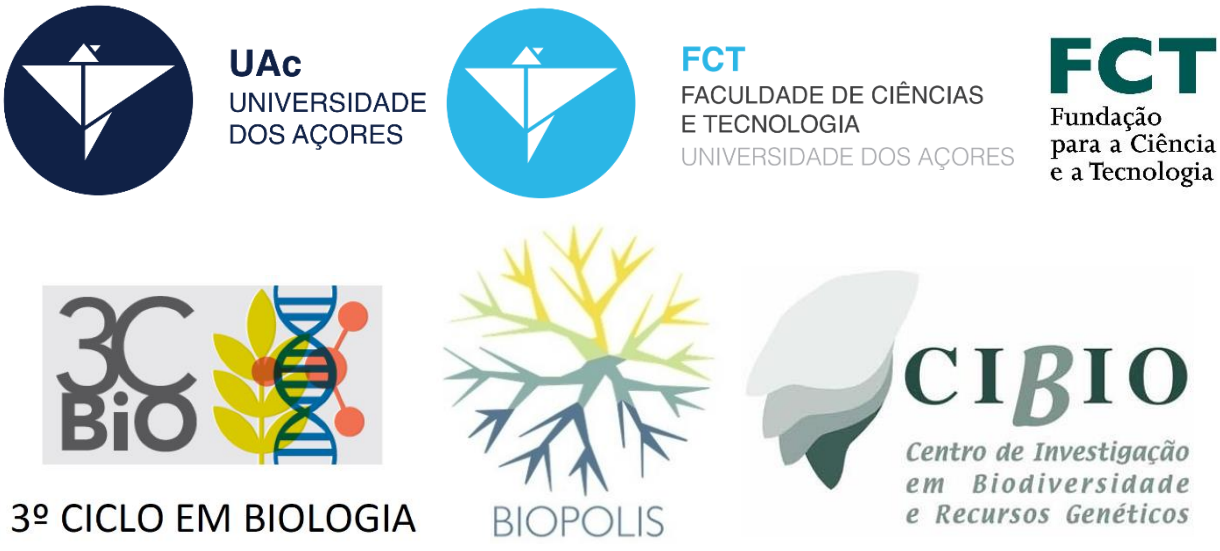

“Research is what I am doing when I do not know what I am doing.”

Wernher von Braun

Ad perpetuam memoriam

Maria do Espírito Santo Costa Melo Cláudio (1943-2018)

Jacinto Humberto Aguiar Pavão (1934-2017)

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Resumo

Estudos em dendrocronologia são mais escassos em áreas com humidade relativa alta, baixa amplitude térmica e sazonalidade pouco pronunciada. Por isso, esta lacuna de conhecimento cria uma oportunidade para explorar os anéis de crescimento de espécies arbóreas da floresta Laurissilva e montana dos Açores. Esta trabalho teve como objetivo reduzir esta lacuna e compreender melhor o papel da dendrocronologia na modelação ecológica, sendo que para tal, foram recolhidas mais de 900 amostras de madeira de três espécies arbóreas nativas dos Açores: *Juniperus brevifoli*a (Seub.) Antoine (Cupressaceae), *Ilex azorica* Gand. (Aquifoliaceae) e *Laurus azorica* (Seub.) Franco (Lauraceae). Dez diferentes locais foram escolhidos em duas ilhas, São Miguel e Terceira, e foram aplicados métodos padrão da dendrocronologia e dendroclimatologia, que incluem o alinhamento, detrending e exclusão de amostras ou porções de cronologias. Várias opções de modelação (por exemplo, Modelos Lineares Generalizados e Random Forest) foram usadas para determinar os principais fatores climáticos que afetam o crescimento radial das árvores. Todas as três espécies estudadas mostraram alguns limites de anéis parcialmente indistinto. No entanto, após a aplicação rigorosa de métodos dendrocronológicos, mostraram um potencial aceitável para investigação em dendrocronologia. A madeira de *J. brevifolia* apresentou uma distinção de cores entre o alburno (tons amarelados) e o cerne (tons avermelhados). No *I. azorica*, foi encontrada uma linha de vasos associada à fronteira dos anéis na maioria das amostras. Ambas as cronologias maiores e mais pequenas foram encontradas para o *I. azorica*, respetivamente nas Sete Cidades com 47 anos de comprimento e na Terra Brava com 128 anos. Diversas relações foram encontradas entre o crescimento das árvores e temperatura, principalmente um efeito positivo da temperatura da primavera (*I. azorica* e *L. azorica*) e efeito negativo das temperaturas de verão (todas as três espécies). A precipitação da primavera também

afetou o crescimento radial do *I. azorica*. O clima do ano anterior foi também relevante no crescimento das árvores do *I. azorica* e *L. azorica*, indicando efeitos fisiológicos tardios. Nos Açores, as limitações nos estudos de dendrocronologia estão relacionadas com a baixa amplitude térmica entre estações do ano, com a sazonalidade pouco pronunciada, e com a elevada variação dos padrões dos anéis de crescimento. A variação encontrada entre as populações está relacionada com perturbações naturais (elevação, diferenças de solo e processos de sucessão e regeneração) ou antropogénicas (corte de árvores e plantação de espécies exóticas). Ambos, são fatores que influenciam os diferentes comprimentos das cronologias construídas e das pequenas variações das relações de clima-crescimento. Os resultados globais sugerem que, no futuro, ao usar ferramentas dendrocronológicas com medições refinadas de anéis de crescimento, pode ser possível calcular as taxas de crescimento e integrar esta informação como variáveis preditoras em modelos de distribuição de espécies, embora necessitem de validação com dados de campo ou de deteção remota. O sinal de temperatura encontrado nas relações de crescimento climático é alarmante, porque espera-se que as temperaturas de verão aumentem (alterações climáticas), o que pode levar à extinção local de espécies. Assim, os métodos utilizados nesta tese sugerem que, esta abordagem pode ser utilizada para compreender o impacto das alterações climáticas no crescimento das árvores. Também, esta abordagem complementada com outras medidas de crescimento radial das árvores e uso de dendrómetros, pode ser aplicada a outras espécies nativas dos Açores em baixa altitude, como *Morella faya* e *Picconia azorica*, espécies exóticas, como a *Cryptomeria japonica*, ou outras espécies já estudadas em climas temperados na Europa. Com a base de dados criada neste trabalho, uma análise global com diferentes métodos de detrending e de abordagens de modelação pode ser aplicada, de forma a dar pistas para uma metodologia abrangente adequada para a região.

Abstract

Dendrochronological studies are scarcer in areas with high relative humidity, low thermal amplitude and without a very pronounced climatic seasonality, such as the Azores Islands. Hence, this knowledge gap extends to the native and endemic Azorean tree species, for which almost no tree ring research was available at the beginning of the present work, despite the available knowledge about their ecological amplitudes, occurrences, and potential distribution. This research aimed to start fulfilling that gap and to clarify if dendrochronological research could support ecological modelling and, consequently, a better understanding of forest dynamics in the Azores. To accomplish this, more than 900 wood cores were collected from three Azorean endemic woody species: *Juniperus brevifoli*a (Seub.) Antoine (Cupressaceae), *Ilex azorica* Gand. (Aquifoliaceae) and *Laurus azorica* (Seub.) Franco (Lauraceae). Ten different stands were sampled in São Miguel and Terceira islands, applying standard dendrochronological and dendroclimatic methods, including crossdating, detrending, and the exclusion of samples or chronology portions, due to tree ring anomalies or to low sampling depth. Likewise, several modelling options were used, such as Pearson correlation, Generalized Linear Models and Random Forest, to determine the most relevant climatic drivers of tree growth. Although the three species showed some partially indistinct ring boundaries and wedging rings, globally, the samples we considered as adequate for dendrochronological research. A clear separation between a yellowish sapwood and the reddish-brown heartwood was found in *J. brevifolia*. For *I. azorica*, a layer of vessels associated to the ring boundary was found in most growth rings. Both the shortest and longest chronologies were found for *I. azorica*, respectively in Sete Cidades with a length of 47 years and in Terra Brava with a length of 128 years. Diverse relations between tree growth and temperatures were found, mainly a positive effect of spring temperature (*I. azorica and L. azorica*) and a negative effect of

summer temperatures (all three species). Precipitation also affected tree radial growth, especially the positive effect of spring precipitation (*I. azorica*). Additionally, previous year climate was also relevant on tree growth in *I. azorica* and *L. azorica*, indicating lagged physiological effects. In the Azores, limitations in dendrochronological studies are related to the low thermal amplitude, to the absence of a pronounced climatic seasonality, and to the high within stand variation in tree ring patterns. Moreover, the high variability found between stands is likely related to natural (e.g., elevation, terrain and soil differences, succession and regeneration processes) or anthropogenic disturbance (e.g, tree cutting, plantation and spread of exotic species), thereby contributing for a considerable variation in chronology length and to slightly different climate-growth relationships at different sites. Nevertheless, the global results suggested that, in the future, by using this dendrochronological approach with refined tree-ring measurements, it would be possible to calculate radial growth rates and to integrate this information in species distribution models, to be validated using field and remote sensing data. The temperature signal found in climate-growth relationships raises concern, because summer temperatures are expected to increase, which could lead to local extinctions. Our results also suggest that this approach could be used to better understand the impact of climate change on tree growth. Also, this approach, complemented with other radial growth proxies and the use of dendrometers, could be extended to other native species with lower elevation distribution ranges, such as *Morella faya* and *Picconia azorica*, or to exotic species, such as *Cryptomeria japonica* and tree species already studied in temperate Europe. Additionally, a global analysis of the entire dataset, exploring different detrending and modeling methods could also be undertaken, providing hints for a comprehensive methodology suitable for the region.

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List of Abbreviations

TBP – t-value

ITRDB – International Tree-Ring Data Bank

TRW – Tree-ring width

DBH – Diameter at breast height

DB – Diameter at base

Hmax – Maximum height

TRWi – Tree-ring indices

EPS – Expressed population signal

Rbar – Mean Pearson correlation or mean interseries correlation

CHELSA – Climatologies at high resolution for the earth's land surface areas

T - Temperature

P - Precipitation

AC1- First order autocorrelation

GLM – Generalized Linear Model

PCA – Principal Component Analysis

VIF – Variation Inflation Factor

AIC - Akaike Information Criterion

AICc – Corrected Akaike Information Criterion

RF- Random Forest

List of Publications

This thesis contains data and information also present at the following publications:

Pavão, D.C., Jevšenak, J., Petrillo, M., Camarinho, R., Rodrigues, A., Silva, L.B., Elias, R.B., Silva, L., 2022. Dendrochronological potential of the Azorean endemic gymnosperm *Juniperus brevifolia* (Seub.) Antoine. Dendrochronologia 71, 125901. https://doi.org/10.1016/j.dendro.2021.125901

Pavão, D.C., Jevšenak, J., Engblom, J., Silva, L.B., Elias, R.B., Silva, L., 2023. Tree growth-climate relationship in the Azorean holly in a temperate humid forest with low thermal amplitude. Dendrochronologia 77, 126050. https://doi.org/10.1016/j.dendro.2022.126050

Pavão, D.C., Jevšenak, J., Silva, L.B., Elias, R.B., Silva, L., 2023. Climate-Growth relationships in *Laurus azorica* - a dominant tree in the Azorean laurel forest. Forests, *In Press*.

CHAPTER 1

General Introduction

CHAPTER 1

General Introduction

1. Chapter outline

In this first chapter, a general overview of the research framework is provided, including an introduction to the main topics in dendrochronology, as well as a description of two branches of dendrochronology that are focused on in this dissertation: dendroclimatology and dendroecology.

This chapter also briefly describes the data analysis approaches followed in dendrochronology, from the process of building tree-ring chronologies to the determination of the relationship between tree growth and climate, also including the importance of modelling in forest ecology and management.

A brief introduction of the study area, the Azores archipelago is also included, focusing on the Azorean natural forests within the context of the Macaronesian forests, but also addressing previous tree growth ring research conducted in the region.

Finally, this chapter also clarifies the motivation for this research program, and introduces the research questions and main goals of the investigation. It ends with a global outline of this dissertation, which includes three research chapters, corresponding to accepted scientific articles, and a final chapter regarding a general discussion and conclusion.

2. Dendrochronology

2.1. Tree growth rings

Tree growth rings are a distinctive source of information, providing data with a precise temporal resolution, usually on an annual scale. Moreover, growth ring research can be applied in many biogeographic regions, including those where trees show dormancy during drought or cold seasons (Fritts, 1976; Cook and Kairiukstis, 1990; Speer, 2010).

Tree growth rings are formed by the vascular cambium that is composed by a thin layer of meristematic cells positioned between the secondary xylem (wood) and the secondary phloem (living bark) (Larson, 1994; Rowe and Speck, 2005). Generally, growth rings include earlywood and latewood. Along the growing season, the cambium initially forms thin-walled xylem cells with large-lumen (i.e., earlywood) followed by thick-walled xylem cells with narrow-lumen (latewood) (Figure 1). In general, latewood provides strength and structure, while earlywood allows conduction of water and nutrients (Larson, 1994; Cutler et al., 2008; White, 2012; Lopez and Barclay, 2017).

Dendrochronology is a research area using tree growth ring measurements, such as tree-ring widths and xylem vessel areas, dated to their exact year of formation, to analyze temporal and spatial patterns of a diverse array of processes on interest in physical and social sciences (Douglass, 1928).

Several proxies can be extracted from those measurements. The most used proxy is total tree-ring width, where early and latewood widths can be measured separately (Briffa, 1999; Speer, 2010). Other proxies include wood density, which translates into the maximum density of latewood, usually reflecting the effect of temperature on radial

growth (e.g., Blake et al., 2020; Kaczka and Wilson, 2021) or stable carbon and oxygen isotopes used in climate reconstructions (e.g., Schollaen et al., 2017).

Independently from the chosen proxy, growth ring dating can be used in different sub-areas, and thereby co-analyzed with other variables, such as climatic data. Hence, dendrochronology is a multidisciplinary field combining principles from biology, ecology, climatology, and geology (Douglass, 1928; Fritts, 1971; Sheppard, 2010; Speer, 2010).

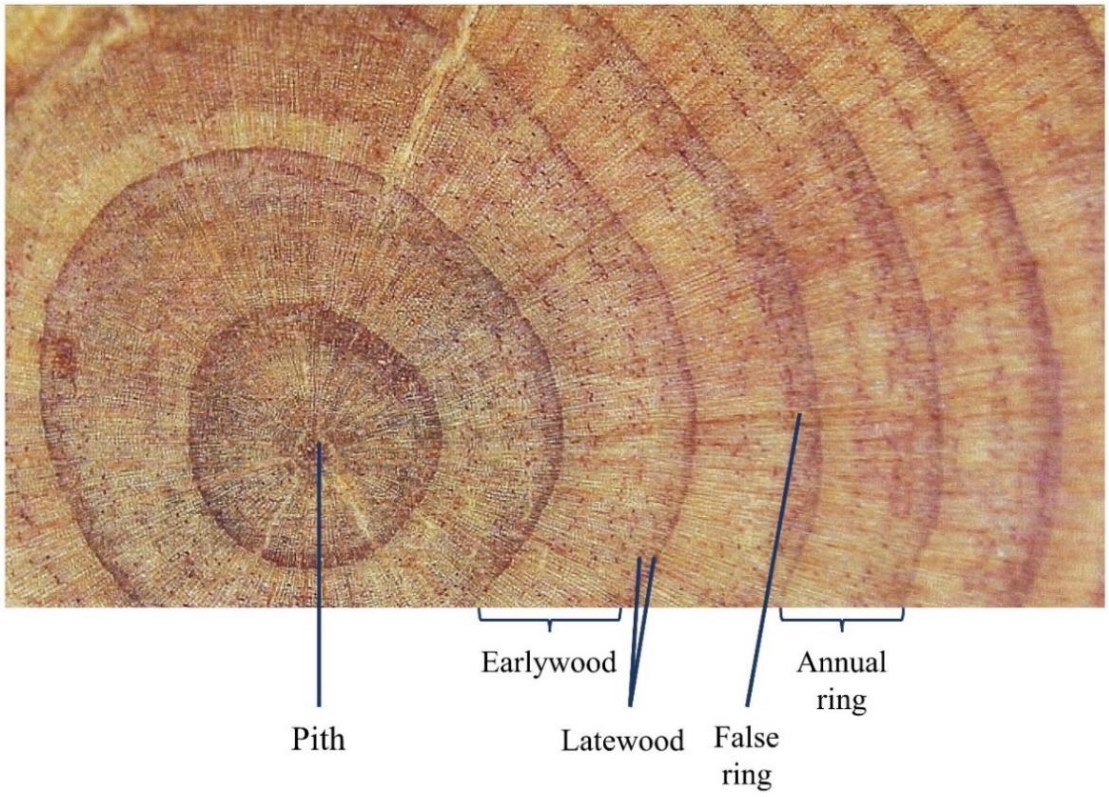

Figure 1. A scheme of *Juniperus brevifolia* wood (cross-section), representing the organization of an annually resolved growth ring.

2.2. Principles of dendrochronology

Dendrochronology follows several principles and quality control methods (Fritts, 1971, 1976). These principles include the selection of appropriate sites, species, and trees, as well as the use of standardized methods for defining tree-ring variables, crossdating, replication, standardization, and detrending (Fritts, 1976; Cook and Kairiukstis, 1990). Adhering to these guidelines helps to ensure the accuracy and validity of dendrochronological analyses.

The *Uniformitarian Principle* acknowledges that physical and biological processes that are related to current patterns of tree growth, must have also worked in the past. Therefore, understanding environmental conditions that affect tree growth rings in the present allows reconstructions of past environments based on the respective tree growth ring data (Fritts, 1976; Wilmking et al., 2017).

The *Principle of Limiting Factors* affirms that plant growth and development are more constrained by the primary environmental variables that are most limiting. For example, in arid and semiarid ecosystems, temperatures are usually high but precipitation low or even missing. Thus, precipitation will be the primary environmental variable affecting or limiting tree growth (Fritts, 1976). However, for forest tree species growing in temperate conditions, instead of climatic variables, non-climatic factors related to stand dynamics, such as competition, may be the most limiting to tree growth (Speer, 2010).

The *Principle of Aggregate Tree Growth* ascertains that any individual tree-growth chronology can be "decomposed" into an aggregate of environmental factors that affected the pattern of tree growth over time. That is, the total variability of the tree-ring series, expressed in tree-ring chronologies, should be examined taking into account: i) the age-related growth trend, ii) the climatic signal of a specific region, iii) the exogenous and

endogenous conditions, and iv) the remaining unexplained "noise" (Fritts, 1976; Cook and Kairiukstis, 1990; Speer, 2010).

The *Principle of Ecological Amplitude* states that trees growing near the extremes of their ecological amplitude are subject to substantial climatic stress, being more susceptible to a climatic limitation (Fritts, 1971; Hughes et al., 1982; Speer, 2010). Consequently, several biogeographic constraints should be considered, such as arid versus wet areas. Moreover, there are certain habitats, such as tropical perhumid forests, where trees grow along the entire year impeding the formation of distinct growth rings (Babst et al., 2018).

The *Principle of Site Selection* is extremely connected to the *Principles of Limiting Factors* and *of Ecological Amplitude*, ascertaining that site selection should be based on criteria that maximizes the environmental signal being investigated (Fritts, 1976; Speer, 2010). For example, trees growing in drought conditions (such as rocky outcrops) may be sensitive to changes in precipitation, making them a good choice for studying historical patterns of precipitation. On the other hand, trees growing in wetter sites (such as wetlands) may be more sensitive to temperature changes and could be a better choice for analyzing temperature trends.

Due to interannual climatic variability, trees develop a characteristic sequence of wide and narrow annual growth rings. The synchronization of growth patterns of various trees from the same location, allows the exact dating of the wood from a specific stand. However, in addition to the general signal of the growth rings, each individual tree can present an individual response to climatic events, given slight differences in their habitat or ecotype (Fritts, 1976; Speer, 2010). When these climatic events are not growth-favorable, there is a possibility that growth rings can develop anomalies such as "missing rings" or “false rings” (Larson, 1994; Speer, 2010). Such anomalies can be detectable

when comparing growth ring patterns from multiple samples from the same tree, or from several trees at the same site – The *Principle of Crossdating* (Fritts, 1976; Sheppard, 2010; Speer, 2010). This process is the most important principle of dendrochronology and is described by Fritts (1976) as "matching of ring-width patterns among specimens; examining the synchrony; recognizing any lack of coincidences; inferring where rings may be absent, false, or improperly observed; testing the inference by examining carefully the ring structure in other specimens; and finally arriving at the correct regional chronology with agreement among the growth sequences of trees in neighboring stands".

This alignment allows all rings to be recognized and assigned to the correct year (Fritts, 1976; Speer, 2010) and, consequently, it is also crucial to establish different chronologies for distinct species, due to the different tolerance to a range of environmental conditions and large plastic responses of distinct tree species (e.g. Sáenz-Romero et al., 2017). Likewise, each different climatic region and the increased distance between trees, decreases the correlation between tree ring series, thus requiring a different chronology for each ecoregion (Mörner and Karlén, 1984).

The *Principle of Replication* defines that sampling more than one stem radius per tree and more than one tree per site, reduces non-desirable environmental signal peculiar of a specific tree. Likewise, by ensuring replication, the environmental signal being investigated can be maximized, and the amount of noise minimized (Fritts, 1976; Speer, 2010). Connecting to the *Principle of Crossdating*, a single tree-ring sample is not enough to build a chronology (Fritts, 1976; Speer, 2010), thus the importance of tree replication in the alignment process.

3. Dendroclimatology

As mentioned before, the interannual variability of the radial increment, from both early and latewood, is determined predominantly by climatic factors. Since growth rings reflect the annual changes of the climate at the region under study, tree-ring and climate patterns of the region should be similar (Fritts, 1976; Speer, 2010).

Dendroclimatology, as a sub-area of dendrochronology, relates tree-ring measurements with climatic data. Moreover, this area works under the same principles as dendrochronology, especially those involving the sampling of trees where the climatic conditions are limiting growth. That is, habitats where precipitation limits tree growth are more adequate to reconstruct past precipitation patterns (e.g., Qin et al., 2003; Treydte et al., 2006; Opała-Owczarek and Niedźwiedź, 2019), while at stands where temperature is the growth-limiting factor, the same is possible for temperature reconstructions (e.g., Chen et al., 2015; Ratcliff et al., 2018; Gaire et al., 2019).

Thus, based on the *Uniformitarian Principle*, it is possible to estimate and reconstruct past climate, before the existence of meteorological stations' records, among other applications (Fritts, 1976; Hughes et al., 1982; Sheppard, 2010; Speer, 2010). Therefore, it is necessary to acquire reliable climatic data from individual or multiple weather stations (Blasing et al., 1981; Hughes et al., 1982).

When data from local stations is unavailable, high-resolution databases that are available for the entire globe can be used, through a process of reanalysis and interpolation. For example, CHELSA database (Climatologies at high resolution for the Earth’s land surface areas) enables the extraction of monthly, weekly, daily, or even hourly data, for different climatic variables, especially precipitation and temperature, the

most commonly used in dendroclimatological studies (Fritts, 1976; Briffa, 1999; Karger et al., 2017; Karger and Zimmermann, 2018).

4. Dendroecology

Dendroecology is also a branch of dendrochronology, which deals with the relationships between patterns in tree-ring series and all the ecological factors that may influence those patterns (Fritts, 1971). Besides climate, it can consider competition, predation, among other biotic and abiotic factors. Whereas dendrochronology has made important contributions to a wide array of different areas, such as climatology, archaeology, or wood formation, the ecological input that dendrochronological research has provided is fundamental to a deeper understanding of forest ecology and management (Amoroso et al., 2017).

Indeed, dendroecological studies have essentially changed modern views of forest ecology and forest dynamics, especially in temperate forests (Manzanedo and Pederson, 2019; Martin-Benito et al., 2022). For instance, dendroecology contribution is essential to perceive how forest ecosystems can respond to the many threats resulting from global environmental change. These threats are not limited to changing climatic conditions, but also include other ecological factors, such as biodiversity loss (e.g., Fyllas et al., 2022), impacts of invasive species (e.g., Xavier et al., 2021), disturbance regimes (e.g., Šamonil et al., 2018), and the variety of potential interactions among them (Amoroso et al., 2017). Therefore, dendroecology supplies important historical context for adapting existing forest management strategies to mitigate and respond to current and future global environmental change (Veblen et al., 2011; Amoroso et al., 2017).

Both dendroclimatology and dendroecology aim to understand the relation between environmental factors and tree growth. While the former uses the information in tree ring chronologies to extract climatic information, the latter also deals with other changes in the local environment (Amoroso et al., 2017). Nevertheless, both areas are connected by some of the methods used and by their shared principles (Rozendaal and Zuidema, 2011; Amoroso et al., 2017; Pearl et al., 2020).

5. Statistical analyses in dendrochronology

5.1. Crossdating

A graphical way to crossdate tree-ring series was developed in the early 20th century by creating a graphic representation of growth ring patterns, known as a "skeleton plot", in which narrow rings were highlighted and characteristic ring features noted. The goal of this technique was to compare and identify all missing and double rings in all the series under study (Douglass, 1935; Cropper, 1979). After a series was correctly crossdated, a summary master chronology was developed and used to visually crossdate new specimens (Schweingruber, 1988).

Nowadays, new software allows the use statistical methods as well as visual tools to support crossdating and to determine the likelihood between the overlapping rings. For example, in the PAST5 (SCIEM) software, statistics such as t-values (Eckstein and Bauch, 1969) and a Gleichläufigkeit Value (Baillie and Pilcher, 1973) can be used to ensure the quality of the crossdating process, as illustrated in numerous recent studies (e.g., Jacob et al., 2020; Bernabei and Marchese, 2022; Bernabei et al., 2022).

5.2. Detrending

The previously mentioned age-related growth trend - the best-known trend in dendrochronological studies - is the gradual decline of tree-ring width from the innermost layer to the outermost layer. In general, this trend can be described by a negative exponential function or by a hyperbola function, in solitary trees on undisturbed environments (Cook, 1985; Cook and Kairiukstis, 1990).

Historically, the process of removing these age-related trends, known as "detrending", was basically an adjustment of curves or lines to the tree-ring series of individual trees, which represented either one increment core or a tree (Cook, 1985). While also removing age trends, differences in tree growth rates would also be removed, because the process will homogenize the gradual decrease of ring widths of all samples. This is important, for example, to prevent fast-growing individual tree-ring patterns from mastering the interannual variability of the average mean chronology (e.g., Sullivan et al., 2016).

Moreover, most chronologies do not present low-frequency variations (i.e., long-term variations over the time period) (Cook and Kairiukstis, 1990; Esper et al., 2003), which can range from several years to several decades, depending to studies time period (e.g., Mazza and Sarris, 2018; Savard et al., 2020). Therefore, several detrending approaches depend not only on the frequency (i.e., variation in tree-ring widths along time) present in the individual chronologies under study, but also on the length of the same chronologies and on the specific conditions of the local study (Fritts, 1976; Speer, 2010; Bontemps and Esper, 2011; Peters et al., 2015; Sullivan et al., 2016; Mazza and Sarris, 2018).

One of the most common approaches of detrending is stochastic detrending, where digital filters are used for curve fitting (Cook and Peters, 1981; Cook and Kairiukstis, 1990). Cubic smoothing spline with a known frequency cutoff at a given frequency is the most frequently used filter. In this approach, a cubic smoothing spline with a 50% frequency response cut-off at *n* years is fitted to each individual ring-width series.

Though, applying this method to a tree-ring dataset with varied ages can introduce a temporal bias in the variation of tree-ring widths within a chronology. Choosing a known frequency cutoff (*n* years) will affect differently the oldest and the youngest chronologies (Cook and Peters, 1981; Cook, 1985; Cook and Kairiukstis, 1990). For example, applying a more flexible spline on the youngest and shortest tree-ring samples, long-term trends in tree-ring width variation (i.e., low-frequency variation) can be removed. On the contrary, on the oldest and largest chronologies it will remove short-term trends (i.e., high-frequency variation).

The temporal bias in the frequency variations can influence further analysis, such as climate-growth relationships. Hence, the introduction of the auto-regressive modeling ("pre-whitening"), that will remove any persistence in the tree-ring data (low or high frequency trends), related to biological carry-over effect of trees, and therefore avoiding the temporal bias (Cook, 1985; Speer, 2010; Cailleret et al., 2019; Klesse, 2021).

5.3. Quality assessment of tree-ring chronologies

There are various approaches that can be used to assess the quality and reliability of mean chronologies, which show how strongly and reliably they represent a population.

Mean Pearson correlation (Rbar) is a commonly used statistic for assessing the quality of mean chronologies. It estimates the strength of the shared growth patterns within the

chronologies by calculating the mean correlation between all pairs of individual tree-ring series for the overlapping time period. The resulting value provides an overall measure of the similarity between the tree-ring series (Wigley et al., 1984; Cook and Kairiukstis, 1990; Speer, 2010).

The Expressed Population Signal (EPS) is another statistical parameter that is widely used to evaluate the reliability of tree-ring chronologies. EPS calculations depends on Rbar and the size of the subsample, where high values (generally, above 0.85) indicates that tree-ring series are a good representation of a theoretically infinite population (Wigley et al., 1984; Cook and Kairiukstis, 1990; Speer, 2010). However, low EPS values most likely indicates low sample size and/or low Rbar, but not necessarily lower representative power of a population (Buras, 2017).

Tree-ring chronologies may become increasingly less well-replicated further back in time due to factors such as low sample depth. To outline this, Subsample Signal Strength (SSS) appropriately indicates the subset that most strongly and accurately defines the tree-ring signal (Wigley et al., 1984; Cook and Kairiukstis, 1990; Speer, 2010; Buras, 2017). This approach is strictly related to EPS as both rely on Rbar, although SSS estimates the representative strength of a subsample in a finite population instead of in a theoretically infinite population (as it happens with EPS) (Wigley et al., 1984; Buras, 2017).

5.4. Growth rings and climate

Various statistical methods can be applied to quantify a relationship between tree rings and climate. This process of extracting climatic information from annually resolved tree-ring chronologies is called “calibration”. The most basic and common approaches include correlations or response-function analysis, both with their respective confidence

intervals to assess significance (Hughes et al., 1982; Fritts and Wu, 1986). Correlation approaches uses Pearson's correlation estimations, while response function is a variant of an indirect regression method (Speer, 2010; Christiansen, 2011). The latter intends to diminish the effect of predictor multicollinearity by regressing the proxy record against the principal components of the climatic data (Cropper, 1984; Speer, 2010).

Nonetheless, novel modelling approaches can be applied to encompass data in one or several regions, with a certain period or with the entire length of the tree-ring chronologies. Using modeling analysis in dendroclimatology, the independent variables or predictor variables (climatic variables) are used to explain or predict changes in dependent variables (tree-ring measurements) (e.g., Pecchi et al., 2019). In this type of statistical analyses, many factors need special attention when choosing the appropriate variable predictors, such as the purpose of the study, data availability, and redundancy between variables (Burkhart and Tomé, 2012).

Moreover, different modelling approaches can be used in dendroclimatology. For example, linear models are usually applied to perceive the mentioned relationship between tree growth and climate, although there is a growing trend assuming that linear assumption between dependent variables and predictor variables is not accurate (Sun et al., 2017; Jevšenak et al., 2018a). Non-linearity can be found when a particular growth-limiting factor becomes excessive and there is no increased response in tree growth (Cook and Pederson, 2011).

Therefore, as trees can grow in a range of environmental conditions, the non-linear response should be considered as approaching an optimized spectrum of environmental conditions (Bhuyan et al., 2017; Sun et al., 2017; Jevšenak et al., 2018b). For this reason, nonlinear models (e.g., machine learning methods) are gaining some popularity in dendroclimatological research. This may be related to climate change, due to the upsurge

of the average temperature in the last decades and, consequently, the increased variation of the observed response of tree growth to climate (Jevšenak et al., 2018a; Khaleghi, 2018; He et al., 2019).

Several studies have used novel modeling analyses for tree-ring data. For example, linear models were previously used to analyze climate responses of tree species (e.g., Marcon et al., 2019; Rodríguez-Ramírez et al., 2020) and to reconstruct climate from tree-ring chronologies (e.g., Aragão et al., 2019; Tejedor et al., 2020). Machine learning methods have also been applied to tree-ring research in various ways, such as using image processing techniques to detect tree rings (e.g., Nakajima et al., 2020; Poláček et al., 2022), predicting basal area increment (e.g., Jung et al., 2013; Jevšenak and Skudnik, 2021) and understanding the relationship between climate and tree-ring proxies (e.g., Jevšenak et al., 2018a; Sahour et al., 2021). One of the major advantages of these models is their ability to consider multiple factors, such as species biodiversity, spatial occurrence and density, and growth (e.g., Liu et al., 2022).

5.5. Modelling in forest ecology and management

The awareness of the present and future dynamics of forest ecosystems is a key issue for biodiversity conservation, especially under global concerns such as climate change (Walentowski et al., 2017; Pecchi et al., 2019). Forest productivity and changes in forest distribution/composition are of great interest to global and regional ecological studies, given the crucial role of forests in the provision of essential ecosystem services and in biodiversity conservation (Gaucherel et al., 2008; Jandl et al., 2019; McDowell et al., 2020; Borges Silva et al., 2022).

There is a growing recognition of the need for knowledge about the spatial occurrence of forest species and their influence on ecological drivers (such as soil and climate) using modeling analyses (McDowell et al., 2020). Modeling can be used to understand the connection between tree growth rates and carbon sequestration, which is important for identifying opportunities for anthropogenic carbon storage (Fatichi et al., 2019; Pugh et al., 2019; Brienen et al., 2020; Walker et al., 2021). In fact, the role of terrestrial ecosystems on carbon sink is already well-established, since it was first recognized by the United Nation's REDD+ initiative in 2008 (UNFCCC, 2008).

However, the drivers of this sink are not fully understood, and modeling tree growth rates could help to fill this gap and improve our understanding of the role of forest restoration in global climate change mitigation efforts (Di Sacco et al., 2021). This information can support spatial prioritization decisions for management actions and strengthen regulatory decision-making, especially in endangered areas where necessary measures and habitat suitability assessments are critical (DeAngelis and Diaz, 2019; Pecchi et al., 2019; Sofaer et al., 2019).

Accordingly, modeling in forest research has been widely used, incorporating or not the effect of predicted climate change scenarios. This analysis can have different and varied approaches and algorithms at global level (e.g. Hickler et al., 2012; Kiviste et al., 2015; Shifley et al., 2017; Carr et al., 2020; Shabani et al., 2021; Bannister et al., 2022). Likewise, in the Azores archipelago different approaches have also been used (e.g. Hortal et al., 2010; Costa et al., 2013; Ferreira et al., 2016; Dutra Silva et al., 2017, 2021).

Moreover, modelling can be used to predict habitat expansion (while predicting the future distribution of invasive species) and habitat loss (especially on circumscribed species – i.e., island species). Since the emergence of modeling techniques, spatial data including aerial images, cartographic layers, and forest inventory, have been key

resources for a supported and reliable statistical model. Considering this fact, trustworthy data sets and statistical models promptly became integral tools in decision-making goals regarding the use of forest resources under a changing climate (Pecchi et al., 2019; Sofaer et al., 2019).

6. Azorean Forests

6.1. Azores Islands

The Azores (36°55'–39°43' N and 25°00'–31°15' W) is a Portuguese archipelago situated in the North Atlantic Ocean, about 1500 km from nearest continent (Europe). Due to its geological and ecological features, belongs to Macaronesia bioregion, comprising nine islands of volcanic origin, organized into three groups (Figure 2). The archipelago has a total land surface of 2323 km^2 (Forjaz et al., 2004) and maximum altitude of the islands ranges from 405 (Graciosa) to 2351 m (Pico Mountain), with several islands reaching more than 1000 m in elevation.

The age of the emerged land areas of the Azores archipelago varies from about 0.25 million years in Pico up to about 6 million years in Santa Maria (Ramalho et al., 2017). The archipelago has an unstable geologic nature with constant volcanic activity, due to its location in an area of seafloor with a complex tectonic setting and an average depth of 2000 m, near the triple junction between the North American, Nubian and Eurasian plates. Hence, soil formation consists in incoherent materials resulting from volcanic explosions, such as trachytic pumice stone and basaltic slag. Various soil types have been described for the Azores (Machado, 1946; Madruga, 1986, 1990; Pinheiro, 1999; Pinheiro et al., 2001; Madeira et al., 2002): andosols derived from trachytic deposits, ferruginous

andosols; inceptisols; brown earth soils; mollisols; vertisols; and young shallow soils, namely litholic soils, regosols, and allophanic soils on lava flows.

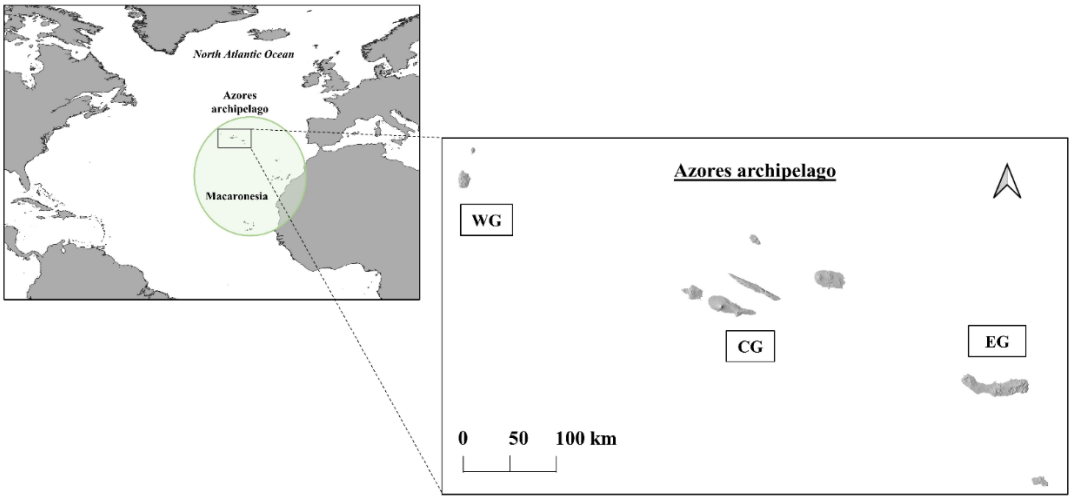

Figure 2. Map of the Azores archipelago (WG – Western Group, CG – Central Group, and EG – Eastern Group), framed on the North Atlantic Ocean and, more specifically, in Macaronesia.

The general climate classification of the Azores archipelago is temperate oceanic with a mean annual temperature of 17ºC at sea level, relative humidity is high, and rainfall ranges from 1500 to 3000 mm per year (Azevedo, 2001). Though, considering the Koeppen-Geiger climate classification system (data from 1971 to 2000), the archipelago climate is mainly temperate (type C), namely Cfb (temperate with no dry season and with a mild summer) (Couto, 2012).

6.2. Azores natural forests and Macaronesian forests

Macaronesia biogeographic region comprises five volcanic archipelagos in the North Atlantic Ocean, specifically Azores, Madeira, Canary Islands, Selvagens and Cabo Verde.

Natural forest of the Azores archipelago, is associated to laurel and mountain forests that usually occurs in areas with high relative humidity and mild average temperatures (Walter, 1970). This type of forests, exist in regions where the oceanic moisture intercepts trees canopy and is collected as horizontal precipitation (occult precipitation) (Fernández-Palacios et al., 2017; Keith et al., 2020), which happens in some archipelagos of the Macaronesia biogeographic region (Azores, Madeira and Canary Islands). Macaronesian natural forests established before the Quaternary glaciations, originating from thermophilous forest types that dominated Europe and Northern Africa for more than 50 million years during the Tertiary period (Mai, 1991; Rodríguez-Sánchez et al., 2009; Fernández-Palacios et al., 2011; Nogué et al., 2013).

Several descriptions have been given regarding the zonal/altitudinal vegetation of the Azores. In the 19th century, Seubert (1844) and Morelet (1860) identified different types of altitudinal vegetation. In the 20th century, there were descriptions based on the occurrence of certain species (Guppy, 1917), recognition of three belts of altitudinal vegetation for the entire archipelago by Tutin (1953), a detailed work on the natural ecosystems of the Azores (Dansereau, 1970) and sintaxonomic classification approaches (Sjoegren, 1973; Luepnitz, 1975). At the end of the 20th century, Dias (1996) classified the vegetation of the Azores, based not only on forest data, but also based on structural data (biovolume) regarding forests. More recently, Elias et al. (2016) gave the first statistically based classification of Azorean natural zonal vegetation and the first potential distribution maps of the zonal vegetation for each island.

Currently, Azores forests are associated with subtropical conditions (i.e., warm temperatures, and relative high humidity and rainfall) that can be found in only a few regions of the planet, which include islands with temperate climate (i.e., moderate temperatures, with relatively mild winters and warm/humid summers) (Dias, 1996).

Depending on weather conditions related to elevation, in particular radiation (i.e., solar exposure), wind and water balance, these natural Azorean forests can be dominated or co-dominated by several endemic tree species, such as *Morella faya* Aiton and *Picconia azorica* (Tutin) Knobl. in sub-humid conditions, *Laurus azorica* (Seub.) Franco and *Frangula azorica* Tutin under humid conditions and *Ilex azorica* Gand. and *Juniperus brevifolia* (Seub.) Antoine in hyper-humid conditions (Elias et al., 2016). In addition to the species mentioned above, Elias et al. (2016) also mention other species, such as *Calluna vulgaris* (L.) Hull that exist mostly in high elevation areas and *Erica azorica* Hochst. ex Seub., which has a large ecological amplitude (from sea level to 1700 m of altitude), being dominant in coastal areas and sub-alpine scrublands. Elias et al. (2016), identified eight types of vegetation belts: *Erica-Morella* Coastal Woodlands, *Picconia-Morella* Lowland Forests (lowland laurel forests), *Laurus* Submontane Forests (submontane laurel forests), *Juniperus-Ilex* Montane Forests, *Juniperus* Montane Woodlands, *Calluna-Juniperus* Altimontane Scrblands, *Calluna-Erica* Subalpine Scrublands and *Calluna* Alpine Scrublands.

In general, the remaining fragments of native vegetation of the Azores are dark green dense spots in the landscape (Figure 3), dominated by the previously mentioned species, even though better preserved in Pico, Terceira and Flores islands (Elias et al., 2016). Likewise, are usually associated with the presence of other species, such as *Viburnum treleasei* Gand., *Vaccinium cylindraceum* Sm. or *Myrsine africana* L. Each type of vegetation described by Elias et al. (2016) is composed of a typical set of species, yet there are similarities in the composition, especially among neighboring communities. This is a result of the great ecological amplitude and low number of vascular species native to the Azores archipelago.

Based on the same data, Pavão et al. (2019) concluded that the communities of vascular plants native to the Azores are distributed as a continuum, with the partitioning of ecological niches among the dominant species. Therefore, despite the dominance, co-dominance and varied occurrence of native vascular species, this study suggests the existence of metacommunities in the archipelago, given the existence of interactions and sharing of ecological niches. Those two latest studies, refer to the ecological amplitude of the native tree species of the Azores and their distribution/occurrence in the archipelago (Elias et al., 2016; Pavão et al., 2019).

6.3. Land cover change

In his work "Saudades da Terra" (Frutuoso, 1589a,b,c), Gaspar Frutuoso (1522-1591) gives the most detailed and complete description of the native vegetation of the Azores (mainly in Santa Maria and São Miguel), at the time of Portuguese settlement in the 15th century. This work also reports that the natural land cover of the islands in the 16th century has been changed with human inducing changes in the landscape and that before the actual human settlement, domestic cattle were released to the wild in order to increase the suitability of the islands to support human populations (Dias, 2007). Indeed, considerable changes occurred in the Azorean land use in the 1950's, with several activities impacting natural communities, replacing the native vegetation with the introduction of numerous crop, forage, forest, ornamental and hedgerow plant species (Costa, 1952; Silva and Smith, 2004).

Although widespread before human settlement in the Azores archipelago (Elias et al., 2016), the remains of those forests are presently located at slopped terrain, and associated with acidic andosols along with a substantial amount of organic matter (Borges

Silva et al., 2022). Natural forests in the archipelago mostly correspond to submontane and montane forests which occur in the thermotemperate-hyperhumid and ultrahyperhumid belts, associated to high rainfall and occult precipitation (cloud forests), with high structural diversity (Borges Silva et al., 2022). Nevertheless, an altitudinal distribution, from sea level up to the highest mountains, is still present in the Azores, from coastal scrubland and woodland up to mountain forests, woodlands and alpine scrubland (Elias et al., 2016; Pavão et al., 2019).

Figure 3. One of the best-preserved stands of natural vegetation of the Azores archipelago - Serra de Santa Bárbara in Terceira Island.

6.4. Dendrochronology in Macaronesia and Azores

The International Tree Ring Data Bank (ITRDB) is a global and comprehensive database of tree growth rings, which contributes to areas of environmental sciences, incorporating this unique space-time coverage. Moreover, according to the ITRDB, there is a gap in the research dedicated to tree rings in the laurel forest, given the lack of strong seasonality. This fact underlies the increased demanding for data in different spatial and

temporal coverage (Babst et al., 2018; Zhao et al., 2019). With this purpose, dendrochronological data have already proven to be an important resource. This approach provides valuable information on ecological (e.g., Charney et al., 2016), geomorphologic (e.g., Stoffel and Bollschweiler, 2008), paleoclimatic (e.g., He et al., 2019) and large-scale climate processes with a space-time coverage and resolution difficult to obtain in other scientific approaches.

However, the knowledge about tree rings in the Macaronesian region, is still quite limited and only a few studies have been published. Fortunately, this view is changing, with tree ring research being listed in several native tree species from Madeira (e.g., Pupo-Correia, 2016) and Canary Islands (e.g., Peraza Oramas and López De Roma, 1967; Morales et al., 2002; García-López et al., 2022). However, the potential for studying the different proxies and its response to climate fluctuations in the region, remains systematically unexplored. Considering the Azores archipelago, Wunder (2013) in his report, was the first to use tree-rings in which age of *Juniperus brevifolia* individuals were estimated, from a small patch in Terceira island - indicated the existence of 150 years old individuals but with the presence of irregular growth rings and wedging rings. To understand forest dynamics, Câmara (2016) estimated the age of two laurel forest sites, using growth rings of several endemic species (*Morella faya, Erica azorica, Ilex azorica* and *Laurus azorica*) and an exotic species (*Pittosporum undulatum* Vent.). In the following years, more detailed studies were carried out with *Pittosporum undulatum*, in which allometric equations were developed to estimate above-ground biomass, using dendrochronological tools (Borges Silva et al., 2017, 2018).

Later, Vieira et al. (2017) developed the first dendroclimatological work focused on the region (low altitude site in Pico island), wherein it related *Pinus pinaster* Aiton growth rings with climatic data and determined that precipitation is the main driver of this species

growth. Finally, the most detailed work with a native tree species of the Azores archipelago, was focused on the species *Laurus azorica*. Matos et al. (2019) concluded that wood anatomical analysis confirmed the presence of clear annual ring boundaries and that allometric models suggest the effect of local environmental conditions on growth rate.

Ecological amplitudes, occurrences and distributions of the forest tree species of the archipelago are well known (Elias et al., 2016; Pavão et al., 2019). Likewise, this region has a great potential given the knowledge gap regarding growth rings, creating an opportunity to explore tree-rings of natural species of the Azores. Including dendrochronological, dendroclimatological and dendroecological analyses, results from this dissertation can support ecological modelling and, consequently, a better understanding of forest dynamics on terrestrial Azorean ecosystems. Therefore, this provision could be an essential knowledge basis for preservation and conservation measures focusing this unique biodiversity.

7. Thesis scope and outline

7.1. Research objectives and questions

This thesis relies on three main ideas, where its research aims are also supported: (1) the potential of the Azores archipelago tree species for tree-ring research, (2) the knowledge gap that exists in this research topic, and (3) the well-known ecological amplitude of native tree species (a basic principle of dendroclimatology). According to this ecological amplitude, the model region of this thesis, the Azores Archipelago, will be covered by collecting data at the various altitudinal ranges of the dominant endemic forest species, *Laurus azorica*, *Ilex azorica* and *Juniperus brevifolia*.

As the main scientific objective, this work will model tree growth-climate relationships in the three selected species. For this purpose, the following research question will be addressed: i) what are the climatic factors affecting growth of endemic tree species? ii) is there variation among sites regarding climate-growth relationships? and iii) can dendroclimatic data support ecological modelling?

To fulfill the main goal of this thesis more than 900 wood cores were collected from three Azorean endemic woody species at 10 different sites in two islands. Standard dendrochronological and dendroclimatic methods were applied, as well as several modelling options to determine the most relevant climatic drivers of tree growth, and the potential of this approach to improve species distribution modelling and tree growth rates.

7.2. Thesis outline

This thesis includes this introductory chapter, three research chapters corresponding to three published scientific papers, and a final chapter dedicated to a global discussion.

Chapter II. Dendrochronological potential of the Azorean endemic gymnosperm* Juniperus brevifolia *(Seub.) Antoine

This chapter evaluates the dendrochronological potential of *Juniperus brevifolia*, analyzing growth rings patterns, crossdating capacity, and the relation between radial growth and climatic factors. Basic dendroclimatology approaches were used, such as using Trephor to collect samples for the wood anatomy analysis and Pearson's correlation to comprehend the climate-growth relationship in two different populations of two different islands (Terceira and São Miguel). In this chapter, several topics regarding tree-ring analyses are discussed. For example, despite the clear transition between earlywood and latewood in *J. brevifolia*, some samples contained partially indistinct ring boundaries

and wedging rings, which affected the crossdating procedure. However, the establishment of ring width mean chronologies was possible and, consequently, allowed to understand the climate-growth relationship - negative correlation with late summer temperatures in both populations.

Chapter III. Tree growth-climate relationship in the Azorean holly in a temperate humid forest with low thermal amplitude

The third chapter focused on the understanding of tree-ring patterns in *Ilex azorica* and examined the relationship between radial tree growth and main climatic drivers. Wood increment cores were sampled from six populations (four populations from São Miguel Island and two from Terceira Island). Firstly, diffuse-ring porous wood was found with a common layer of vessels associated to the ring boundary, which was critical to identify annual tree-rings. Secondly, to relate temperature and precipitation with radial growth, generalized linear models were used, resulting in diverse climate-growth relationships in different populations, while the composite chronology exhibited a pronounced effect of temperature. Overall, *I. azorica* presented reliable annual tree-rings, which could be statistically related to climate, mostly temperature.

Chapter IV. Climate-growth relationships in* Laurus azorica *- a dominant tree in the Azorean laurel forest

The fourth chapter was dedicated to an important species of the Azores natural forest with close taxa in Macaronesian laurel forests, *Laurus azorica*. To quantify climate-growth relationships, four stands at São Miguel and two stands at Terceira islands were sampled. After following standard dendrochronological methods and rigorous sample selection procedures, relatively low within stand correlation, and high temporal autocorrelation were obtained. In this chapter, climate-growth relationships were

discussed, after using a stepwise Random Forest and Generalized Linear Models analysis. Pronounced effects of temperature, low precipitation signal and an effect of previous year climate on growth rings were found. Likewise, variation of the climate-growth relationships among stands was discussed. Those results were compared with other broad-leaved species with diffuse porous wood, contributing to increase the baseline dendroclimatic knowledge about Azorean forests.

Chapter V. General discussion, conclusions, and future perspectives

In this final chapter, a general discussion and the main breakthroughs of the previous chapters and the thesis in general are presented. At the same time, both implications and limitations of the proposed study are discussed, as well future perspectives since this study allows to perceive opens doors for future investigations in the Azores.

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CHAPTER 2

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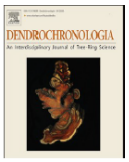

ORIGINAL ARTICLE

Dendrochronological potential of the Azorean endemic gymnosperm *Juniperus brevifolia* (Seub.) Antoine

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Abstract

Tree-ring inter-annual pattern variation is crucial in dendrochronology, allowing the identification of possible limiting factors on growth. Thus, trees exposed to subtropical or tropical climates without a marked seasonality may show a low degree of interannual variation, impeding a straightforward dendroclimatological approach. Meanwhile, subtropical regions, and areas in transitional climates such as the Azores archipelago, are widely unexplored in terms of dendroclimatology, providing opportunities to work with endemic trees, including the dominant Azorean tree *Juniperus brevifolia* (Seub.) Antoine. To evaluate the dendrochronological potential of *J. brevifolia*, we analyzed tree-ring patterns, crossdating capabilities, and correlation with climate parameters. We sampled 48 individual trees from two natural populations (São Miguel and Terceira islands) using an increment borer. Besides, a Trephor tool was used to obtain wood microcores for micro-anatomical analysis. Although the transition between early and latewood was evident, partially indistinct ring boundaries and wedging rings were present in some cases, affecting the crossdating process, but not impeding the establishment of reliable ring-width chronologies. Following detrending, master chronologies were built and correlated with monthly temperature and precipitation data using the treeclim R package. The climate-growth relationships indicated negative correlations with late summer temperature in both populations. Considering our results and the importance of *J. brevifolia* as a dominant tree in the Azores natural forests, we conclude that it shows an acceptable potential for dendrochronological research. Thus, this study provides baseline information to help fill the knowledge gap regarding the climate-growth relationship of Azorean trees.

Keywords: Azores; climate response; crossdating; dendroclimatology; *Juniperus*.

1. Introduction

Tree-ring analyses are widely used for tree age determination and growth rate estimation, allowing to relate tree growth and environmental factors affecting tree-ring features, such as tree-ring width (TRW) and presence/absence of tree-ring boundaries (Haines et al., 2016; Misi et al., 2019; Shengtao et al., 2019). One of the crucial steps in dendrochronology is the crossdating procedure that presumes the effect of a large-scale external factor on the high-frequency variability in tree-ring width (Black et al., 2016; Fritts, 1976). Hence, a crossdated chronology primarily reflects the temperature and moisture variation (Fritts, 1976; Speer, 2010; Nieminen et al., 2015; Qaderi et al., 2019), allowing for dendroclimatological applications such as climate reconstructions, growth-limiting factor analyses or dendro-provenience studies (Nechita, 2013; Haines et al., 2016; Chen et al., 2019b). Trees growing in subtropical and tropical climates, without a pronounced seasonality, tend to show a low degree of annual variation in TRW (Rozendaal and Zuidema, 2011), which might explain the difficulties in crossdating complacent trees (Sass-Klaassen et al., 2007; Speer, 2010; Wils et al., 2011a). Studies focusing on the potential of subtropical trees for climate studies revealed difficulties in the delimitation of ring-width due to the occurrence of non-annual growth rings and of ring anomalies such as wedging, false, and absent rings (Heinrich and Allen, 2013; Haines et al., 2018, 2016).

In the Azores archipelago, the climate might be classified as temperate oceanic and wet mesothermic but with altitudinal variation and slight differences among the islands (Azevedo, 2001). The mean annual temperature varies from 18°C at sea level to 12°C at higher altitudes, and the average annual precipitation ranges from 730 to 1600 mm near the coast up to 4000 mm at high elevation, increasing with altitude and from east to west (Azevedo, 2001; Couto, 2012). Regarding Köppen Climate Classification (data from

1971-2000), the Azores climate is temperate (type C), although with subtypes depending on elevation (Couto, 2012). The predominant type is temperate with no dry season and with a mild Summer (Cfb), but it ranges from temperate with hot and dry Summer (Csa) to tundra (ET, only observed in Pico Mountain above 1600 m). Nevertheless, daily and annual temperature variation is relatively low, and precipitation is well distributed throughout the year (Azevedo, 2001; Couto, 2012; Elias et al., 2016). Therefore, natural forests in the Azores evolved under relatively homogeneous climatic conditions, and relatively far from the mainland, including a limited number of native woody species (Silva et al., 2010; Elias et al., 2016; Pavão et al., 2019), such as *Picconia azorica* (Tutin) Knobl., *Morella faya* Aiton, *Laurus azorica* (Seub.) Franco, *Ilex azorica* Loes., *Erica azorica* Hochst. ex Seub. and *Juniperus brevifolia* (Seub.) Antoine (Elias et al., 2016). Only a few dendrochronological studies targeted the Azorean woody species, therefore this region constitutes a major gap in the International Tree-Ring Databank (ITRDB) (Zhao et al., 2019). Borges Silva et al. (2017, 2018) using dendrochronological tools developed allometric equations to estimate the above-ground biomass of the woody plant invader *Pittosporum undulatum* Vent. The only climate-growth correlation study applied on the Azorean archipelago, was focused on the introduced *Pinus pinaster* Aiton (Vieira et al., 2017) at a low elevation site, reporting a positive response to spring precipitation but no temperature signal in the tree-ring width chronology. Finally, the only study addressing a native species was presented by Matos et al. (2019), who studied *Laurus azorica* and aimed to describe the growth ring anatomy, and to understand the relationship between dendrometric traits and the number of growth rings. The wood anatomical analysis confirmed the presence of clear annual ring boundaries, and a significant relationship between trunk diameter and tree age was found.

The endemic gymnosperm *Juniperus brevifolia* is one of the more important woody species in the Azores, being dominant or co-dominant in many types of natural forests and woodlands (Elias et al., 2011, 2016; Adams, 2014; Elias and Dias, 2014; Pavão et al., 2019). *Juniperus* comprehends 75 accepted species, being the second most diversified genus of conifers (The Plant List, 2013; Adams, 2014). Besides *Juniperus procera* Hochst. ex Endl., that occurs south of the equator, in the east and south of tropical Africa, this genus is mostly distributed in the northern hemisphere, from the subarctic tundra to the semi-desert (Adams, 2014). *Juniperus* species have become less dominant in certain regions because their populations have been considerably reduced due to overexploitation (Assefa and Abate, 2018; Kahveci et al., 2018; Warrag et al., 2019). This has contributed to a relatively low number of dendrochronological studies addressing this genus. Nonetheless, *Juniperus* is important in tree-ring networks in the Mediterranean Basin, the mid-Atlantic region of USA, the Middle East, and in Asia (Qin et al., 2003; Touchan et al., 2005; Shi et al., 2010; Maxwell et al., 2011, 2012; Wils et al., 2011a; Wang et al., 2014, 2015; Chen et al., 2015, 2019b; Nie et al., 2017; Yang et al., 2017; Li et al., 2019; Opała-Owczarek and Niedźwiedź, 2019). Moreover, the factors influencing the establishment and growth of juniper, in relevant habitats where it is a dominant element, have been studied (Wang et al., 2008; Liang et al., 2012; Seim et al., 2016; Chen et al., 2017, 2019a, 2020; Pandey et al., 2020; Mu et al., 2021).

In 2010 an exploratory study of *J. brevifolia* trees in Terceira island revealed a maximum age of 150 years (Wunder and Elias, 2013), suggesting it to be a promising target for dendrochronological applications, such as climate reconstruction or dendroecological studies. Considering the peculiar climate of the archipelago, we analyzed tree-ring annual patterns, possible crossdating difficulties, and the correlation of TRW with climatic parameters using samples from two different islands. Given a

previous work on the wood anatomy of Macaronesian *Juniperus* (De Palacios et al., 2014), here we just confirm those observations. Though, this research aims to evaluate the dendrochronological potential of *J. brevifolia*, identifying specific tree-ring issues related to crossdating and prevailing climate signal in this species. Therefore, our main hypotheses are that 1) *Juniperus brevifolia* chronologies can be crossdated and 2) both populations will have similar prevailing climate signal driving tree growth.

2. Materials and Methods

2.1. Study area

The Azores archipelago (36°55'–39°43' N and 25°00'–31°15' W) comprises nine volcanic islands located in the North Atlantic Ocean (Figure 4). With a total land surface of 2323 km^2 (Forjaz et al., 2004), the archipelago is divided into three main groups, which lie on an area of seafloor with a complex tectonic setting, near the triple junction between the Eurasian, Nubian, and North American plates (Miranda et al., 2014).

Our study sites are located at two different islands (Figure 4), Terceira (Serra de Santa Bárbara, 900 m a.s.l.) and São Miguel (Serra da Tronqueira, 600 m a.s.l.), where there are two of the best preserved and more representative natural forests in the archipelago. Both islands have the best-preserved vegetation belts located above 600 m a.s.l., *Juniperus-Ilex* montane forests, and *Juniperus* montane woodlands, where *J. brevifolia* is dominant, located in the upper thermotemperate-hyperhumid zone (Elias et al., 2016; Pavão et al., 2019). According to Köppen Climate Classification, the climate at both sites (Appendix 1, Figure 5) is temperate with no dry season, and a mild Summer (Couto, 2012).

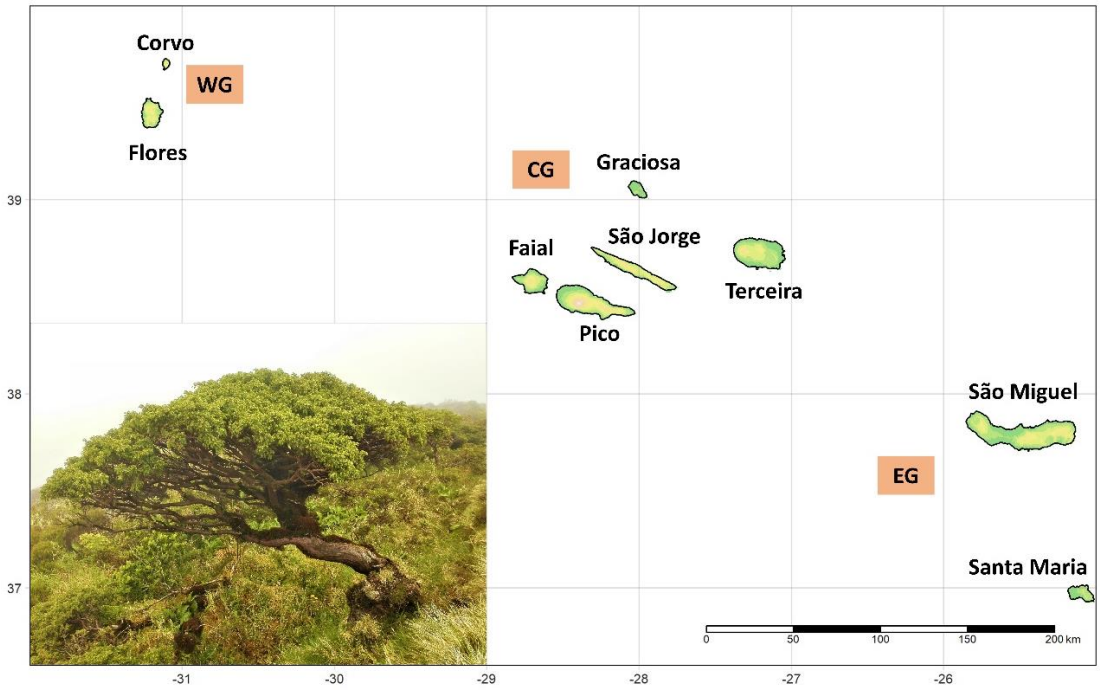

Figure 4. Map of the Azores archipelago (WG – Western Group, CG – Central Group, and EG – Eastern Group) and an example of an individual of *Juniperus brevifolia*. Red arrows indicate study area locations.

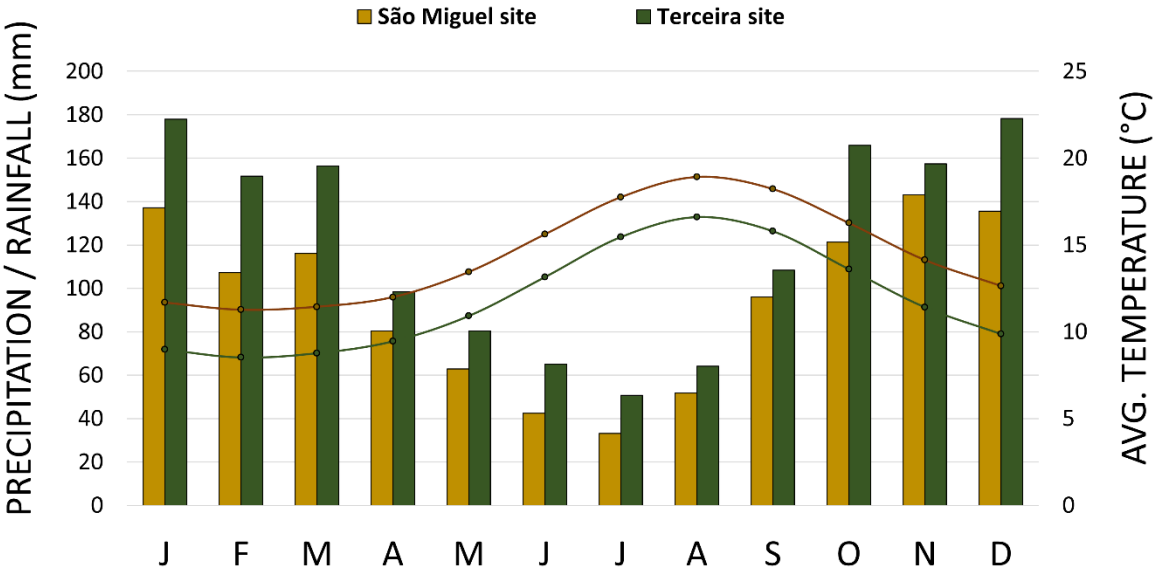

Figure 5. Average monthly temperatures (lines) and monthly precipitation (bars) for the two study sites. Data was extracted from CHELSA timeseries dataset with a spatial resolution of 30-degree seconds.

At Tronqueira the forest cover was dominated by *Laurus azorica*, *Ilex azorica*, *Erica azorica*, *Clethra arborea*, and *Juniperus brevifolia*, also including many understory elements, with a total of 29 vascular plant taxa, a density of 4100 shrubs/trees per hectare

and a medium height of 3.8 m. At Santa Bárbara, the forest cover was dominated by *Ilex azorica*, *Laurus azorica* and *Juniperus brevifolia*, also including many understory elements, with a total of 19 vascular plant taxa, a density of 2700 shrubs/trees per hectare and a medium height of 4.3 m. Figure 6 shows one example of the environment where *Juniperus brevifolia* is usually found.

Figure 6. Example of an individual of *Juniperus brevifolia* in its environment. This photo also represents a small patch of a preserved natural forest in the archipelago.

2.2. Target Species

Juniperus brevifolia is a wind-pollinated, dioecious tree or shrub (Adams, 2011, 2014) and is one of the dominant woody plants in the Azorean forests, especially in mountainous areas above 500 m (Elias, 2007). Due to its ecological amplitude, this

species occurs in a wide range of habitats – from coastal to subalpine scrublands – being a keystone species for ecological restoration plans because of its considerable importance on the Azorean natural forest ecology (Elias et al., 2011). *Juniperus brevifolia* is internationally protected under the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention) and its conservation status is currently "Vulnerable" according to the IUCN (International Union for Conservation of Nature) criteria (Thomas, 2011).

2.3. Sampling

All sampling was adopted and conducted following standard dendrochronological methodologies and protocols (Speer, 2010). Sampling was performed between January and March 2019 and in July 2019 including adult trees with acceptable size (i.e., more than 10 cm in trunk diameter), avoiding trunk distortion to obtain optimal cores. A Pressler borer (Haglöf Sweden AB) was used to collect 86 wood increment cores (5 mm in diameter) from a total of 45 individuals (25 from São Miguel and 20 from Terceira), with 2 cores per tree. Sampled trees were randomly selected among the areas given as dominated by *J. brevifolia* in the Regional Forest Inventory. In addition, to provide wood-anatomical sections, microcores were collected from different individuals using the Trephor tool (Rossi et al., 2006). The purpose of wood anatomical sampling was to provide microscopic images of tree-ring features.

For each tree, additional information was collected regarding dendrometric traits, namely Diameter at Breast Height (DBH) at 130 cm, Diameter at Base (DB) at 20 cm, and Maximum Tree Heigh (HMax). A diameter measuring tape was used to measure diameters and a Vertex IV 360 and Transponder T3 (Haglöf Sweden AB) were used to

measure tree height (Speer, 2010; Sedmakova et al., 2016). Tree location was collected using a Garmin Montana 680 GPS, to allow assembling accurate geographic information for future climate data extraction.

2.4. Sample preservation and preparation

After sampling, wood microcores were immediately transferred into Eppendorf microtubes filled with formaldehyde-ethanol-acetic acid (FAA) fixative solution. The increment cores were stored into paper straws and, at the laboratory, placed in wood supports for air-drying for at least one week, and then glued in the respective supports. Sample surface preparation was carried out by sanding with progressively finer grades of abrasive paper - up to grid 600 - (Orvis and Grissino-Mayer, 2002; Speer, 2010) until the xylem cellular structure, tree-ring boundaries and individual tracheids were clearly visible under magnification.

2.5. Microanatomy

Wood microcores were handled following a standard protocol (Prislan et al., 2014). After the fixation step with FAA, an automatic tissue processor was used, performing a progressive dehydration with alcohol, clearing with D-limonene and paraffin infiltration. Microcore samples were paraffin blocked, trimmed, and sectioned in a rotary microtome (8 μm in thickness). Sections were transferred to Glycerin-Albumin coated slides and stored at 37◦C overnight. Before the staining process, paraffin was removed using D-limonene, and the sections rehydrated with alcohol solutions with decreasing concentration. The staining process was adapted from van der Werf et al. (2007): a water solution was prepared with 100 ml demineralized water, 150 mg Astrablue, 40 mg

safranin, and 2 ml acetic acid. Slides were immersed in the staining solution for 10 minutes and then dehydrated and mounted in DPX (Distrene Plasticizer Xylendene).

2.6. Image acquisition

To obtain microscopic images, mounted slides were observed under a light microscope (LEICA DM1000), associated with a CoolSnap-Pro camera (Media Cybernetics), using Image Pro-Plus 5.0. software. Next, to acquire ready to measure images of wood increment cores, we used a LEICA S9I Stereozoom stereomicroscope with incorporated 10 M.P. camera (Leica Microsystems Inc., Buffalo Grove, IL, USA). We captured high resolution images (1920 x 1080 pixels) with 10x magnification (in some case 20x was also used, depending on how visible tree-rings were), by manually moving the sample and keeping a 50% overlap of consecutive images to enable reliable stitching which was done with the open-source software Fiji – ImageJ (Schindelin et al., 2012).

2.7. Tree-ring data collection and analysis

Tree-ring width (TRW) was measured from optical images using Cybis CooRecorder (v. 9.3.1) with a 0.01 mm precision and converted into .rwl files on Cybis CDendro (v. 9.3.1), following the visual crossdating on the PAST5 (SCIEM) software. We used t-values (TBP - Baillie and Pilcher, 1973) above 3 and a Gleichläufigkeit Value (Eckstein and Bauch, 1969) above 60%. The biggest challenge was the presence of false and missing rings, therefore two samples from Terceira (TER) and 5 from São Miguel (SM) were removed from the analysis. In the selection of the reference tree for crossdating at each site, priority was given to samples with longer chronologies and clear ring

boundaries. We combined chronologies from the same tree and hierarchically built each site chronology.

The detrending procedure was applied to each tree-ring series using the package "dplR" (Bunn, 2008) for R, and consisted of fitting a smoothing spline curve with a 50% frequency cut-off and response period of 30 years to each individual ring-width series (Cook and Briffa, 1990; Bontemps and Esper, 2011). This process reduces the influence of disturbance (non-climatic biological age-related growth trends) while preserving, as much as possible, the variability in our short tree-ring series, thereby maximizing the climate signal (Fritts, 1976). Tree-ring indices (TRWi) were pre-whitened to remove persistence from tree-ring series and averaged using a robust biweigth mean to reduce the influence of outliers (Cook, 1985; Cook and Briffa, 1990; Cook and Pederson, 2011). Chronology quality was evaluated using expressed population signal (EPS) and mean Pearson correlation (Rbar) as described in Wigley et al. (1984). The autocorrelation was calculated using the *acf() function*, though we used residual chronologies to reduce its effect (Esper et al., 2015b). Finally, we estimated the uncertainty of the mean chronologies by using a bootstrap approach with 1000 replicates, randomly selecting 75% of the individual chronologies, then calculating a temporal mean chronology at each run, and accessing the respective mean and standard deviation (Appendices 2 and 3).

2.8. Climate correlation

Several climate databases were tested in terms of spatial and temporal resolution, namely Climatic Research Unit (CRU) with Japanese Reanalysis data (JRA) (University of East Anglia Climatic Research and Harris, 2019), WorldClim (Harris et al., 2014; Fick and Hijmans, 2017), and Climatologies at high resolution for the earth's land surface areas

(CHELSA) database. We found that data from CHELSA timeseries dataset (Karger et al., 2017, 2018; Karger and Zimmermann, 2019) with a spatial resolution of 30 degree seconds (ca. 1 km^2) was closer to the real climate at the study sites, since other databases seemed to provide values much closer to known climate stations located at low elevation in Angra do Heroísmo (Terceira) and Nordela (São Miguel) (IPMA, 2021). Also, the selected data showed a slightly lower temperature and higher precipitation at Santa Bárbara than at Tronqueira, which is in agreement with the respective temperatures and the general climatic trend with elevation in the Azores (Azevedo, 2001; Couto, 2012). We used exact coordinates gathered on fieldwork to extract climate monthly data for the sample sites.

Subsequently, response function correlation (*dcc_response*) and partial correlation (*seascorr*) from the R package "treeclim" (Zang and Biondi, 2015) were applied to TRWi site chronologies and climate data. A bootstrap procedure was used to obtain more robust parameter estimates, where 1000 bootstrap samples were taken from the original distributions of climate and tree-ring data. We performed partial correlation analysis to avoid possible spurious correlations, to test the strengths of the relationships, and provide a reasonable and objective assessment of the climate-growth relationship (Stahle and Cleaveland, 1994), by controlling the inter-correlation between climatic variables, and testing different season lengths (2, 3, 4 and 6 months) within a 14-month window.

3. Results

3.1. Detection of annually resolved tree-rings

The wood of *J. brevifolia* showed a clear separation between a yellowish sapwood and the reddish-brown heartwood (Figure 7). Tree-ring boundaries could be distinguished

at the macroscopic level, in transverse section (Figure 7). Due to site conditions, particularly slope, most samples showed uneven tree-rings (Figure 7a). We observed periods of suppressed and released wood in the adult phase, but more complacency was observed in the juvenile phase (Figure 7b), with less variation on ring widths near the pit.

Tracheids in latewood tended to have a smaller cellular lumen and thicker cell wall, forming a relatively thin layer of cells, with a somewhat abrupt transition between early and late wood (Figure 8a). More than 50% of cores had problematic ring features such as missing and wedging rings, however the periods of common variability were long enough to correctly crossdate the final batch for both sites. On Figure 8 (b and c), ring boundaries were sometimes less evident, originating false rings. Some samples showed unclear ring transitions or partially indistinct ring boundaries (Figure 8d) and the presence of wedging rings (Figure 8e), making the crossdating process more difficult. More details were provided, microscopically, in Appendix 5.

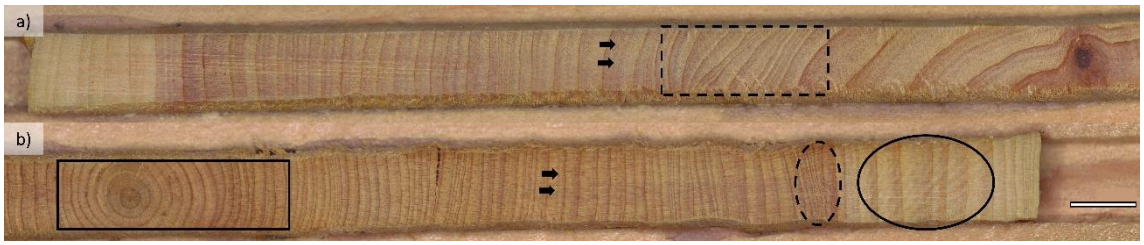

Figure 7. Illustration of two examples of *Juniperus brevifolia* increment cores from the same site: a) Uneven growth rings (black dashed rectangle); (b) Juvenile phase (black solid rectangle), suppressed wood (black dashed circle) and released wood (black solid circle). Scale bar 4 mm.

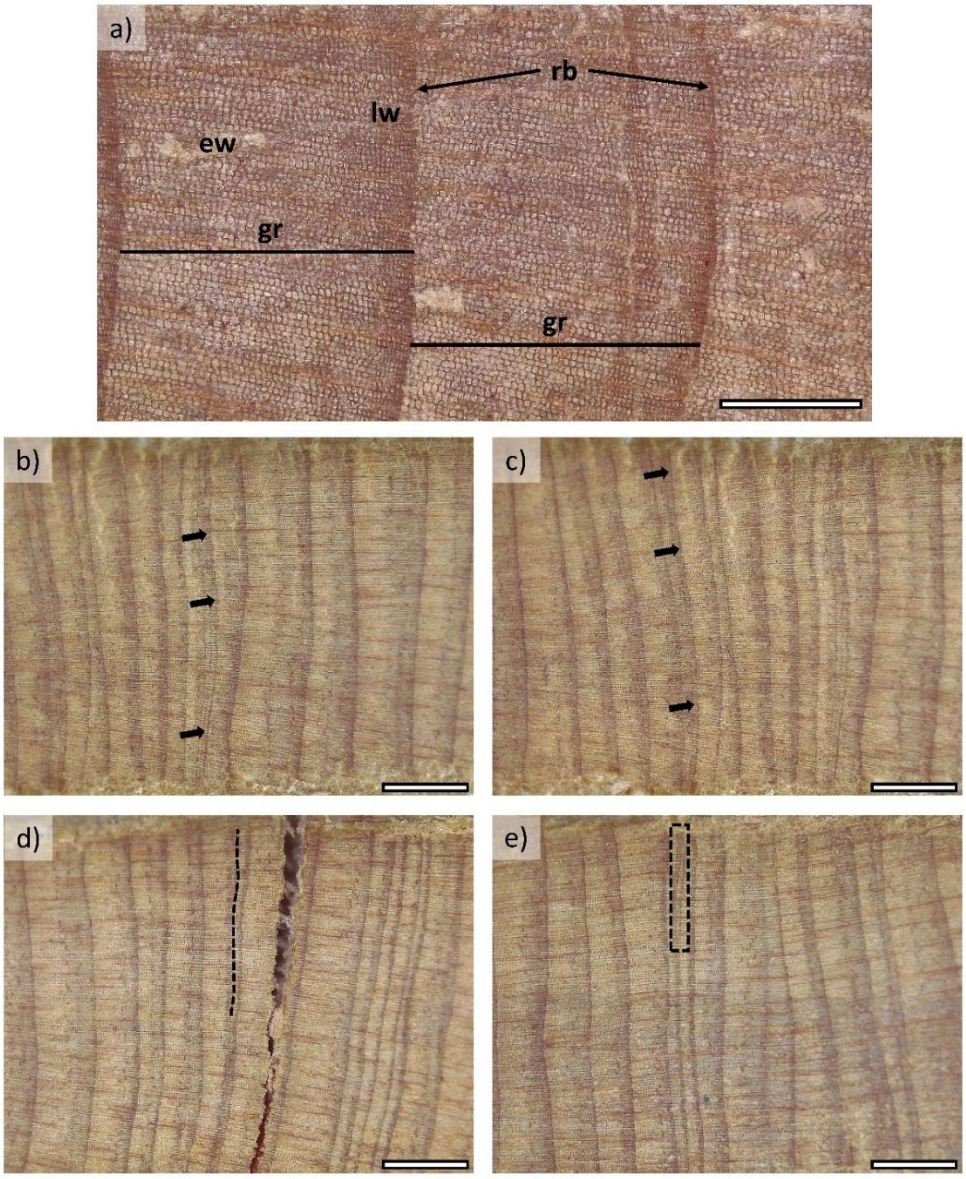

Figure 8. Growth rings of *Juniperus brevifolia* trees obtained from cross-sections: a) detail of growth ring (gr) with thick-wall ring boundaries (rb), earlywood (ew) and latewood (lw), scale bar 500 μm; Examples of frequently present wood anomalies, b) and c) presence of false rings (black arrows), d) partially indistinct ring boundary (dashed line), e) wedging ring (dashed rectangle); scale bar 1 mm.

3.2. Climate-growth correlations

Associated with a higher elevation, lower annual temperature and higher precipitation were found at TER than at SM (Table 1). Highest EPS and Rbar values were

obtained for SM, with a slightly larger sample size, but a higher autocorrelation was found in TER. Figure 9 shows tree-ring widths for SM and TER populations and the estimated mean chronologies with a length of 86 and 117 years, respectively, where variability of individual chronologies was relatively high. the bootstrapped sampling suggested that both mean chronologies were robust (Appendices 2 and 3).

Table 1. Site description with geographical coordinates, annual temperature (T) and precipitation (P) (data extracted from CHELSA timeseries dataset) at the two study sites. Number of trees and cores (N), average maximum tree height (Hmax), average DBH (DBH), mean inter-series correlation (Rbar), Expressed Population Signal (EPS) and the first order autocorrelation (AC1).

Island	**Terceira**	**São Miguel**
Abbreviation	TER	SM
Longitude (º)	-27.3207	-25.1843
Latitude (º)	38.7365	37.7972
Elevation (m)	900	600
N	18 (33)	20 (46)
Annual T (ºC)	14.89	15.09
Annual P (mm)	1546	1162
Hmax (m)	4.72	3.89
DBH (cm)	16.42	17.39
Rbar	0.10	0.25
EPS	0.77	0.93
AC1	0.65	0.33

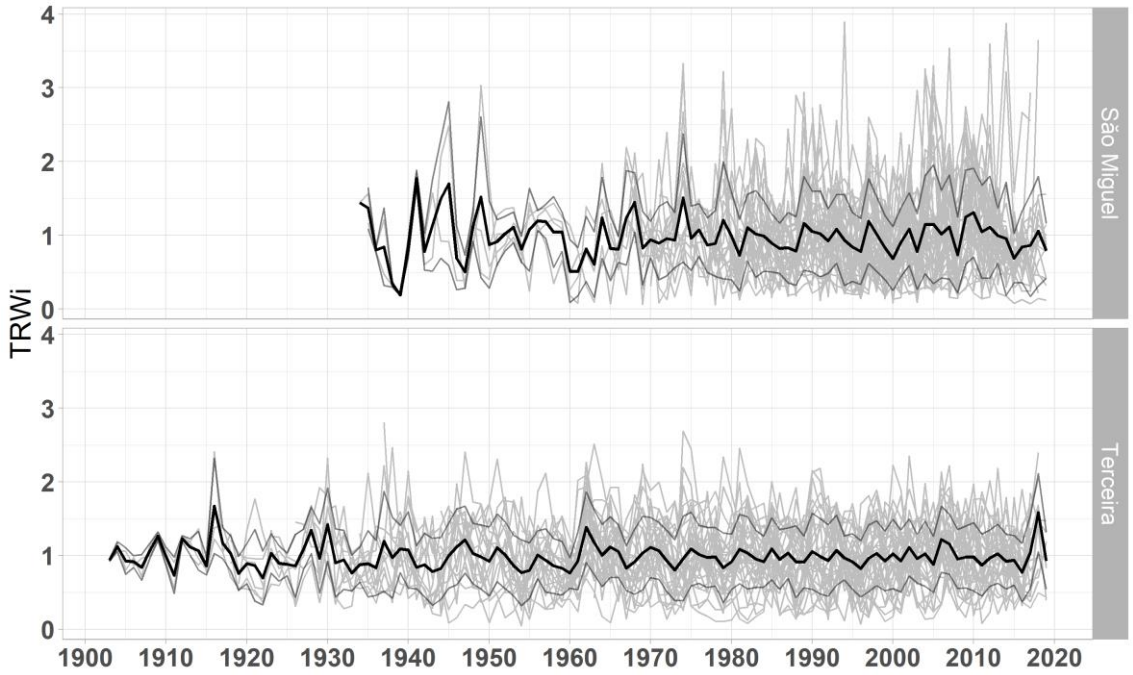

Figure 9. Spaghetti plot of *Juniperus brevifolia* tree-ring indices for two populations at São Miguel and Terceira islands, Azores. Mean chronology (bold line) ± standard deviation (dark grey lines) is shown.

First order autocorrelation (AC1) was higher on Terceira tree-ring chronology, suggesting that the impact of the former year's growth on the present year's was higher at Terceira. Nevertheless, residual chronologies were used to reduce autocorrelation, and, at both sites, they provided negative correlations with summer temperatures (Figure 10), while all correlations between TRWi site chronologies and precipitation were nonsignificant (Appendix 4). The absolute values of the correlations between TRW and temperature were relatively low.

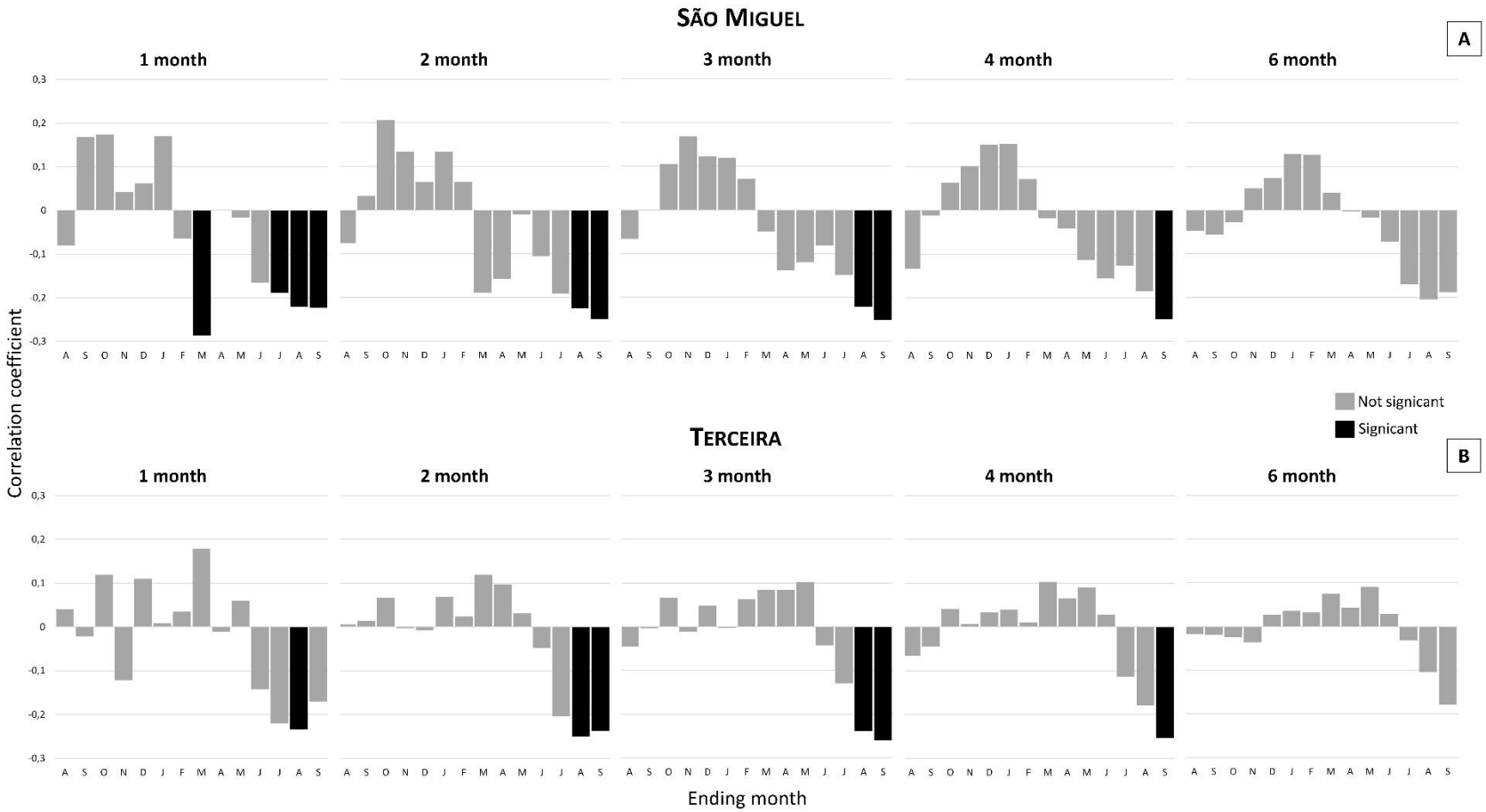

Figure 10. Seasonal climate-growth relationships evaluated (using 1, 2, 3, 4 or 6 consecutive months) from partial correlation coefficients between TRWi site chronologies and climate data. Mean monthly temperatures are used as primary climate variable, while monthly precipitation sum is used as controlling variable. Significant correlations are marked in black.

4. Discussion

We found the presence of several indistinct ring boundaries, false and missing rings, which agrees with previous dendroclimatological studies of *Juniperus* from subtropical or tropical regions (Wils et al., 2009; Wils et al., 2011). Problematic crossdating has also been reported for many other genera, especially on subtropical and tropical areas (Speer et al., 2004; Krepkowski et al., 2012; Groenendijk et al., 2014), and also other regions, for example in the Mediterranean with olive trees (Cherubini et al., 2013) or in New Zealand with two *Prumnopitys* species (Boswijk et al., 2021). Wils (2009) and Wils et al. (2009) analyzed the crossdating capacity of *Juniperus procera* in Ethiopia and concluded that successful crossdating may be inhibited by the formation of multiple or indistinct rings. This can be explained by the presence of moderately wet slopes fed by continuous moisture and rainfall, and consequently wet terrain, which causes an abnormal growth pattern and the formation of missing, wedging, and false rings, due to cambial activity maintained throughout the year (Wils, 2009). Previous studies reported the same observations for other Juniperus species, at least in a portion of the observed samples, successful crossdating depending on a careful consideration of wood anatomical anomalies (De Luis et al., 2007; Wils et al., 2011a). In the Azores, low elevation sites exhibit less pronounced seasonality, therefore we decided to sample trees at higher elevations. Despite that, our crossdating evaluation parameters showed relatively low values indicating that tree-growth was not exclusively limited by climate and that different factors might affect tree-growth, namely competition, sloped terrain, among other factors (Wils et al., 2011a; Krepkowski et al., 2012; Chi et al., 2015; Islam et al., 2019; Zalloni et al., 2019; Liu et al., 2020; Nelson et al., 2020). Regarding the wood anatomy of *Juniperus brevifolia*, our results agree with the comparative wood anatomical study by De Palacios et al. (2014). Both studies were able to detect the presence of ring

boundaries, which is the main pre-requisite for dendrochronological studies. The somewhat abrupt transition between early and late wood was delimitated by tracheids in latewood that tended to show a smaller cellular lumen and thicker cell wall. This sudden transition has also been reported by De Palacios et al. (2014) in a comparative anatomical study of Macaronesian *Juniperus*, but also for other conifer species such as *Pinus sylvestris* L. (Martín et al., 2010).

Autocorrelation values were considerable high on both sites, meaning that the former year's growth affects the present years (Cook, 1985). Therefore, pre-whitening procedure had to be undertaken in order evaluate the climate signal on reliable mean chronologies (Hassan, 2016; Coulthard et al., 2020). Although the bootstrapped mean chronologies showed consistent results (Appendices 2 and 3), the variation among trees was considerable, resulting in low Rbar values (Table 1). Low Rbar values have been reported in previous studies, particularly when considering shrub-ring data or low arboreous species (e.g., Buras, 2017; Le Moullec et al., 2020), or regions where climate ranged from tropical or subtropical to areas in transitional climates (e.g., Zuidema, 2005; Brienen and Espinosa et al., 2018; Granato-Souza et al., 2018; Vasconcellos et al., 2019; Shi et al., 2020; Ali et al., 2021). This suggests that further sampling is needed to improve the average correlation among series, although not invalidating the responsiveness of tree-ring data to climate variability (Buras 2017). Another factor that might have affected the Rbar values in our study was the relatively small distance between trees, possibly leading to competition and affecting tree growth (e.g. Chi et al., 2015; Sánchez-Salguero et al., 2015; Zhang et al., 2016; Ford et al., 2017; Zalloni et al., 2019; Luo et al., 2020).

Correlation analysis at SM showed that spring and summer temperatures tended to significantly affect tree radial growth, while at TER only late summer temperatures had a negative effect on tree radial growth. Although this could be the result of relatively

higher temperature and lower precipitation in SM as compared to TER, these slight differences could also be explained by specifics of stand conditions that could prevail, rather than climate factors (e.g., Evans et al., 2017; Liu et al., 2020). These factors include tree density, which differed among the two sites, usually associated with higher temperatures and lower rainfall (Nelson et al., 2020), which agrees with our results, and plant community composition differences that might be associated with different competition levels (Chi et al., 2015; Zalloni et al., 2019). In addition to stand conditions and tree competition, natural disturbances are often related to low or reduced climate signal, being a predominant growth limitation (Rydval et al., 2015, 2018). The only dendroclimatological study reported for the archipelago focused on *Pinus pinaster* Ait., on a different island and at a lower elevation site, where there was a positive response to spring precipitation but no temperature signal in the tree-ring width chronology (Vieira et al., 2017). In a study of *Juniperus thurifera* L. in central Spain, tree-ring series contained information on late spring and early summer drought conditions (Esper et al., 2015a). *Juniperus brevifolia* subsp. *brevifolia* is adapted to wet/very wet conditions and low/mild temperatures (Elias and Dias, 2014), which is in agreement with our results, as precipitation in late spring and early summer showed a tendency to have a positive effect, although not significant (Appendix 4). Moreover, the negative effect of summer temperatures could indicate the occurrence of summer drought, since low precipitation, water drainage/infiltration along steep terrain and increased evapotranspiration could limit the amount of water available to sustain cell division and expansion during this season (Camarero et al., 2014). High temperature would likely increase potential evapotranspiration, reducing soil moisture content but also leading to stomatal closure, potentially inhibiting tree growth (Sigdel et al., 2018; Harvey et al., 2020). The effect of topography on water availability has been described in several studies as influencing tree

growth, even if on a small scale (He et al., 2017; Kim et al., 2017; Dearborn and Danby, 2018a,b; Fortunel et al., 2018).

Juniperus is one of the most important genera for climate reconstructions and dendrochronology research (Treydte et al., 2006; Sano et al., 2013; DeRose et al., 2015; Mokria et al., 2018; Opała-Owczarek and Niedźwiedź, 2019; Yang et al., 2019). Thus, considering subtropical regions and areas in transitional climates like the Azores, where tree growth is generally not limited by precipitation, and seasonal temperature fluctuations are not extreme (Worbes, 2002; Brienen et al., 2016; Żywiec et al., 2017), a future approach could rely on the analysis of sub-annual tree growth using dendrometers or on a xylogenetic approach (Poljanšek et al., 2019). Meanwhile, we conclude that our results suggest an acceptable dendrochronological potential of *J. brevifolia*, which could be further evaluated by i) increasing sample size to obtain more representative chronologies with higher EPS and Rbar, ii) studying additional tree-ring proxies, such as stable carbon and oxygen ratios (Shestakova and Martínez-Sancho, 2021), wood-anatomy (Arnič et al., 2021) and blue reflectance (Kaczka and Wilson, 2021) and long chronologies of wood-anatomical characteristics; and iii) by sampling populations at new locations, to have a broader view of the TRW/climate relationship in the archipelago.

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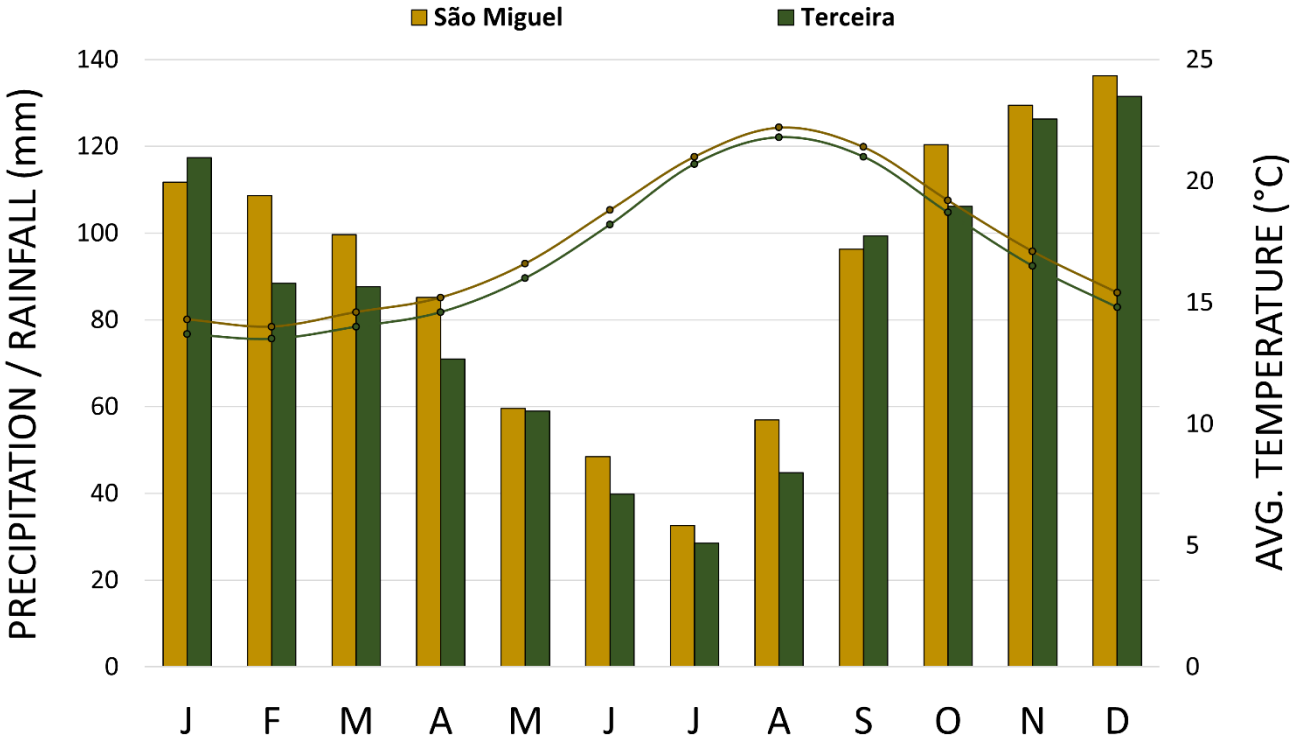
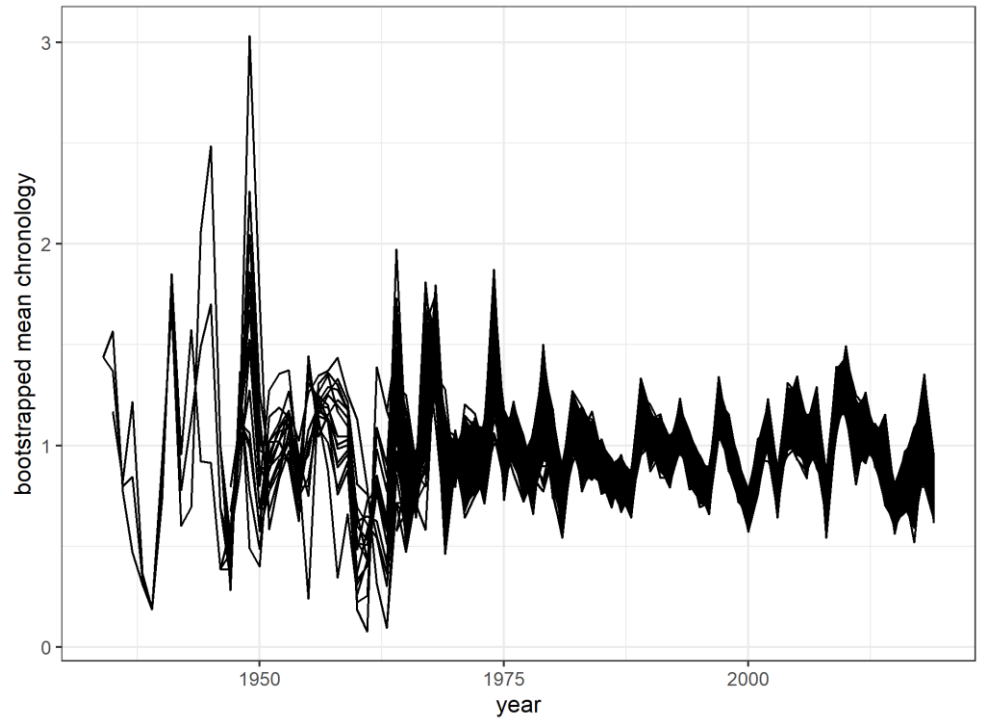
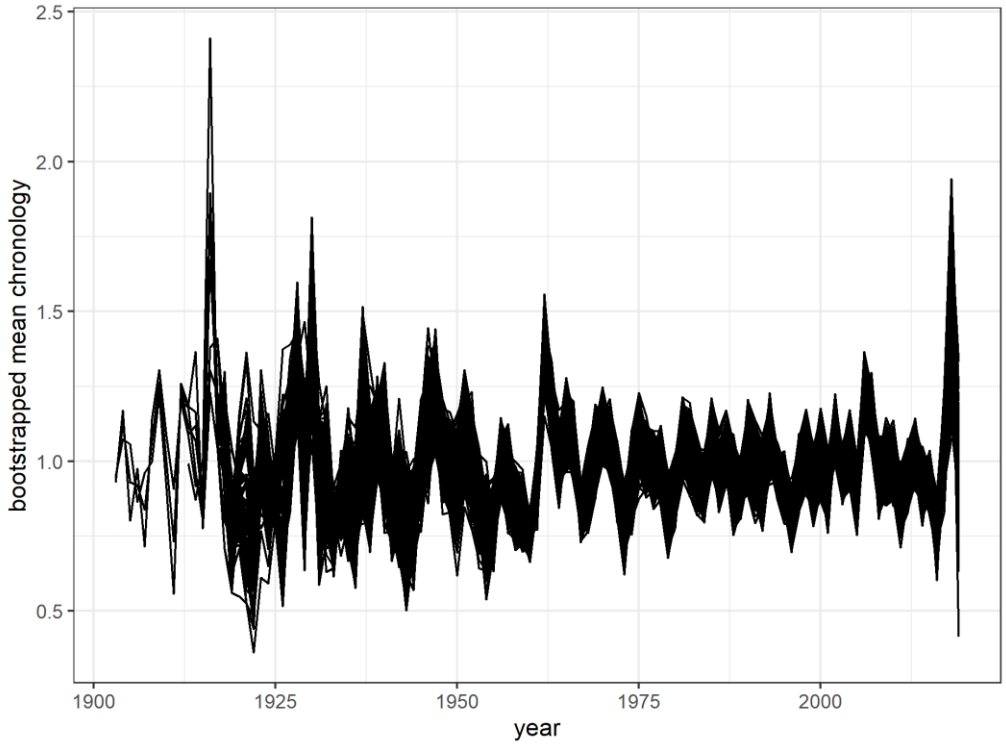
CHAPTER 2 – Supplementary Material



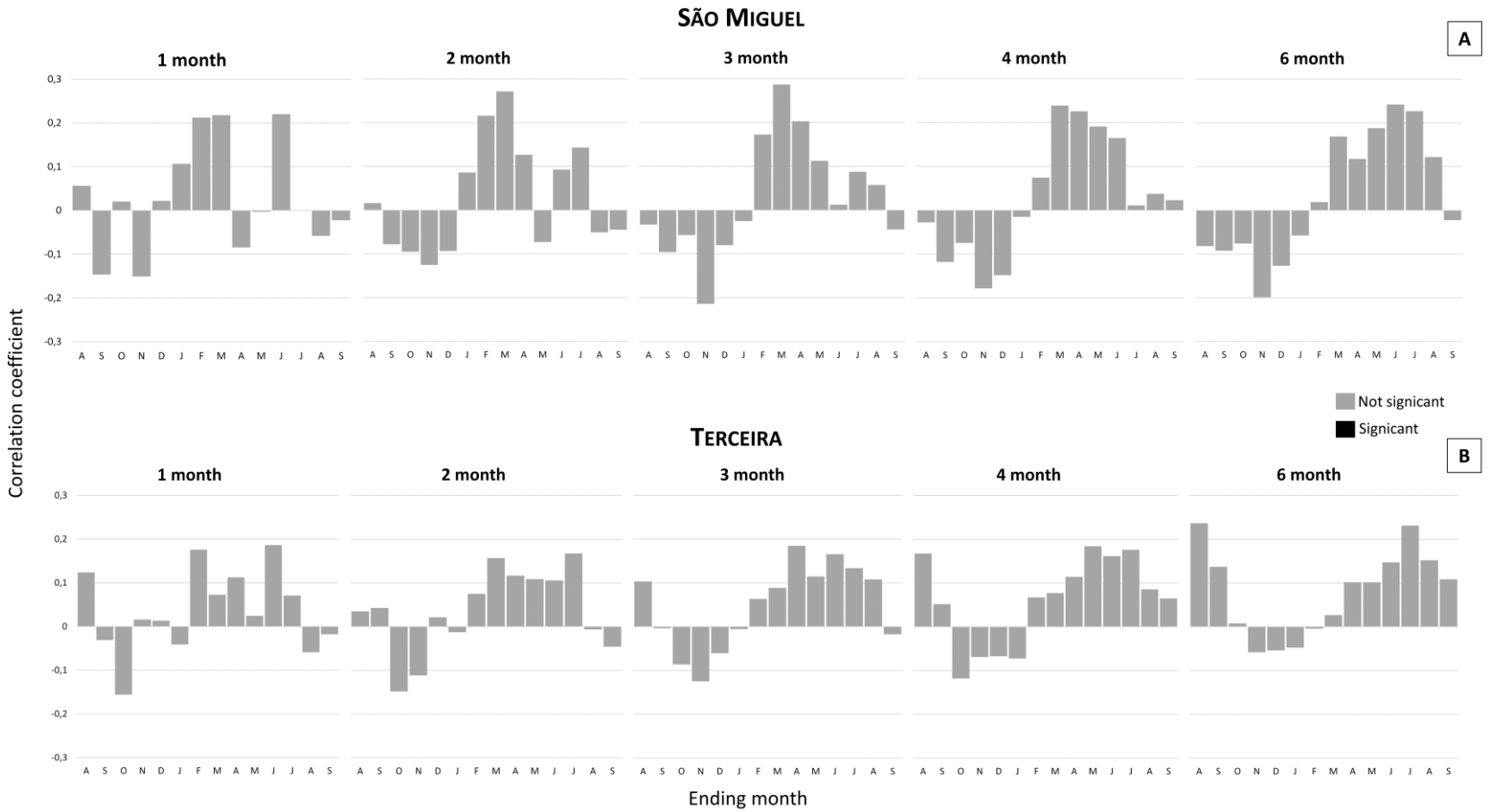
Appendix 1. A general comparison of average monthly temperatures (ºC, lines) and sum of monthly precipitation (mm, bars) for the islands targeted in this study (São Miguel and Terceira). Both climatic variables data was retrieved from climate normals (1971-2000) of Portuguese Institute for Sea and Atmosphere (IPMA).



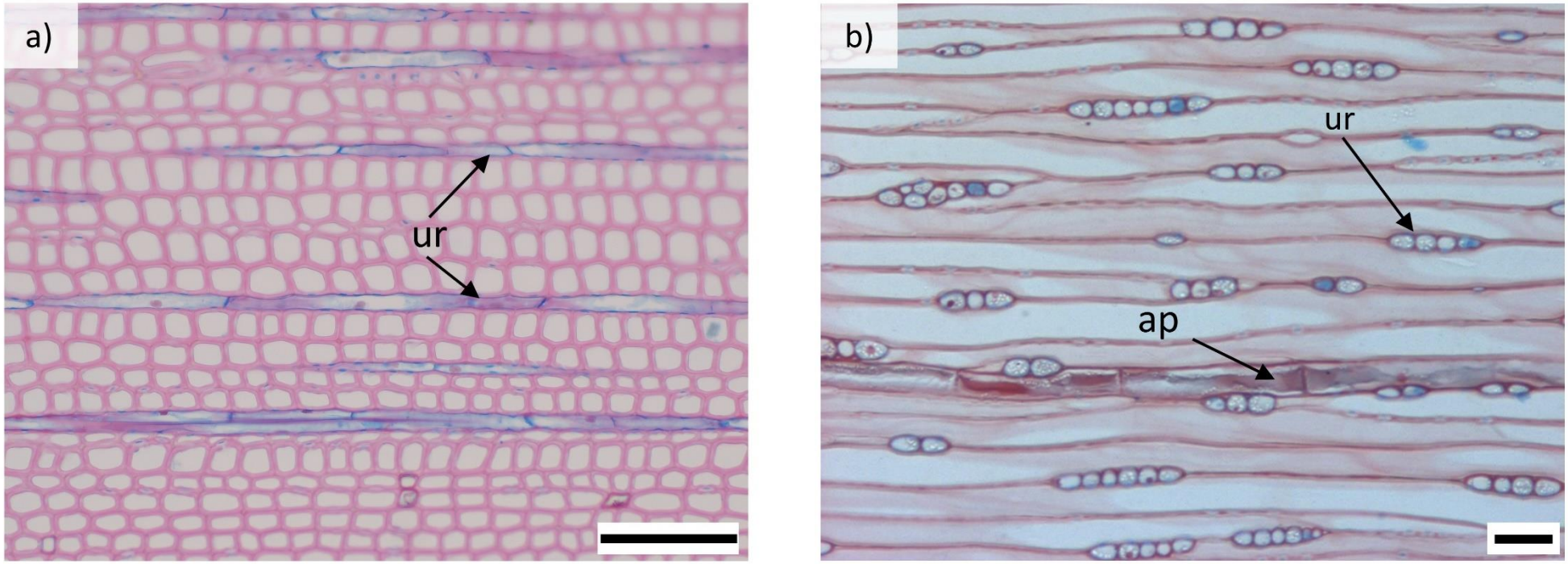
Appendix 2. São Miguel bootstrapped mean chronology.



Appendix 3. Terceira bootstrapped mean chronology.



Appendix 4. Seasonal climate-growth relationships evaluated (using 1, 2, 3, 4 and 6 consecutive months) from partial correlation coefficients between TRWi site chronologies and climate data. Monthly precipitation sum is used as primary climate variable, while mean monthly temperatures are used as controlling variable. Significant correlations are marked in darker color.



Appendix 5. Cross-section (a) and tangential section (b) views of *Juniperus brevifolia* wood under transmission microscope: a) tracheids with relatively homogeneous cross-section size, and uniseriate rays (ur) distributed along an annual ring; scale bar 100 µm; b) A detailed view (scale bar 50 µm) showing a closer perspective of uniseriate rays (ur) and the presence of axial parenchyma. Tracheids with equal size are visible and uniseriate rays are distributed along an annual ring. Ray parenchyma is visible, very abundant, and diffuse with dark-coloured cell content, and rays (2-7 cells high) were uniseriate.

CHAPTER 3

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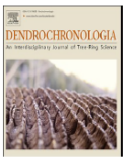

Original article

Tree growth-climate relationship in the Azorean holly in a temperate humid forest with low thermal amplitude

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Title

Tree growth-climate relationship in the Azorean holly in a temperate humid forest with low thermal amplitude

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Abstract

Dendroclimatic records in areas with high relative humidity and low thermal amplitude are manifestly scarcer and only a few studies are applied to species that are present in areas with weak seasonality. The Azores archipelago with temperate climate, with low thermal amplitude, has unique biodiversity, including the Azorean holly, *Ilex azorica* Gand., that is dominant in most extant natural forests. Hence, the importance of understanding its behavior and relation with climate. In this study, we try to understand tree-ring patterns of this species and examine the relationship between radial tree growth and main climatic drivers. For this purpose, we sampled four populations from São Miguel Island and two from Terceira Island. We found a diffuse-ring porous wood with a common layer of vessels associated to the ring boundary, which was critical to identify annual tree-rings. Generalized linear models were used to relate different variations of temperature and precipitation parameters, resulting into a diverse climate-growth relationships of different populations, while the composite population exhibited pronounced effect of temperature. We conclude that, *I. azorica* forms reliable annual tree-rings, which can be statistically related to climate, mostly temperature. However, there are differences among specific sites, thus the climate sensitivity depends on other site characteristics, such as soil and slope, but probable also to other ecological drivers, such as the competition, water drainage, among others.

Keywords:

Azores; Aquifoliaceae; Dendroclimatology; GLMs; Humid forest.

1. Introduction

Humid forests influence global hydrological cycles (Avissar and Werth, 2005) and show high biodiversity levels (Harvey et al., 2020; Lima et al., 2020), playing an important role as carbon sinks (Durigan et al., 2017; Borges Silva et al., 2022). However, dendroclimatic records in regions with high relative humidity and low thermal amplitude are manifestly scarcer than in areas with a more pronounced seasonality (Worbes, 2002; Rozendaal and Zuidema, 2011; Fichtler, 2017; Babst et al., 2018; Zhao et al., 2019; Pearl et al., 2020; Giraldo, 2021). For example, Cherubini et al. (2003) found that trees growing under Mediterranean climate could show non-stopping cambial activity. Likewise, in the Canary islands, a study dedicated to species growing under reduced variation of annual temperature and daily mean temperature, obtained robust tree-ring chronologies for a third of the species only (García-López et al., 2022). In fact, only a few tree-ring chronologies have been established for those environments, since the formation of clear annual growth rings in those conditions raised doubts (Rozendaal and Zuidema, 2011; Quintilhan et al., 2021). Despite comparatively low scientific attention in the past, work in dendrochronology continued, leading to a better understanding of the complexity of growth ring formation and to the detection of growth ring boundaries in broad-leaved species in areas with low climatic seasonality (Worbes, 2002; Dezzeo et al., 2003; Brienen and Zuidema, 2005; Wils et al., 2011; Brienen et al., 2016; Fichtler, 2017; Pavão et al., 2022). At humid forests, despite the heterogeneity of sampling sites and species, tree growth usually correlates positively with precipitation, apart from mountain habitats, where growth is usually stimulated by higher temperatures (David et al., 2014; Vlam et al., 2014; Pucha-Cofrep et al., 2015; Pavão et al., 2022).

Azorean forests are associated with temperate humid conditions that can be found only in a few regions of the planet, including temperate islands (Brienen et al., 2016; Elias

et al., 2016; Fichtler, 2017; Pavão et al., 2019, 2022). The oceanic temperate climate is reflected in high annual precipitation, high relative humidity, persistent wind and low thermal amplitude (Agostinho, 1941; Bettencourt, 1979; Calado et al., 2011). Spatial distribution of precipitation in the archipelago is regulated by altitude and the exposure to dominant winds (Marques et al., 2008). About 75% of annual precipitation occurs in winter, and its distribution is highly influenced by topography, with very wet high elevation zones and drier coastal areas (Santos et al., 2004). Moreover, horizontal precipitation resulted from the interception of air humidity and mountain forests (also designated as cloud forests), very common in the archipelago, still increases the amount of available water (Gabriel and Bates, 2005; Dias and Melo, 2010; Elias et al., 2011). Nonetheless, depending on climate conditions, particularly wind, water balance and radiation, the forests of the Azores can be dominated and co-dominated by distinct endemic trees (Elias et al., 2016; Pavão et al., 2019). Despite the ecological view that the Azorean forests are distributed as a continuum, with some niche partitioning between dominant species, the zonal vegetation is characterized by eight vegetation belts, in which the dominant species change with altitude (Pavão et al., 2019). However, most of the dominant forest species have not been targeted with dendrochronological studies, for example the Azorean holly, *Ilex azorica* Gand. Thus, the importance of studying the dendrochronological potential of *I. azorica* and its relationship with climate, since this species dominates between 600 and 1000 m a.s.l. and is present in the *Juniperus-Ilex* montane forests in the upper thermotemperate-hyperhumid zone, with rainfall ranging from 3000 to 5000 mm/year (Elias et al., 2016; Pavão et al., 2019).

In fact, the Azores still represent one of the major gaps in the International Tree-Ring Databank with only a few studies (Zhao et al., 2019). For the invasive tree *Pittosporum undulatum* Vent., dendrochronological tools, developed from allometric equations, were

used to estimate above-ground biomass (Wunder, 2010; Teixeira et al., 2015; Borges Silva et al., 2017). A study of the introduced species *Pinus pinaster* Aiton, focusing a low elevation site, resulted with a positive response to precipitation and no temperature signal in the tree-ring chronology (1961 to 2010) (Vieira et al., 2017). A description of growth ring anatomy allowed to understand the relationship between dendrometric traits and the number of growth rings in the endemic tree *Laurus azorica* (Seub.) Franco (Matos et al., 2019). More recently, a dendroclimatological approach, showed negative correlations between tree-ring widths and late summer temperature (1903 to 2019), in two mountain populations of *Juniperus brevifolia* (Seub.) Antoine (Pavão et al., 2022). Moreover, the lack of more extended dendrochronological research, impairs more detailed estimations of the carbon sequestration capability of the different Azorean forests, since carbon stocks have been estimated (Borges Silva et al., 2022), but tree age and growth rates are largely unknown.

The family Aquifoliaceae with *Ilex* as the only genus, includes dioecious shrubs or trees with simple and alternate leaves (Powell et al., 2000; Loizeau et al., 2005). It shows diffuse to semi-porous wood and tree rings that are mostly distinct in temperate and subtropical areas, but faint or entirely absent in tropical species (Baas, 1973; Scheweingruber et al., 2013; García-López et al., 2022). Dendrochronological research has covered several species of this family. In South America, *Ilex microdonta* Reissek - one important species of the tropical cloud forests in Brazil - forms distinct growth rings and its tree growth is mainly related to summer minimum temperature and precipitation (Miranda, 2019). In continental Europe, *Ilex aquifolium* L. has been shown to increase vessel clustering in contrast to radial growth, under drought stress conditions, suggesting that carbon allocation depended on the stem water conduction system in drought-induced environments (Rita et al., 2015). Considering the Canary Islands, *Ilex canariensis* Poir.

often showed indistinguishable rings (Scheweingruber et al., 2013; García-López et al., 2022). In the Azores, Câmara (2016), while aiming to understand temporal forest dynamics, first reported the use of growth ring analysis of *I. azorica* to estimate tree age distribution, considering that growth rings showed an intermediate level of reading difficulty, with some indistinct rings, and several prominent vessels (Worbes, 2004).

In this research we aimed to better understand tree-ring patterns in *I. azorica*, and to make a first evaluation of the relationship between climate and tree-ring width. The specific aims of this study were i) to build reliable *I. azorica* site chronologies from main natural populations in the archipelago and ii) to evaluate the statistical relationship between climate and *I. azorica* tree-rings widths chronologies, separately for individual populations and, as a whole, for the composite chronology resulting from the average between populations. We used an extensive sampling approach in two islands, with six populations and a total of 175 trees. Since regression techniques have been widely used in dendrochronological research worldwide (Fritts, 1976; Cook and Kairiukstis, 1990; Li et al., 2014; Ciapała and Adamski, 2015; Rita et al., 2015; Coulthard et al., 2017; Jevšenak et al., 2018; Cui et al., 2022), we used generalized linear models (GLMs) to assess the relationship between tree-ring chronologies and climate factors. We expect to find diffuse porous wood in the Azorean holly with the occasional occurrence of some undefined boundaries, although generally clear growth rings and, consequently, significant relationships between radial growth and climate.

2. Methods

2.1 Azorean holly

The Aquifoliaceae comprehend more than 400 species of dioecious shrubs or trees with simple and alternate leaves (Powell et al., 2000; Loizeau et al., 2005). Mostly occur in the tropics, but widening into temperate regions of America, Eurasia and Africa, being commonly found in humid habitats (Manen et al., 2010; Sosa et al., 2013). Species are mostly recognized on whether they are deciduous or evergreen, by the size and shape of the leaves, among other characteristics, although Ilex taxa are difficult to distinguish only using wood or leaf anatomy (Baas, 1973), or pollen characteristics (Lobreau-Callen, 1975). In Portugal, only three species of Ilex are present: *Ilex aquifolium* L. in the mainland, *Ilex canariensis* in Madeira, and *Ilex azorica* in the Azores. The latter is characterized by obovate, acute, or obtuse and relatively small leaves (Appendix 6). In the Azores, Ilex forests appear in areas with high vertical precipitation and horizontal (i.e., occult) precipitation, associated with the more permeable rocky substrates, and incipient soil. *Ilex azorica* is classified as 'Least Concern' according to IUCN criteria (Rivers, 2017), and considered a mature species that regenerates in the forest (Elias and Dias, 2009). Its important role in the Azores ecosystems is well-established due to its dominance in several habitats (Ribeiro et al., 2005; Elias et al., 2016; Pereira et al., 2016; Pavão et al., 2019).

2.2. Study area

Located in the North Atlantic Ocean, the Azores archipelago (36◦55'–39◦43' N and 25◦00'–31◦15' W) includes nine volcanic islands (Figure 11), with a total land surface of 2323 km2 (Forjaz et al., 2004). Divided into three main groups, the archipelago lies on

an area of seafloor with a complex tectonic setting, near the triple junction between the Eurasian, Nubian, and North American plates (Miranda et al., 2014). According to the most recent Koeppen-Geiger climate classification (data from 1971 to 2000) (Couto, 2012), the Azores climate is predominantly temperate (type C), namely Cfb (temperate with no dry season and with a mild summer). The age of islands varies from the youngest (Pico island) of 0.186 My (Costa et al., 2015), to the oldest (Santa Maria island) with 6.01 My (Ramalho et al., 2017). We selected four sites in São Miguel Island, with 0.8 My (Sibrant et al., 2014), and two in Terceira Island, with 0.39 My (Hildenbrand et al., 2014), within the *Juniperus-Ilex* montane forests (Elias et al., 2016).

The types of vegetation and the dominant taxa found at each site were the following: Serra de Santa Bárbara and Terra Brava – dominant presence of arboreous species (*I. azorica*, *L. azorica* and *J. brevifolia*) also with an abundant pteridophyte cover of *Dryopteris azorica* (Christ) Alston and *Culcita macrocarpa* C. Presl); Nordeste and Pico Bartolomeu – besides the three mentioned taxa, *Erica azorica* Hochst. ex Seub. and the invasive *Clehtra arborea* Aiton. also dominated at the tree layer, and *Athyrium filix-femina* (L.) Roth. was common at the understory; Sete Cidades and Lombadas - with similar abundance and dominance of the vegetation from the previously described sites, but with the presence of the invasive species *Hedychium gardnerianum* Sheppard ex Ker Gawl. and without the presence of *J. brevifolia*, *E. azorica* or *C. arborea*.

The climate present at our study sites, based on the data obtained from the CHELSA database (Karger and Zimmermann, 2018, 2019), was summarized in Appendix 7, where mean monthly temperature and monthly precipitation are shown.

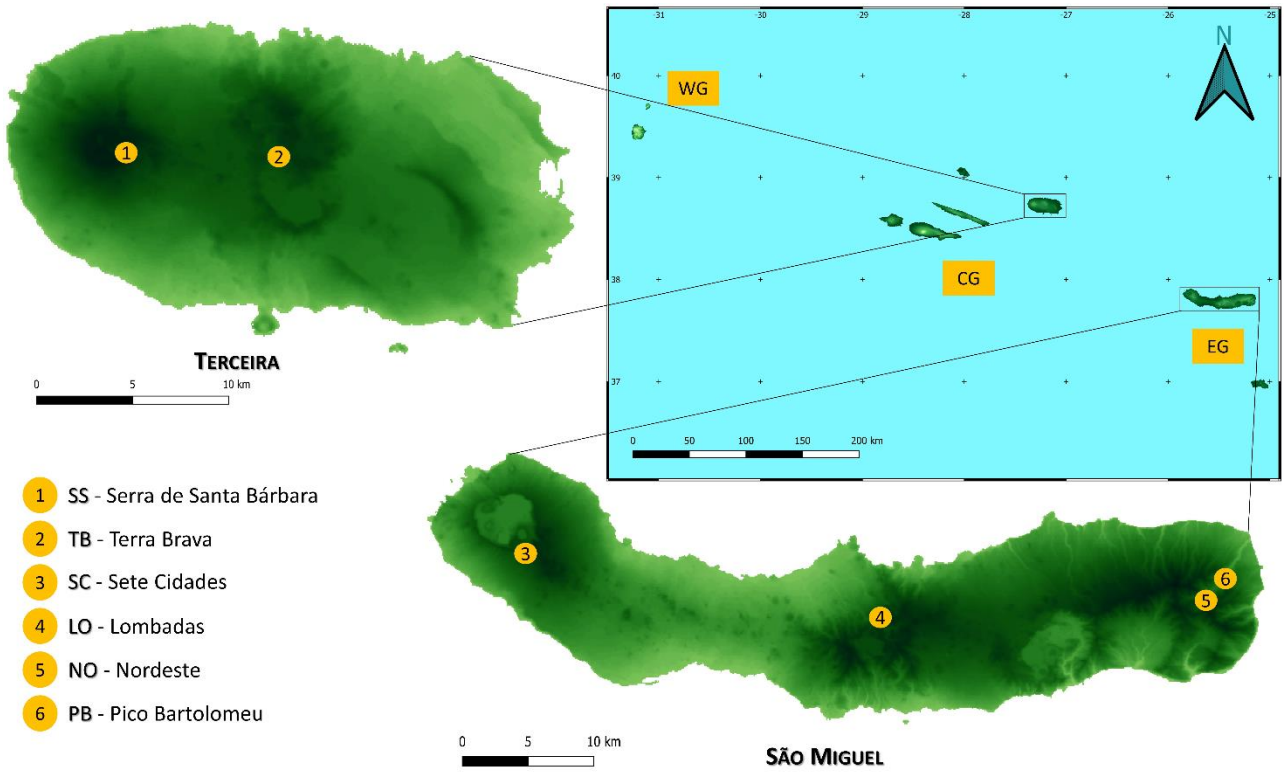

Figure 10. Map of the Azores archipelago (WG – Western Group, CG – Central Group, and EG – Eastern Group) and a focus of both islands in the study (Terceira and São Miguel). Yellow circles indicate *Ilex azorica* populations and the respective abbreviations/names of the sites.

2.3. Tree core sampling and preparation

Field surveys were conducted during 2019 and 2021, mainly in summer. In total, 175 trees were sampled, with two to four wood cores per tree, resulting in total of 416 cores. Laboratory analyses were based on dendrochronological dating techniques described by Speer (2010). Wood samples were extracted with a 5 mm diameter Pressler borer from, at least, 30 individual trees at each site. The diameter at breast height and the height of each tree were measured. The cores were kept in paper straws to prevent possible damage. In the laboratory, increment cores were air dried and glued onto wooden mounts. Cores were sanded with progressively finer grades of abrasive papers (up to grid 600) until a suitable polished surface was achieved. Next, to acquire ready to measure images of wood

increment cores, we used a LEICA S9I Stereozoom stereomicroscope with incorporated 10 M.P. camera (Leica Microsystems Inc., Buffalo Grove, IL, USA), keeping a 50% overlap of sequential images to enable reliable stitching which was done with the open-source software Fiji – ImageJ.

2.4. Tree-ring data collection and analysis

Annual tree-ring widths (TRW) were measured to an accuracy of 0.01mm using Cybis CooRecorder (v. 9.3.1) and converted into .rwl files on Cybis CDendro (v. 9.3.1). Visual crossdating was performed on the PAST5 (SCIEM) software, and was based on measures of GLK (Gleichläufigkeit) (Schweingruber, 1988; Buras and Wilmking, 2015), T-Test and Pearson's correlation coefficient. We started the crossdating process within trees, with the more readable samples (i.e., no ring anomalies and clear tree-ring boundaries), and hierarchically built each site chronology. Cores which could not be correctly crossdated, were excluded from further analysis.

The detrending procedure and the construction of site chronologies were performed with the R package "dplR" (Bunn, 2008). Individual tree ring-width series were subjected to detrending to remove non-climatic variability (age-related growth trends that are due to biological or stand effects), whereas preserving, as much as possible, the variability in our tree-ring series, thus maximizing the climate signal (Fritts, 1976). The growth trend was processed using cubic splines with 50% frequency, and a cutoff of 0.30 × L years, where L is the length (in years) of the longest individual chronology available for the site (Cook and Peters, 1981; Cook and Kairiukstis, 1990). Afterwards, tree-ring indices (TRWi) were pre-whitened to eliminate persistence from tree-ring series. Prior to the site chronologies building process, a second selection was performed by removing 25% of

the individual timeseries with the lowest correlation coefficients, to improve the signal of the mean site chronologies.

A TRWi chronology was therefore built for each study site, averaging residual tree-ring series, to reduce the effect of autocorrelation while preserving the climatic information (Esper et al., 2015; Brienen et al., 2016), using Tukey's biweight robust mean, which minimizes the effects of outliers (Cook, 1985; Cook and Kairiukstis, 1990; Cook and Pederson, 2011). To estimate the uncertainty of the mean chronologies, a bootstrap approach with 1000 replicates was used, by randomly selecting 75% of the individual chronologies, while calculating a temporal mean chronology at each run (Appendix 8). Assessment of the bootstrapped chronologies quality was performed using: mean Pearson correlation (Rbar) as a measure of the strength of the common growth 'signal' within the chronologies (Wigley et al., 1984); Subsample Signal Strength (SSS), calculated from data on sample size and between mean interseries correlation (Rbar) (Buras, 2017); and to calculate the coefficient of correlation between two consecutive values in a time series (autocorrelation), we used the *acf() function* in R, that retrieves the carry-over effects of previous years.

2.5. Climatic data

For this approach average minimum, maximum and mean monthly temperature and monthly sum precipitation was extracted from CHELSA timeseries dataset (Karger et al., 2017; Karger and Zimmermann, 2018, 2019) with a spatial resolution of 30 arc seconds (ca. 1 km2), using exact coordinates of the sample sites gathered during fieldwork. The following climatic variables were used in modelling:

i) Temperatures of the current year (year of the current growing season) – Average annual minimum, mean and maximum temperatures; Average monthly minimum, mean and maximum temperatures (January to December); Average Winter minimum, mean and maximum temperatures (December-February); Average Spring minimum, mean and maximum temperatures (March-May); Average Summer minimum, mean and maximum temperatures (June-August); and Average Autumn minimum, mean and maximum temperatures (September-October).

ii) Temperatures of the previous year (year of the previous growing season) – Average annual minimum, mean and maximum temperatures; Average monthly minimum, mean and maximum temperatures (January to December).

iii) Precipitation of the current year (year of the current growing season) – Annual precipitation; monthly precipitations (January to December); Winter precipitation (December-February); Spring precipitation (March-May); Summer precipitation (June-August); and Autumn precipitation (September-October).

iv) Precipitation of the previous year (year of the previous growing season) – Annual precipitation; and monthly precipitations (January to December).

2.6. Dendroclimatic models

We applied Generalized Linear Models to estimate the relationship between TRWi and climatic variables (Table 2). This method has been effectively used in growth ring analyses before (Jevšenak et al., 2018; Cui et al., 2022). By estimating parameters with a high efficiency (O'Hara and Kotze, 2010; Dobson and Barnett, 2018), it evaluates the possible effects of the selected climatic variables on tree growth (e.g. Bigler and Bugmann, 2004; Tsen et al., 2016; Rossi et al., 2018; Cui et al., 2022). Indeed, this method

examines how the mean response (i.e., tree growth) relates to a set of predictors (i.e., climate variables) (Wood, 2006), one of the main objectives of dendroclimatology. The models were calculated for the whole data set, and individually for each site. This way, we aimed for a better understanding of the differences between sites, as only the common period of 1983–2019 (common years from all populations with SSS≥ 0.85) was studied, also giving us the opportunity to study the common signal of all sites with the composite population of *I. azorica*.

The complete list of tested models is shown in Table 2. All seasonal models encompassed all four seasons (Winter, Spring, Summer, and Autumn). Minimal adequate models were also calculated, starting with a specific saturated model, and reducing the number of variables, based on the value of the respective AIC (see below), and including only those variables with significant ($p < 0.05$) regression coefficients. Finally, combined models (models that include temperature and precipitation variables) were also calculated, starting from the best temperature and precipitation models. Furthermore, climatic variables were selected according to the results of a Principal Component Analysis (PCA) and a Variance Inflation Factor (VIF) analysis, to remove the correlated variables, resulting into final minimal adequate models. These last steps allowed us to exclude correlated and redundant variables.

2.7. Model selection

The decision of selecting the most informative and parsimonious model was based on Akaike Information Criterion (AIC) (Akaike, 1973), in a corrected version (AICc) to address potential overfitting due to low sample size (Burnham and Anderson, 2002). Goodness-of-fit of the tested models (i.e. adjusted R^2) was calculated as the percentage

of the sum of squares explained by the model (Zuur et al., 2007). We used principal component analysis (PCA) to remove correlated climatic variables and reduce redundancy of the best models (Legendre and Legendre, 1998) and VIF (variance inflation factor) to measure of the amount of multicollinearity among the regression variables (Theil, 1971). After having removed redundant variables, based on the PCA and VIF results, *stepAIC() function* from "MASS" R package (Ripley et al., 2022) was used to further evaluate possible model simplification. The final models only considered those variables with significant regression coefficients ($p<0.05$) and corresponded to AICc values clearly below the null model.

Table 2. List of all calculated models and reference to the inclusion of current year, previous year or both (current and previous year) climatic data.

Models	*Current year*	*Previous year*	*Both*
1 - Mean annual temperature	x	x	
2 - Mean annual minimum temperature	x	x	
3 - Mean annual maximum temperature	x	x	
4 - Mean seasonal temperatures	x		
5 - Mean seasonal minimum temperatures	x		
6 - Mean seasonal maximum temperatures	x		
7 - Monthly temperatures	x	x	x
8 - Minimal adequate monthly temperatures	x	x	x
9 - Monthly mean temperatures	x	x	
10 - Minimal adequate monthly mean temperatures	x	x	
11 - Monthly minimum temperatures	x	x	
12 - Minimal adequate monthly minimum temperatures	x	x	
13 - Monthly maximum temperatures	x	x	
14 - Minimal adequate monthly maximum temperatures	x	x	
15 - Minimal adequate combined temperatures			x
16 - Annual precipitation	x	x	
17 - Seasonal precipitation	x		
18 - Monthly precipitations	x	x	x
19 - Minimal adequate monthly precipitations	x	x	x
20 - Minimal adequate combined precipitations			x
21 - Combined minimal adequate temperature and precipitation			x
22 - Combined minimal adequate model (after PCA and VIF)			x
23 - Final minimal adequate model (after *stepAIC ()*)			x

3. Results

3.1. Detection of annual growth rings in Ilex azorica

Throughout our samples, we found diffuse porous wood with recognizable growth ring boundaries. A layer of vessels associated to the ring boundary was found in most growth rings (Figure 12). This feature helped to detect false rings along the crossdating process. Moreover, separation between early and late wood was identifiable but abrupt, with cells showing bigger cellular lumen and thinner cell walls in the earlywood and the opposite in latewood (Figure 12). Possible unclear ring transitions were noted and corrected accordingly during crossdating. As for other ring anomalies, wedging rings were not common and were usually associated with the juvenile phase.

3.2. Assessment of tree-ring chronologies

The evaluation of the tree-ring series is summarized in Table 3. In total, we removed 115 samples (25.2%), mostly due to lower correlations with mean site chronologies, or due to unreliable crossdating. The maximum length of the chronologies was 128 years (1891 to 2019) in Terra Brava - Terceira, while the minimum was 47 years in Sete Cidades – São Miguel (1973 to 2020) (Figure 13). Also, to decrease the uncertainty arising from lower sample depth, bootstrapped chronologies (Appendix 8) were cut off and only years with SSS $\geq$ 0.85 were included in the analysis (thresholds are indicated in Figure 13). Rbar ranged from 0.29 to 0.11, while the first-order autocorrelation ranged from 0.31 to 0.54. Although SSS values were low in certain years, almost all surpassed the recommended criteria of 0.85 (Figure 13), allowing to securely progress with the analysis of climate signal in TRWi chronologies.

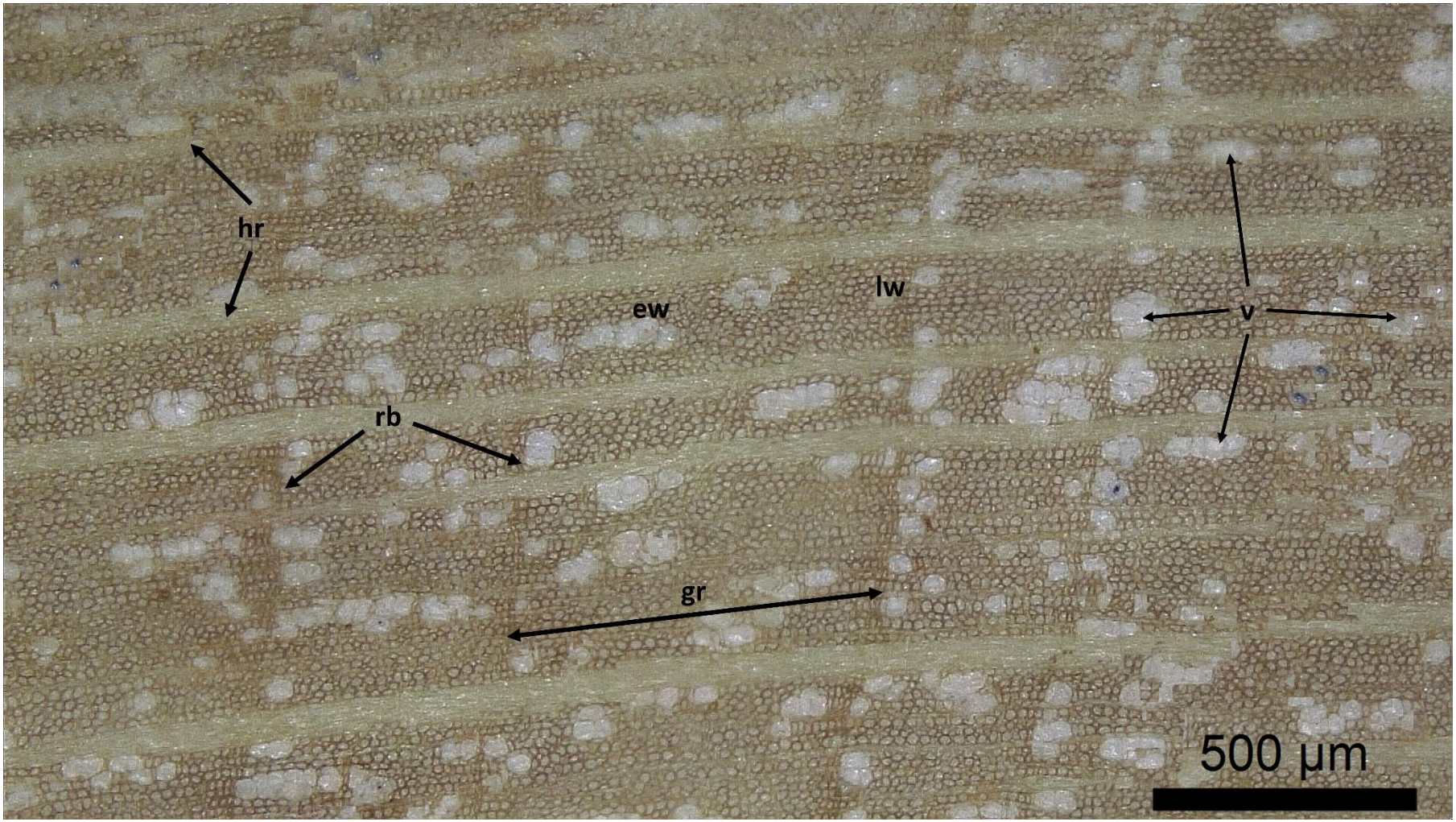

Figure 12. Cross-section showing *Ilex azorica* growth rings: detail of growth ring (gr) with ring boundaries (rb) evident, earlywood (ew) and latewood (lw); heterogeneous rays (hr) occurred, mainly perpendicularly to the ring boundaries; vessel clusters (v) were found both dispersed in the xylem but also aligned with the ring boundary.

Table 3. Site name and abbreviation, geographical coordinates, annual mean temperature (T) and annual precipitation sum (P) at the six study sites. Number of trees, number of cores before crossdating process (N^1) and the final number of cores for dendroecological analysis (N^2), average maximum tree height (Hmax), average diameter at breast height (DBH), mean inter-series correlation (Rbar) and the first order autocorrelation (AC1).

Site	***Serra de Santa Bárbara***	***Terra Brava***	***Sete Cidades***	***Lombadas***	***Nordeste***	***Pico Bartolomeu***
Abbreviation	SS	TB	SC	LO	NO	PB
Island	Terceira	Terceira	São Miguel	São Miguel	São Miguel	São Miguel
Longitude (º)	-27.3075	-27.2060	-25.7900	-25.4687	-25.1842	-25.1701
Latitude (º)	38.7356	38.7326	37.8354	37.7883	37.7974	37.7978
Elevation (m)	860	700	510	580	590	620
N Trees	17	30	33	33	31	31
N^1 Samples	62	79	63	88	65	59
N^2 Samples	46	59	47	66	49	44
Annual T (ºC)	13.76	14.02	14.92	14.81	14.70	14.41
Annual P (mm)	1497	1486	1330	1354	1294	1294
Hmax (m)	6.20	5.43	5.18	5.48	5.11	5.65
DBH (cm)	15.79	14.47	10.10	13.90	10.95	15.04
Rbar	0.18	0.13	0.11	0.12	0.23	0.29
AC1	0.45	0.47	0.35	0.32	0.51	0.54

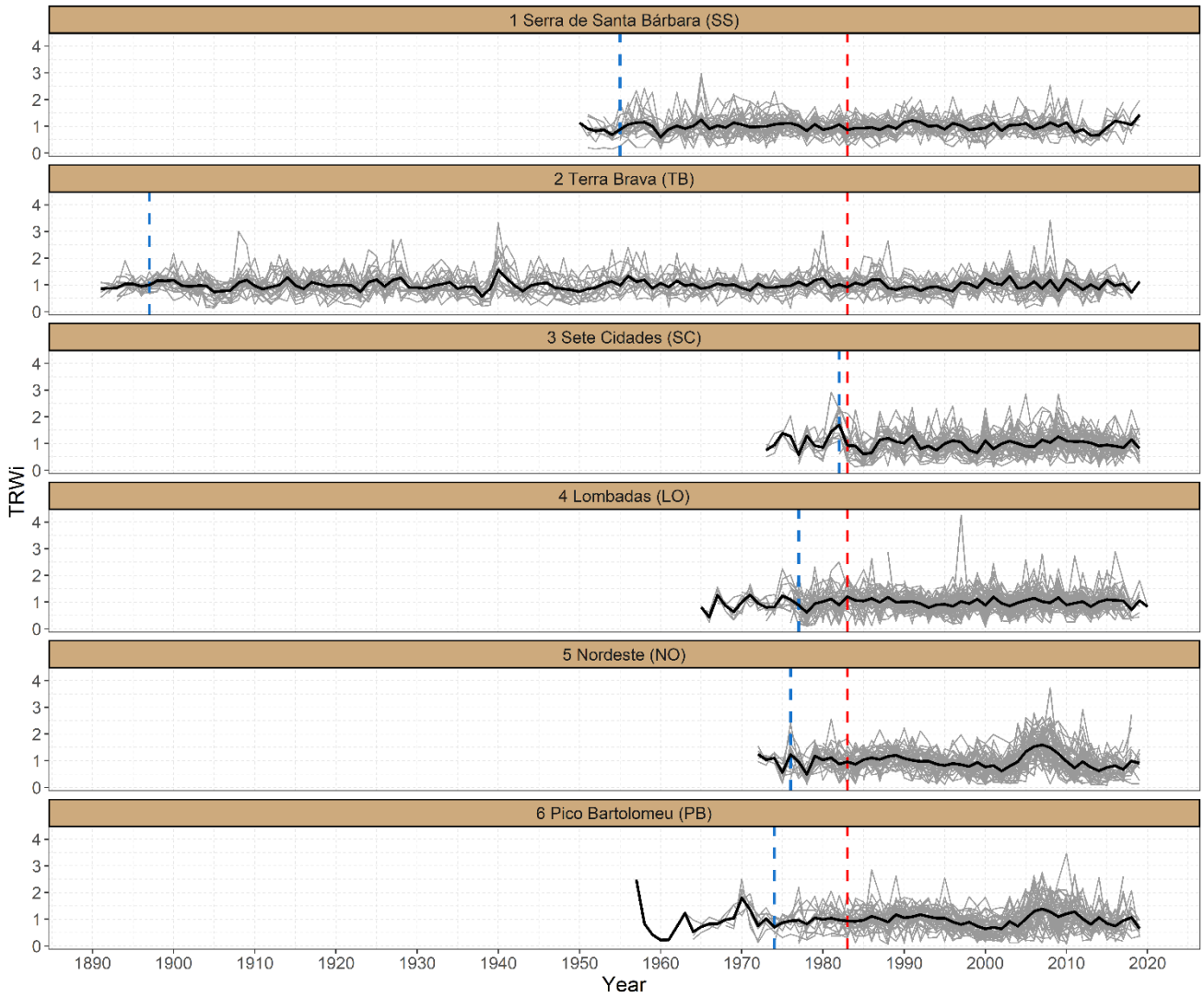

Figure 13. Spaghetti plots of *Ilex azorica* tree-ring indices for two populations at Terceira Island and four populations at São Miguel Island, Azores. Bootstrapped mean chronologies are represented in the bold black line. Vertical dotted blue line represents the threshold SSS ≥ 0.85 while vertical dotted red line is the cut-off used for GLM analysis.

3.3. Climate-growth relationships

Climate characterization

Climate data extracted from CHELSA timeseries dataset showed the same pattern at all the sites with the highest temperature in August and lowest in February, and highest precipitation in December and lowest in July (Appendix 7). Nevertheless, sites from

Terceira Island showed more precipitation and lower temperature than those from São Miguel Island (Table 3).

Model selection

A global view of the calculated models highlights the effect of temperature and precipitation of mainly February and April over the past 36 years, despite some variation (see Table 4 and 5 for a summary, and Appendix 9 for a full description of modelling results). Overall, all best fitted models for each site and for the composite chronology, showed an AICc value that was lower than that of the null model. The effect of temperature was more evident and prevailed among most models (Table 4).

Composite chronology

The composite chronology shows the common climate signal of all study sites. Models focusing on temperature presented better results while models with precipitation were mostly non-significant (Table 4). The final minimal adequate model included a negative effect of February minimum temperature of the current year and a positive effect of April minimum temperature of the previous year.

Serra de Santa Bárbara

Only monthly temperatures from the previous year resulted into acceptable models (models 10, 12 and 14 – Table 4). The final minimal adequate model included a positive effect of February mean temperature of the previous year, and negative effects of August minimum temperature and May precipitation of the previous year (Table 5).

Terra Brava

Although acceptable models included monthly temperatures of the current year (models 10, 12 and 14 – Table 4) and monthly precipitation of the current year (model

19), the final minimal adequate model included only a positive effect of April precipitation of the current year (Table 5).

Table 4. An overall evaluation of all calculated models.

Variable	**Models**	*Year*	*Composite population*	*SS*	*TB*	*SC*	*LO*	*NO*	*PB*
Temperature	1	*Previous*	X	X	X	X	X	X	X
		Current	**	X	X	X	X	X	X
	2	*Previous*	**	X	X	X	X	X	X
		Current	**	X	X	X	X	X	X
	3	*Previous*	X	X	X	X	X	X	X
		Curent	X	X	X	X	X	X	X
	4	*Current*	**	X	X	X	X	*	X
	5	*Current*	*	X	X	X	X	X	X
	6	*Current*	**	X	X	X	X	*	X
	7	*Both*	X	-	-	-	-	-	-
		Previous	X	-	-	-	-	-	-
		Current	X	-	-	-	-	-	-
	8	*Both*	**	-	-	-	-	-	-
		Previous	**	-	-	-	-	-	-
		Current	**	-	-	-	-	-	-
	9	*Previous*	**	X	X	X	X	X	X
		Current	**	X	X	X	X	X	X
	10	*Previous*	**	**	X	*	**	*	X
		Current	**	X	*	*	**	*	X
	11	*Previous*	**	X	X	X	X	X	X
		Current	*	X	X	X	X	X	X
	12	*Previous*	**	**	X	*	**	*	X
		Current	**	X	*	*	**	X	X
	13	*Previous*	X	X	X	X	X	X	X
		Current	**	X	X	X	X	X	X
	14	*Previous*	**	**	X	*	**	X	X
		Current	**	X	*	*	**	*	X
Precipitation	15	*Both*	**	**	*	*	**	X	X
	16	*Previous*	X	X	X	X	X	X	X
		Current	X	X	X	X	X	X	X
	17	*Current*	X	X	X	X	X	X	X
	18	*Previous*	X	X	X	X	X	X	X
		Current	X	X	X	X	X	*	X
	19	*Previous*	X	**	X	**	X	**	*
		Current	X	X	**	**	*	**	X
Both	20	*Both*	X	**	**	**	**	**	**
	21	*Both*	**	**	**	**	X	X	**
	22	*Both*	X	**	*	**	X	*	**
	23	*Both*	**	**	**	**	**	**	**

** The model included variables with significance < 0.001 and an AICc value lower than the null model; * The model included variables with significance < 0.05 and an AICc value lower than the null model; X The model showed a high AICc value and/or no significant variables; - The model was not calculated because the number of explanatory variables was higher than the number of observations of the dependent variable itself.

Sete Cidades

Models that included monthly temperatures and precipitation from both previous and current year resulted into acceptable models (models 10, 12, 14 and 19 – Table 4). The final minimal adequate model included positive effects of April precipitation of the current year, July maximum temperature and August precipitation of the previous year (Table 5).

Lombadas

Models with monthly temperatures either from the previous and current years (models 10, 12 and 14 – Table 4), and with monthly precipitation of the current year were all significant. The final minimal adequate model only included a positive effect of June mean temperature of the current year (Table 5).

Nordeste

Regardless some good models included monthly temperatures (models 10, 12 and 14 – Table 4), models with monthly precipitation (models 18 and 19) showed lower AICc, with the final minimal adequate model including a positive effect of February precipitation of the previous year and a negative effect of December precipitation of the previous year.

Pico Bartolomeu

The only population without good models based on temperature variables, with only one model with monthly precipitation from the previous year (model 19 – Table 4) with significant results. The final minimal adequate model included a positive effect of February precipitation of the previous year.

Table 5. Performance of the best models for each studied site and composite population, with respective Coefficients of each explanatory variable, AIC, AICc, Null Model AIC and R^2. Specific climatic signal presented for each study site, whereas composite chronology represents the common signal of all sites.

Sites	*Model*	*Coefficients*	*AIC*	*AICc*	*Null Model AIC*	*R^2*
Composite chronology	TempMin2 **	-0.049	56.369	56.559	74.012	0.095
	TempMinPre4 *	-0.042				
SS	TempPre2 **	0.076	-6.303	-4.303	5.929	0.391
	TempMinPre8 **	-0.143				
	PrecPre5 **	-0.001				
TB	Prec4 **	0.002	-1.718	-0.968	6.705	0.244
SC	TempMaxPre7 *	0.094	-21.948	-19.948	-3.041	0.494
	Prec4 **	0.001				
	PrecPre8 *	0.002				
LO	Temp6 ***	-0.130	-20.927	-20.177	-10.611	0.283
NO	PrecPre2 **	0.002	-19.809	-18.519	-5.361	0.395
	PrecPre12 **	-0.001				
PB	PrecPre2 **	0.002	-8.466	-7.716	0.536	0.256

Coefficients (+) and (-) indicates positive and negative effect while *, ** and *** are related to significance level (0.05, 0.01 and 0.001, respectively). Temp is temperature for different months and Prec is precipitation for different months (1 to 12), e.g., Temp2 is the mean temperature for February, TempMin2 is minimum temperature for February and Prec4 is precipitation for April. Previous year temperatures or previous year precipitations were given the suffix Pre, thus TempMaxPre7 is the maximum temperature of July from the previous growing season. AICc is the corrected AIC, a bias correction used when the sample size is not much larger than the number of fitted parameters.

4. Discussion

4.1. Identification of annual growth rings

Ilex azorica showed diffuse-porous wood with solitary or clustered vessels, as expected for the genus (Scheweingruber et al., 2013). Growth rings were generally well delimited, with xylem vessels associated to the very beginning of the earlywood. *Ilex* wood is mostly diffuse-ring porous with recognizable growth ring boundaries, with an exception for *Ilex canariensis* (Scheweingruber et al., 2013). Baas (1973) working with wood anatomy in the *Ilex* genus, stated that *Ilex azorica* wood features were characterized by conspicuous growth rings, as found in homonymous subtropical species, but less marked ring boundaries as in tropical lowland species. The occurrence of rings anomalies, such as false rings and wedging rings, has not been reported for this species. Nevertheless, a study focusing on the endemic tree *Laurus azorica*, found that ring anomalies could be caused by reaction wood, due to slope differences in the habitat, the formation of knots and/or compartmentalization by fungi or putrefaction (Matos et al., 2019). This could also explain the anomalies found in our study, since both species co-exist at many sites.

4.2. Chronology quality

To improve the quality of our tree-ring widths series, 105 samples were removed from dendroclimatic analysis due to lower correlations with each mean site chronology. Removed samples presented some ring anomalies (indistinct ring boundaries and false rings), thus low crossdating statistical values, which showed low regionally synchronization patterns (Theuerkauf et al., 2019). Other studies with tree-ring width proxy, also state the removal of samples from climate-growth relationship analysis (e.g. TT, 2016; Zhou et al., 2019; Thomte et al., 2021). The inter-series correlation (rbar)

results revealed different growth pattern among individual trees, because of the relatively low values in all sites, which is common at regions with low thermal amplitude (e.g., Brienen and Zuidema, 2005; Espinosa et al., 2018; Granato-Souza et al., 2018; Vasconcellos et al., 2019) and was also reported for another endemic Azorean tree (i.e., Pavão et al., 2022). This might be explained by the small distance between trees, possibly leading to competition and affecting tree growth (e.g., Chi et al., 2015; Ford et al., 2017; Zalloni et al., 2019; Luo et al., 2020). Autocorrelation values were considerably high at all the sites, meaning that the previous year's growth impacts the present years (Cook, 1985), as further discussed below.

4.3. Climate-growth relationships

Composite chronology

Modelling the relationship between TRWi of the composite chronology and climate variables, allowed to analyze the common climate response of all study sites. The best models revealed a complex temperature effect on *I. azorica* growth, predominantly a negative effect of the temperature from the previous year. Similar negative relationships between temperature and TRWi have been observed in tropical sites at high elevation (e.g., Buckley et al., 2007; Sinha et al., 2017; Dearborn and Danby, 2018a), in broadleaf ring porous trees at Mediterranean forests (Castagneri et al., 2017; Martínez-Sancho et al., 2017; García-López et al., 2022), and in temperate regions (Rita et al., 2015, 2016; Tumajer and Treml, 2016). The final minimal adequate model included a negative effect of February and April minimum temperatures of the current year, what might be explained by the balance among evapotranspiration and adequate soil moisture at the beginning of radial growth (Dawadi et al., 2013; Thapa et al., 2015). The negative effect

of temperature on tree growth, right before the beginning of the growing season, may be due to reduced carbon assimilation rates, resulting from an increased effect of autotrophic respiration rates (e.g. Clark, 2007) and a direct negative impact on photosynthesis rates (e.g. Galbraith et al., 2010).

Site chronologies – Previous year effect

Models revealed effects from previous year temperature and precipitation in all populations, except for TB and LO. Our relatively high first order autocorrelation values confirm this effect since the width of a ring will directly affect ring growth in the following year. Likewise, several studies concluded that, in ring-porous species as *I. azorica*, earlywood width was influenced by growth in the previous growing season, probably because cambial activity initiation precedes bud burst and leaf expansion (García González and Eckstein, 2003; Tardif et al., 2021; Gričar et al., 2022). Similarly, water deficiency conditions on previous year will lead to the accumulation of carbohydrate reserves instead of a biomass increase, generally influenced by environmental factors (Gallé et al., 2007), favoring water conduction in the following growing season (Michelot et al., 2012; Islam et al., 2019). Other lag effect was observed in the NO population, with a negative effect of December precipitation from the previous year that. Combining the mountainous terrain with pronounced slopes and the hydrological seasonality, both could influence the correct level of soil moisture for tree growth (Tsui et al., 2004; Dawadi et al., 2013; Khan et al., 2013; Thapa et al., 2015; Toure et al., 2015).

Site chronologies – Current year effect

On TB, SC and other populations, a positive effect of April precipitation was revealed, what might be explained by the upkeep of the level of moisture needed during

the growing season (Camarero et al., 2014; Pavão et al., 2022), which has a direct effect on stomatal conduction and could increase CO_2 assimilation (Gallé et al., 2007; Rita et al., 2015, 2016). Similarly, the negative effect of June temperature at LO population could be due to an increase in evapotranspiration, a decrease in water availability, negatively affecting cell division and turgor pressure-mediated enlargement (Castagneri et al., 2017; Martínez-Sancho et al., 2017; Souto-Herrero et al., 2018). Tree growth limitation reduced by water availability has also been reported for subtropical mountains (Morales et al., 2004; García-López et al., 2022). Moreover, the effect of landscape morphology on water availability and, consequently, on tree growth has been described in numerous studies (He et al., 2017; Kim et al., 2017; Dearborn and Danby, 2018a,b; Fortunel et al., 2018).

Differences among site chronologies

When modelling each of the site chronologies, separately, we observed slightly different results what might be explained due to competition with other native or exotic species (Primicia et al., 2015; Lu et al., 2019; He et al., 2022), high variability among stands (low rbar values), differences between the microclimates (e.g. Wang et al., 2020; Yang et al., 2020) and different site conditions (i.e. altitude) existing in the archipelago (see Elias et al., 2016; Pavão et al., 2019). Variations among stands of the same species have been commonly found in studies including sites at different elevations (Chen et al., 2011; van der Maaten-Theunissen and Bouriaud, 2012; Yu et al., 2013) or at different locations (Mazza et al., 2014; Misi et al., 2019). However, similarities were also found between closer sites, such as the positive effect of February precipitation on the previous growing season at NO and PB. This exacerbates the importance of obtaining dendrochronological and dendroclimatological information for different locations. In fact, a diverse response of tree growth to climate can be explained by variation among vegetation areas (e.g. Hickler et al., 2012) and at intra-individual scale (e.g. Sun et al.,

2021), consequently affecting forest productivity (Lindner et al., 2010) and leading to conflicting productivity outcomes (Hanewinkel et al., 2013). Indeed, diverse growth responses to climate represents a powerful tool to understand forest dynamics under uncertain climate change scenarios (Fritts, 1976; Schweingruber, 1996; Rita et al., 2014).

Other studies in the Macaronesia

This study was essential to fill the knowledge gap in the International Tree-Ring Databank that exists on the Azores archipelago (Zhao et al., 2019), but also at the Macaronesia. For example Vieira et al. (2017), focusing a conifer species, stated that a positive signal of precipitation was not observed in the trees growing in the Azores, concluding that the absence of a winter precipitation signal indicated that trees did not rely on soil water reserves during the growing season. Working at higher elevation, we mainly found effects of temperature, but with some specific effects of precipitation. Although water availability has hardly been thought as an important limiting factor to tree growth at higher elevations in temperate regions (Morales et al., 2004), these observations should not be generalized to upper tree lines worldwide. Moreover, our results are also in agreement with previous work in Macaronesia, regarding the conifers *J. brevifolia* in the Azores (Pavão et al., 2022) and *Pinus canariensis* (Sweet ex Spreng.) in Canary Islands (e.g., Jonsson et al., 2002; Brito et al., 2016; López et al., 2021) and other species in Canary Islands (e.g. García-López et al., 2022), that found links between tree growth and both temperature and precipitation.

5. Conclusions

We conclude that *I. azorica* forms reliable annual tree rings, which can be statistically related to climate, both temperature and precipitation. Our results demonstrated that

different sites, and consequently different altitudes, soils, slopes, etc., retrieved slightly different effects of climatic parameters. Since only a limited number of broad-leaved tree species have been studied in areas with high relative humidity, low thermal amplitude and without a very pronounced seasonality, our study provided valuable information about the growth-climate relationships in these conditions while suggesting methodological insights, thus filling this specific knowledge gap on the archipelago. Future approaches could be applied, for example studying additional tree-ring proxies, such as stable carbon and oxygen ratios (Shestakova and Martínez-Sancho, 2021), wood-anatomy (Arnič et al., 2021) or early and latewood vessel area (Souto-Herrero et al., 2018), to obtain more refined data and, consequently, improve climate-growth analysis. Moreover, our results give information that could encourage further studies, for example focusing climate reconstructions (e.g. Rozendaal and Zuidema, 2011; Heinrich and Allen, 2013; Pearl et al., 2020). This would allow the assess to long-term variations from average climate (Sheppard, 2010) and/or frequency of extreme climate (Stockton and Fritts, 1971). Likewise, the impact of climate variability tree growth in laurel forests needs to be focused to evaluate their potential responses to climate change. All essential points to better understand forest dynamics and, consequently, influence forest management decisions.

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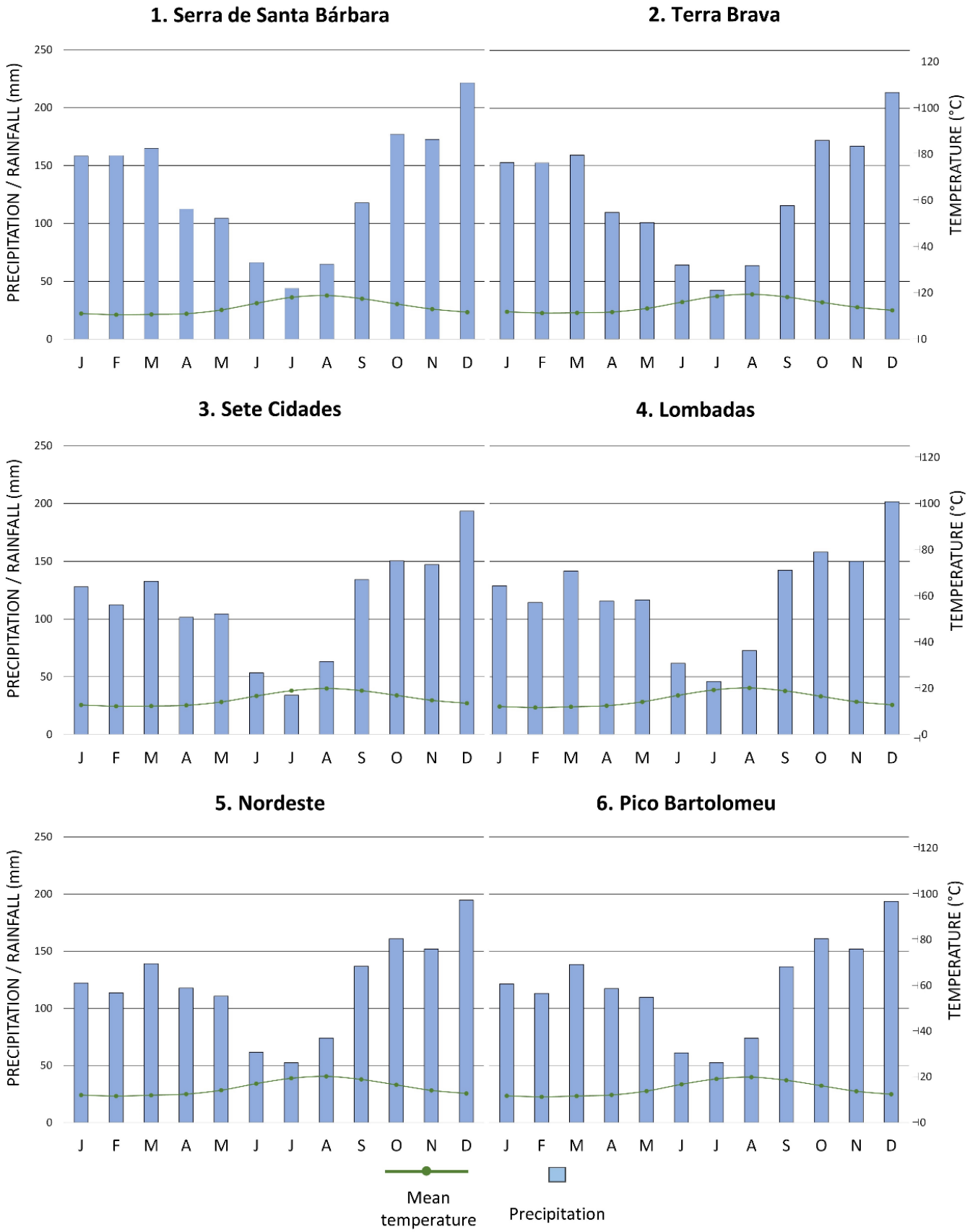
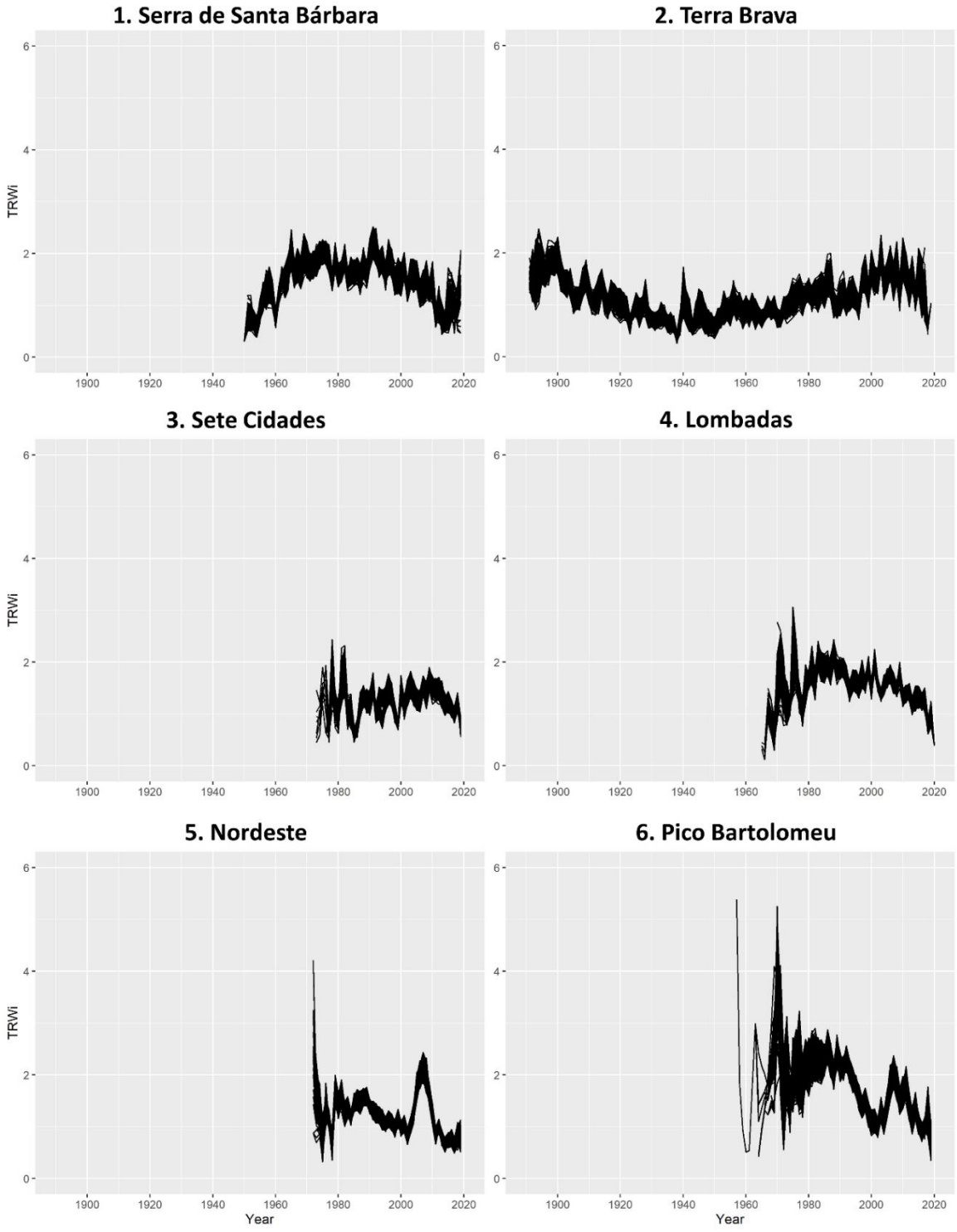
CHAPTER 3 – Supplementary Material

Appendix 6. An example of an adult individual of *Ilex azorica*.



Appendix 7. Average temperatures (lines) and monthly precipitation (bars) for all study sites. Data was extracted from CHELSA timeseries dataset with a spatial resolution of 30-degree seconds.



Appendix 8. Bootstrapped mean chronology for all studied sites. Years on x axis and tree-ring indices (TRWi) on y axis.

Please, use the following link to download Appendix 9 (Excel Sheets): https://figshare.com/s/0d65e4b6b551b6bf91b5

Appendix 9. Performance of all tested models for each studied site and composite population, with respective Coefficients of each explanatory variable, AIC, AICc, Null Model AIC and R^2. "NS", "*", "**" and "***" are related to significance level (not significant, 0.05, 0.01 and 0.001, respectively).

CHAPTER 4

forests

MDPI

Article

Climate–Growth Relationships in *Laurus azorica*—A Dominant Tree in the Azorean Laurel Forest

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Title

Climate-Growth Relationships in *Laurus azorica* - a Dominant Tree in the Azorean laurel forest

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Abstract

Forests in oceanic islands, such as the Azores archipelago, enable interesting dendroclimatic research, given their pronounced climatic gradients over short geographical distances, despite the less pronounced seasonality. The Lauraceae play an essential ecological role in Macaronesian natural forests. An example is *Laurus azorica* (Seub.) Franco, a relevant species given its high frequency and physiognomic dominance in Azorean laurel forests. This study aims to quantify climate-growth relationships in *L. azorica* using a dendroecological approach. We sampled four stands at São Miguel and two stands at Terceira islands, in a total of 206 trees. Following standard dendrochronological methods and rigorous sample selection procedures, we obtained relatively low rbar values and high temporal autocorrelation. Using a stepwise Random Forest analysis followed by Generalized Linear Models calculation, we found prominent effects of present and previous year temperature, but a low precipitation signal on growth rings, with some model variation between stands. Our results agreed with previous observations for broad-leaved species with diffuse porous wood, contributing to increase the baseline dendroecological knowledge about Azorean forests. Due to the high levels of within and between stand variation, and to refine the climatic signal analysis, complementary approaches should be explored in the future.

Keywords:

Azores; Dendroclimatology; Generalized Linear Models; Laurel forest; Macaronesia; Random forest.

1. Introduction

Oceanic islands, particularly those with volcanic origin, are usually distinguished by their peculiar and heterogeneous environments (Mueller-Dombois and Boehmer, 2013; Elias et al., 2016; Pavão et al., 2019; Hanz et al., 2022). These ecosystems have been the focus of research in biogeography, plant ecology and, more recently, in dendrochronology. Orographic precipitation regimes and complex topography lead to considerable spatial variation in temperature and water availability, facilitating studies of climate-growth relationships across environmental gradients (Kier et al., 2009; Weigelt et al., 2013; Zimowski et al., 2014; Hanz et al., 2022), and allowing to better understand the potential impact of a shifting climate on island species. Nevertheless, wood anatomy and growth dynamics of forest trees in oceanic islands remain largely underexplored (Battipaglia et al., 2010; Copenheaver et al., 2010; Vieira et al., 2017; Matos et al., 2019; Christopoulou et al., 2020; Fernández de Castro et al., 2020; Génova et al., 2022; Pavão et al., 2022), namely in Macaronesia (Jonsson et al., 2002; Pérez-De-Lis et al., 2011; Rozas et al., 2011, 2013; Vieira et al., 2017; Matos et al., 2019; Fernández de Castro et al., 2020; Pavão et al., 2022) - a biogeographic region including North Atlantic archipelagos that encompass a wide breadth of climatic conditions. Those archipelagos constitute a hotspot of plant diversity, with laurel forests and the Lauraceae having important ecological roles due to their widespread distribution and predominance in many plant communities (Fernández-Palacios et al., 2017; Hanz et al., 2022). In this type of ecosystem, water balance, depending on precipitation, temperature, and relative humidity, is generally viewed as a key factor with impacts on functional diversity, species richness and tree growth (Vieira et al., 2020). Together with other environmental variables, water availability directly affects photosynthesis and carbon assimilation, required for tree-ring width increment (Cuny et al., 2014; Baldocchi and Penuelas, 2019; Giguère-Croteau et

al., 2019; Marchand et al., 2020). Despite often not being included in dendroclimatological analyses, additional factors may also affect tree growth including topography, soil nutrient availability, competition, herbivory/phytophagy and natural disturbance (Luo et al., 2020; Hanz et al., 2022; He et al., 2022).

The climate of the Azores, one of the Macaronesian archipelagos, is oceanic temperate, with high relative humidity, mild summers and winters, low daily and annual thermal amplitude, and precipitation evenly distributed throughout the year, although scarcer in summer (Azevedo, 2001; Couto, 2012). Meanwhile, a steep altitudinal gradient is clearly expressed in the Azorean natural vegetation belts, with different types of zonal woodlands, forests, and scrubland (Elias et al., 2016; Pavão et al., 2019; Borges Silva et al., 2022). Submontane laurel forest was likely much more common in the past, but still represents one of the more common types of natural extant forests (Elias et al., 2016; Pavão et al., 2019). The Lauraceae are represented in the Azores by *Laurus azorica* (Seub.) Franco, the dominant species in submontane laurel forests, that is also present in four other zonal natural forest and woodland types (Elias et al., 2016; Pavão et al., 2019; Borges Silva et al., 2022).

Previous studies addressed tree-ring growth in the Lauraceae. In Macaronesia growth rings generally showed an abrupt transition between thin and thick cell walls, characterizing early and latewood, and, in some cases, a delimiting marginal parenchyma band (Schweingruber et al., 2013; Reis-Avila and Oliveira, 2017). In Tenerife, *Laurus novocanariensis* Rivas Mart., Lousã, Fern.Prieto, E.Díaz, J.C.Costa & C.Aguiar showed a diffuse porous wood structure, with the entire cross-section of the stem being functional in terms of water transport thereby reducing tree susceptibility to conditions of transient water limitation (Balabasquer, 2021). For this species, García-López et al. (2022) found synchronous annual tree rings, robust tree-ring chronologies, and positive correlations

with annual precipitation. Outside Macaronesia, Reis-Avila and Oliveira (2017) identified growth ring boundaries delimited by radially flattened fibers with thickened cell walls in the wood of *Nectandra amazonum* Nees and *Ocotea porosa* (Nees & Mart.) Barroso. Granato-Souza et al. (2019) found that *Nectandra oppositifolia* Nees & Mart trees responded synchronously but negatively to high temperatures in the summer of the previous year and to high precipitation in the current year growing season. Moreover, previous research has also determined that several Lauraceae exhibit synchronous and climate-sensitive growth dynamics, and are therefore appropriate for dendrochronological analyses (Reis-Avila and Oliveira, 2017; Granato-Souza et al., 2019; Balabasquer, 2021; García-López et al., 2022), raising the same possibility for *L. azorica*.

The Azorean natural forests provide critical ecosystem services, including habitat provisioning for biodiversity and carbon storage (see Borges Silva et al., 2022), but also protection against soil erosion and enhanced capabilities of water intersection and infiltration (Louvat and Allègre, 1998; Fontes et al., 2004; Malheiro, 2006; Borges Silva et al., 2022). However, no estimates of annual tree growth are available, impeding more precise estimations of annual carbon sequestration. Only a few studies have recently addressed dendrochronological topics devoted to Azorean trees (Wunder, 2010; Teixeira et al., 2015; Borges Silva et al., 2017, 2018; Vieira et al., 2017; Pavão et al., 2022), both introduced - *Pittosporum undulatum* Vent. (Pittosporaceae), *Pinus pinaster* Aiton (Pinaceae) - and native - *Juniperus brevifolia* (Seub.) Antoine (Cupressaceae), *Ilex azorica* Gand. (Aquifoliaceae) (Pavão et al., 2023). Câmara (2016) estimated tree ages in two stands of laurel forest within a protected area, and Rego et al. (2017) analyzed growth rings in a laurel forest invaded by *Clethra arborea* Aiton (Clethraceae). More recently, Matos et al. (2019) described the growth ring anatomy and the relationship between

dendrometric traits and the number of growth rings in *L. azorica*, confirming the diffuse porous structure of the wood, with solitary or clustered randomly distributed vessels, oriented perpendicularly to the distinct ring boundaries (Schweingruber et al., 2011; Matos et al., 2019). This suggests a water transport efficiency similar to that reported for *L. novocanariensis* (Balabasquer, 2021), despite the low risk of cavitation in the Azores, due to high water availability, except during the driest Summer months at low elevation sites.

Given the structural importance of the Lauraceae in Macaronesia (Schweingruber et al., 2013; Reis-Avila and Oliveira, 2017; Balabasquer, 2021; García-López et al., 2022), the need to enhance estimations of annual carbon sequestration, and the absence of climate-growth relationship studies for that family in the Azores, our research aimed to use dendroecological approaches to determine the basic climate-growth relationships in *Laurus azorica*. We compiled a large dataset of annually resolved ring-width measurements derived from core samples collected from 203 trees in disjunct forest stands. We used a sequential com-bination of Random Forest and Generalized Linear Models to determine the relationships between radial growth and potential climate drivers. Thus, the main objective of the study was to investigate the limiting climatic factors affecting the radial growth of *L. azorica*. We addressed the following hypotheses: 1) based on a previous study, *L. azorica* will show distinctive tree ring-boundaries that will allow an accurate climate-growth relationship assessment; 2) the effect of previous year climate variables will be relevant because ring-porous broadleaved species are known to build their earlywood before the onset of the growing season, from carbohydrates stored from the previous growing season (e.g., García González and Eckstein, 2003; Buttó et al., 2021); and 3) given the high relative humidity and annual precipitation of the archipelago (Azevedo, 2001; Couto, 2012), temperature will be the

main limiting factor that affects tree growth, as previously shown for other Lauraceae species (e.g., Reis-Avila and Oliveira, 2017) and other studies in the Azores (e.g., Matos et al., 2019; Pavão et al., 2023).

2. Materials and Methods

2.1. Study area

The Azores is a Portuguese archipelago, located in the North Atlantic Ocean (36°55'–39°43' N and 25°00'–31°15' W) within a complex tectonic setting, near the triple junction between the Eurasian, Nubian, and North American plates (Miranda et al., 2014). Included in Macaronesia, it comprises nine volcanic islands (Figure 14) with a total land surface of 2323 km^2 (Forjaz et al., 2004). The age of islands varies from 0.186 My for Pico island (Costa et al., 2015) to 6.01 My for Santa Maria island (Ramalho et al., 2017). The climate in the archipelago is predominantly temperate (type C), namely Cfb (temperate with no dry season and with a mild summer), according to the Koeppen-Geiger climate classification system (data from 1971 to 2000; Couto, 2012). Depending on the climatic conditions, particularly wind, water balance and radiation, Azorean forests are distributed along eight vegetation belts, where plant species dominance and co-dominance change with altitude (see Elias et al., (2016) for a full description). Despite the considerable changes that occurred in the Azorean land use in the 1950's, with subsequent replacement of the natural forests by crops and pastureland (Costa, 1950), the zonal vegetation is nowadays distributed as a continuum, with some niche partitioning between dominant species (Pavão et al., 2019).

In this study we limited sampling to Laurus submontane forest stands (Elias et al., 2016) occurring in two islands - São Miguel and Terceira - where the target species is

dominant. A total of six stands were selected, allowing sampling across an altitudinal gradient to capture a wide range of environmental and climatic conditions (Figure 14): four stands at São Miguel Island – Pinhal da Paz (PP), Lombadas (LO), Povoação (PO) and Nordeste (NO) - and two at Terceira Island – Caldeira do Guilherme Moniz (GM) and Matela (MT). Selected stands were dominated by *Laurus azorica*, although mixed with several Azorean native trees, namely *Picconia azorica* (Tutin) Knobl (Oleaceae) and *Morella faya* Aiton (Wilbur) (Myricaceae) at the lower altitudes, and *Juniperus brevifolia* and *Ilex azorica* at higher altitudes. Invasive species were also present, including *Pittosporum undulatum*, *Clethra arborea* and *Hedychium gardnerianum* Sheppard ex Ker Gawl (Zingiberaceae) (Elias et al., 2016; Borges Silva et al., 2022).

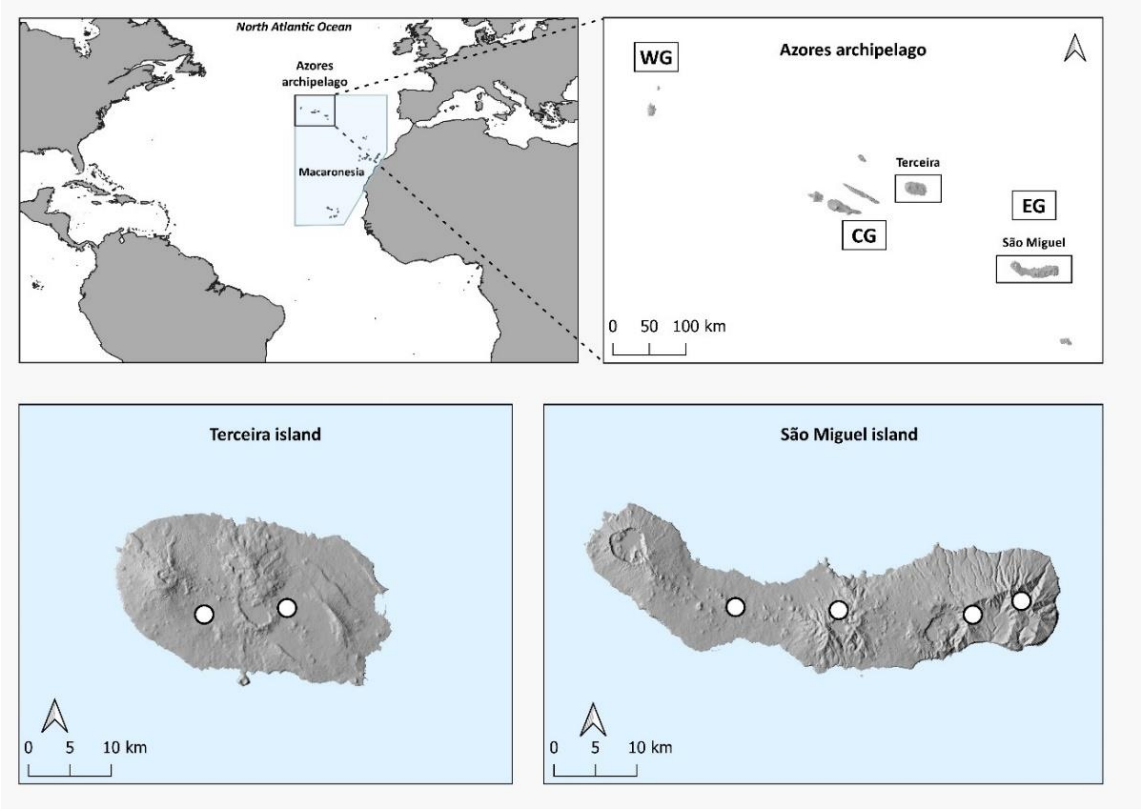
Selected forest stands differed slightly in terms of species composition and soil characteristics:

Caldeira do Guilherme Moniz (GM) – A stand located at a medium elevation site (455 m), with annual mean temperature of 15.8°C, annual precipitation of 1471 mm, almost flat terrain, and a vitric andosol containing more than 60% of unweathered pyroclastic material (Pinheiro, 1999). A large *L. azorica* population with young and old trees that occur spontaneously in a well preserved Laurus submontane forest with other native tree species, such as *Morella faya*, *Erica azorica* Hochst. ex Seub. (Ericaceae), *Ilex azorica* and many native fern species such as *Woodwardia radicans* (L.) Sm. (Blechnaceae), *Culcita macrocarpa* C.Presl. (Culcitaceae) and *Dryopteris* spp. (Dryopteridaceae).

Matela (MT) – A stand located at a medium elevation site (400 m), with annual mean temperature of 16.2°C, annual precipitation of 1327 mm, almost flat terrain, and a ferruginous andosol, composed by trachytic pyroclastic material with a thin ferruginous layer (Pinheiro, 1999). A small *L. azorica* population with young and old trees that occur

spontaneously in the remaining mosaics of natural vegetation with *Morella faya* and *Juniperus brevifolia*.

Figure 14. Map of the Azores archipelago (WG – Western Group, CG – Central Group, and EG – Eastern Group), framed on the North Atlantic Ocean and, more specifically, in Macaronesia. Both islands included in the study (Terceira and São Miguel) are highlighted, and circles indicate *Laurus azorica* sampled sites.



Pinhal da Paz (PP) - A stand located at a relatively low elevation site (320 m), with annual mean temperature of 16.4°C, annual precipitation of 1330 mm, somewhat rocky terrain, and a shallow allophanic regosol (Ricardo et al., 1977). A small population of relatively young *L. azorica* trees that occur spontaneously in a forest recreation park with *Cryptomeria japonica* (Thunb. ex L.f.) D.Don (Cupressaceae) and other introduced species, such as *Pittosporum undulatum*. *Laurus azorica* trees were essentially located at a smooth hillside partly invaded by *Hedychium gardnerianum*.

Lombadas (LO) – A stand located at a relatively high elevation site (600 m), with annual mean temperature of 15.2°C, annual precipitation of 1459 mm, steep terrain (20-

30° slope), and an unsaturated ferruginous andosol (Ricardo et al., 1977). A large *L. azorica* population with young and old trees that occur spontaneously, in the remaining natural vegetation pockets, representing a transition between a *Laurus* submontane forest and a *Juniperus-Ilex* woodland, with *Morella faya*, *Erica azorica*, *Viburnum treleasei* Gand. (Adoxaceae), *Ilex azorica*, *Juniperus brevifolia*, and many native fern species such as *Woodwardia radicans* and *Culcita macrocarpa*. *Cryptomeria japonica* stands occur nearby as well as some invasion by *Pittosporum undulatum* and *Hedychium gardnerianum*.

Povoação (PO) – A stand located at a medium elevation site (470 m), with annual mean temperature of 15.3°C, annual precipitation of 1352 mm, slightly sloped terrain (10° slope), and an allophanic ferruginous regosol (Ricardo et al., 1977). A small *L. azorica* population with relatively old trees that occur spontaneously in a valley, with small patches of natural vegetation, representing *Laurus* submontane forest, with other native trees, such as *Morella faya* and *Erica azorica*, and some native ferns, such as *Woodwardia radicans* and *Culcita macrocarpa*. *Cryptomeria japonica* stands occur nearby as well as some invasion by *Pittosporum undulatum* and *Hedychium gardnerianum*.

Nordeste (NO) – A stand located at a relatively high elevation site (590 m), with annual mean temperature of 15.1°C, annual precipitation of 1434 mm, moderately steep terrain (10-20° slope), and a shallow allophanic ferruginous regosol (Ricardo et al., 1977). A large *L. azorica* population with young and old trees that occur spontaneously in a mountain area, a large cover of natural vegetation, corresponding to a *Laurus* submontane forest, in some cases in a transition to a *Juniperus-Ilex* woodland, with *Morella faya*, *Erica azorica*, *Viburnum treleasei*, *Ilex azorica*, *Juniperus brevifolia*, and many native fern species such as *Woodwardia radicans*, *Culcita macrocarpa*, and *Dryopteris* spp.

Cryptomeria japonica stands also occur nearby as well as some invasion by *Pittosporum undulatum*, *Clethra arborea* and *Hedychium gardnerianum*.

2.2. Target species – Laurus azorica

Distributed in tropical and subtropical climates, Lauraceae is a large family of tree taxa, including approximately 45 genera and 2850 species (Christenhusz and Byng, 2016). This family has an important ecological role in Macaronesia as one of the plant families structuring the laurel forest ecosystems in the Azores, Madeira, and in the Canary Islands (Fernández-Palacios et al., 2017), also contributing to the species richness of this biome (Quinet and Andreata, 2002). Regarding its economic value, this family offers a wide range of applications, including high quality timber and non-timber resources as spices and essential oils (Marques, 2001). Individuals of the Azorean endemic *Laurus azorica* are recognized by a vertical trunk branching usually at a short distance from the base, with alternate glabrous leaves, but with hairy young leaves and shoots (Figure 15). According to the IUCN (International Union for Conservation of Nature) red list category and criteria, *L. azorica* is currently classified as a species of "Least Concern", with the population trend being stable even though available habitats are severely fragmented (Silva and Beech, 2017). In the archipelago, this species is present in four zonal vegetation types (Elias et al., 2016), mainly in *Laurus* submontane forests (300–600 m), but also in lowland laurel forests and montane woodlands. It can also be found in lava flows, coastal and mountain scrubland, and forested wetlands (DRRF, 2017).

2.3. Sample collection and data preparation

Field work was performed mainly in summer, between 2018 and 2022. Two to four wood cores were sampled per tree, resulting in 206 trees and 415 samples. At least 30 individual trees (large, adult trees were prioritized) were randomly sampled at each site,

avoiding trees with any evidence of trunk, stem, or canopy damage. Wood cores were collected using a 5 mm diameter Pressler borer and kept in paper straws to prevent damage. Dendrometric traits, including diameter at breast height (dbh) and tree height, were measured.

Figure 15. *Laurus azorica* forest in São Miguel Island, Azores.

In the laboratory, we followed standard dendrochronological techniques (Speer, 2010; Pavão et al., 2022). Increment core samples were air dried, mounted and glued into wood supports. Cores were then sanded with progressively finer grades of abrasive paper

(up to grid 600) until a proper polished surface was obtained. Ready to measure images of wood increment cores were taken using a LEICA S9I Stereozoom stereomicroscope with incorporated 10 M.P. camera (Leica Microsystems Inc., Buffalo Grove, IL, USA), keeping a 50% overlap of sequential images to enable reliable stitching which was done with the open-source soft-ware Fiji – ImageJ (Schindelin et al., 2012).

2.4. Tree-ring data collection and analysis

Measurements of annual tree-ring widths (TRW) was performed using Cybis CooRecorder (v. 9.3.1) to an accuracy of 0.01 mm. After converting measurements into .rwl files on Cybis CDendro (v. 9.3.1), visual crossdating was performed on the PAST5 (SCIEM) software. To ensure quality of the alignments on crossdating procedure, GLK (Gleichläufigkeit) (Schweingruber, 1988; Buras and Wilmking, 2015), T-Test and Pearson's correlation coefficient statistics were used. Samples that could not be satisfactorily crossdated were eliminated from further analysis.

Detrending procedure was applied to each individual tree-ring series using the package "dplR" for R software (Bunn, 2008). The procedure consisted of fitting a cubic smoothing spline with a 50% frequency response cut-off at 25 years to each individual ring-width series (Fritts, 1976; Cook and Kairiukstis, 1990; Bontemps and Esper, 2011):

$$y_t = \beta_0 + \sum_{j=1}^{p} f_j(x_{tj})\beta_j + \varepsilon \quad (1)$$

where *xtj* is the raw time series, *fj* is the smoothing spline function (i.e., a degree 3 polynomial), β the regression coefficients, and ε the residuals. Response period was chosen given the length of the shorter chronology, which allows a more flexible approach. Subsequently, tree-ring indices (TRWi) were pre-whitened to remove short-term persistence (related to biological carry-over effect of trees) from tree-ring series. Moreover, 25% of the individual chronologies with the lowest correlation coefficients

(within the site chronology) were removed, to enhance the signal of the mean site chronologies. A TRWi chronology for each study site was built, averaging residual tree-ring series, to preserve climatic information while reducing the effect of autocorrelation (Esper et al., 2015; Brienen et al., 2016), and using Tukey's biweight robust mean to reduce the influence of outliers (Cook, 1985; Cook and Pederson, 2011; Brienen et al., 2016). Throughout the chronology building process, 131 samples were removed from further analysis.

Different measures were used to ensure chronology quality. Firstly, we used mean interseries correlation (rbar) as described in Wigley et al. (1984), as a measure of the strength of the common growth 'signal' within the chronologies. Secondly, we used Subsample Signal Strength (SSS) to evaluate the loss of explanatory power due to a decreasing sample size back in time, calculated as:

$$SSS = (nx(1+(N-1)xrbar))/(N*(1+(n-1)*rbar)), \quad (2)$$

where n and N are the number of cores or trees in the subsample and sample, respectively, and rbar is the mean interseries correlation. Only the portion of each chronology with SSS ≥ 0.85 was used in modelling (Buras, 2017). Thirdly, we used autocorrelation (AC1) to retrieve the carry-over effects of previous years, calculated using the *acf() function* in R. Finally, we used a bootstrap procedure to estimate the standard deviation (SD) of each stand-level mean chronology (N=6). Specifically, for each stand, a total of 1000 replicate mean chronologies were generated based on a random selection of 75% of the available individual tree chronologies. A corresponding SD (for each stand) was then computed from the 1000 replicates (Appendix 10). This was used to further evaluate the consistency of the mean chronologies (e.g., Pavão et al., 2022).

2.5. Dendroclimatic models

2.5.1. Climatic variables

Exact coordinates (centroid of each forest stand) obtained from sample sites were used to download minimum, maximum and mean monthly temperature and monthly precipitation from CHELSA timeseries dataset (Karger et al., 2017; Karger and Zimmermann, 2018) with a spatial resolution of 30 arc seconds (ca. 1 km^2). Different combinations of explanatory climatic variables were used for modelling (Table 6). In the case of seasonal values, we considered Winter (December-February), Spring (March-May), Summer (June-August) and Autumn (September-October), based on climate studies for the archipelago (Azevedo, 2001; Couto, 2012). A detailed description of the climate at our study sites, based on CHELSA database (Karger et al., 2017; Karger and Zimmermann, 2018), was summarized and graphically represented in Appendix 11.

2.5.2. Modelling approaches

The relationship between TRWi and climatic variables was modeled by applying a sequential combination of Random Forest (RF) – which belongs to the group of machine learning algorithms – and Generalized linear Models (GLMs); two methods that have been successfully used in growth ring analyses (e.g., Rossi et al., 2008; Jevšenak et al., 2018; Sahour et al., 2021; Cui et al., 2022). A diagram with the analysis flow is presented in Figure 16.

RF is a flexible modeling tool that can accommodate binary, categorical, and high dimensional data, while providing measures of predictor variable importance (Breiman, 2001; Archer and Kimes, 2008). In this study, this method was used to determine climatic variable importance as a first step of climate-growth ring analysis (Jevšenak et al., 2018; Jevšenak and Skudnik, 2021; Li et al., 2021; Sahour et al., 2021). Furthermore, RF models

are nonparametric and can, therefore, consider nonlinear relationships and interactions between variables. RF is often used as an exploratory tool, as this method can identify relationships and interactions between variables without specifying their form, a priori (Lucas, 2020).

Afterwards, we incorporated the most important climatic terms (as selected by RF) in generalized linear models to estimate the strength and direction of their effects on annual radial increment (i.e., tree ring width, TRWi):

$$y_t = \beta_0 + \boldsymbol{\beta X_t} + \varepsilon, \quad (3)$$

where y_t is the response variable (TRWi), β_0 the intercept (model constant), $\boldsymbol{\beta X_t}$ a vector of regression coefficients and independent climatic variables, and ε the residuals.

That is, RF was used as a pre-step to calculate variable importance and reduce the number of potential predictor variables to be used in GLMs, while the latter was used to retrieve the direction of the effect of the selected variables.

2.5.3. Model implementation and variable selection

Globally, we calculated 77 models, with 11 different models for the composite and each of the individual site chronologies (Table 7): nine different models in the first step of the RF; one optimal model in the second step of RF; and one reduced GLM.

RF models were calculated both for the whole data set (composite chronology – CC, where we included the six growth-ring chronologies) and for each individual site chronology. We used the *randomForest() function* from package "randomForest" for R software (Breiman, 2001), with 10000 trees per run, with an optimal value for the mtry parameter (with respect to Out-of-Bag error estimate – Breiman (2001)) that was calculated for each model using the *tuneRF() function*.

Table 6. List of climatic variables used in models to explain the climate-growth relationships in six *Laurus azorica* forest stands in two Azores islands – Terceira and São Miguel.

Climate variable	Year	Variable
Temperature	Current	Mean annual temperature
		Mean annual minimum temperature
		Mean annual maximum temperature
		Mean Winter temperature
		Mean Spring temperature
		Mean Summer temperature
		Mean Autumn temperature
		Mean Winter minimum temperature
		Mean Spring minimum temperature
		Mean Summer minimum temperature
		Mean Autumn minimum temperature
		Mean Winter maximum temperature
		Mean Spring maximum temperature
		Mean Summer maximum temperature
		Mean Autumn maximum temperature
		Monthly mean temperatures
		Monthly minimum temperatures
		Monthly maximum temperatures
	Previous	Mean annual temperature
		Mean annual minimum temperature
		Mean annual maximum temperature
		Monthly mean temperatures
		Monthly minimum temperatures
		Monthly maximum temperatures
Precipitation	Current	Annual precipitation
		Winter precipitation
		Spring precipitation
		Summer precipitation
		Autumn precipitation
		Monthly precipitations
	Previous	Annual precipitation
		Monthly precipitations

In the first RF step we calculated a saturated model, including all the available climatic variables from the present and the previous year, and nine other models based on temperature and/or precipitation from the current and/or the previous years, both for the composite and the individual site chronologies (Table 7). After this step, we retained only those climatic variables with an importance value above 10%, that were used to feed the second RF step.

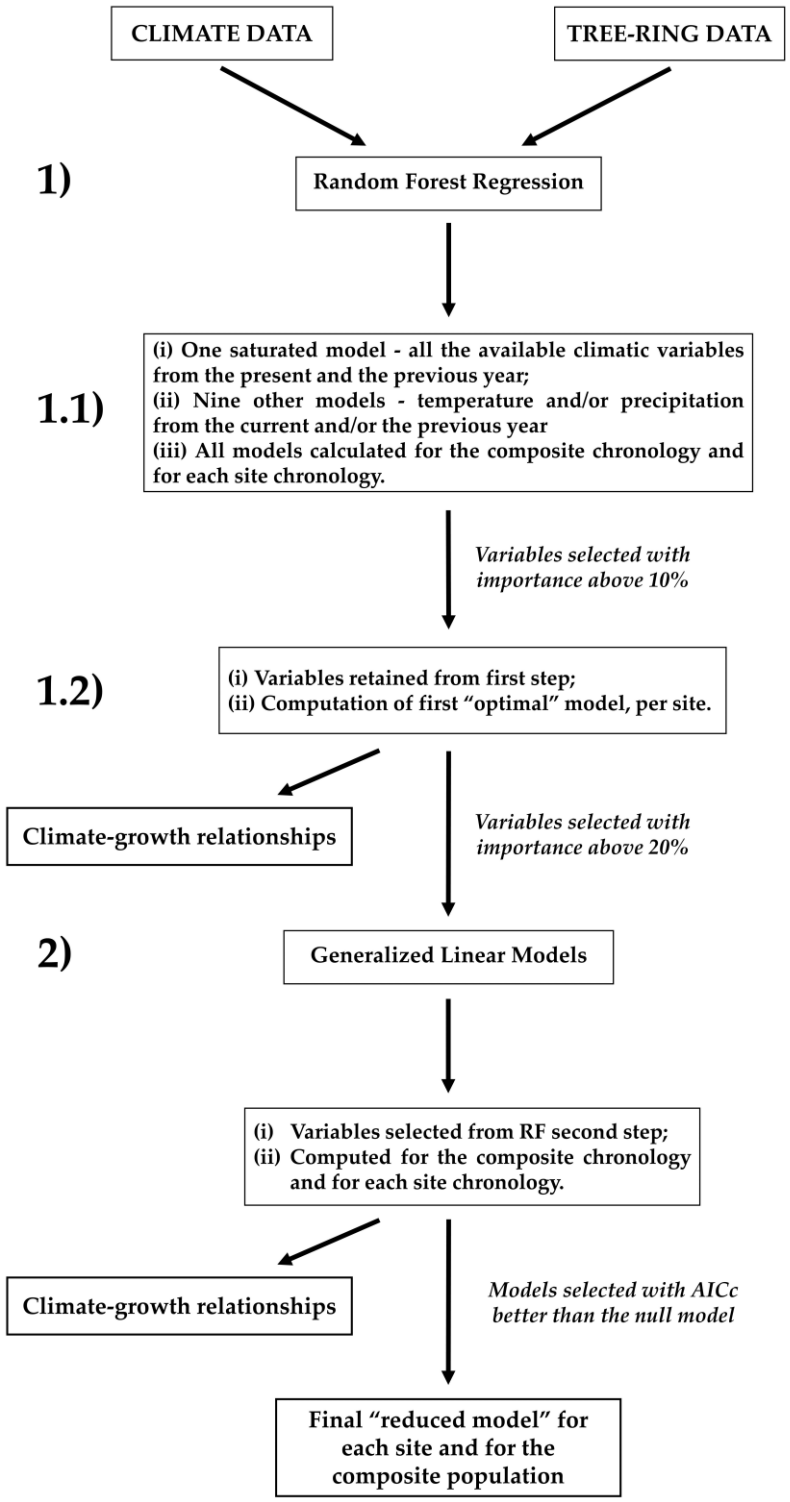


Figure 16. Flow diagram summarizing calculations of all dendroclimatic models used to explain the climate-growth relationships in six *Laurus azorica* forest stands in two Azores islands – Terceira and São Miguel. 1) RF modelling was used to inform the selection of the best explanatory climatic variables; and 2) GLMs used to estimate the direction and strength of the climatic variables on annual radial increment. Italic text indicates the selection parameters used at each step.

The second RF step allowed to build models (designated as "optimal") including only those climatic variables with an importance value close to or above 20% (Table 7).

Table 7. List of all RF models and GLMs calculated to explain the climate-growth relationships in six *Laurus azorica* forest stands in two Azores islands – Terceira and São Miguel. The models included climatic data from the current year, from the previous year or from both. The dependent variables corresponded to the composite or to the individual site chronologies.

Number	Model	Current	Previous	Both
	Random Forest Step 1			
1	Saturated model (All variables)			x
2	Partially saturated model (All variables)	x		
3	Partially saturated model (All variables)		x	
4	Temperature model	x		
5	Temperature model		x	
6	Temperature model			x
7	Precipitation model	x		
8	Precipitation model		x	
9	Precipitation model			x
	Random Forest Step 2			
10	Optimal model (Selected variables)	x	x	x
	GLMs			
11	Reduced model (Selected variables)	x	x	x

These climatic variables were used to feed the GLM analysis that was implemented using the *glm()* and *stepAIC() functions* in R, both for the composite and the individual site chronologies. To select the most parsimonious and informative GLMs we used the following criteria (see Johnson and Omland, 2004; Sheppard, 2010; Ávila et al., 2018; Parelho et al., 2021; Barreiro et al., 2022): i) a corrected version (AICc) of Akaike Information Criterion (AIC) (Akaike, 1973), to address possible overfitting due to low sample size; ii) a comparison of that value with the AIC of the null model; iii) adjusted R^2, an estimate of model fit, calculated as the percentage of the sum of squares explained

by the model (Zuur et al., 2007); and iv) the significance of the regression coefficients ($p<0.05$).

3. Results

3.1. Site chronologies

Chronology length varied from 48 years (1974 to 2019) in Lombadas – São Miguel to 67 years (1953 to 2020) in Povoação – São Miguel. First-order autocorrelation ranged from 0.20 to 0.53 and rbar values ranged from 0.12 to 0.28. The complete assessment of the tree-ring series is summarized in Figure 17.

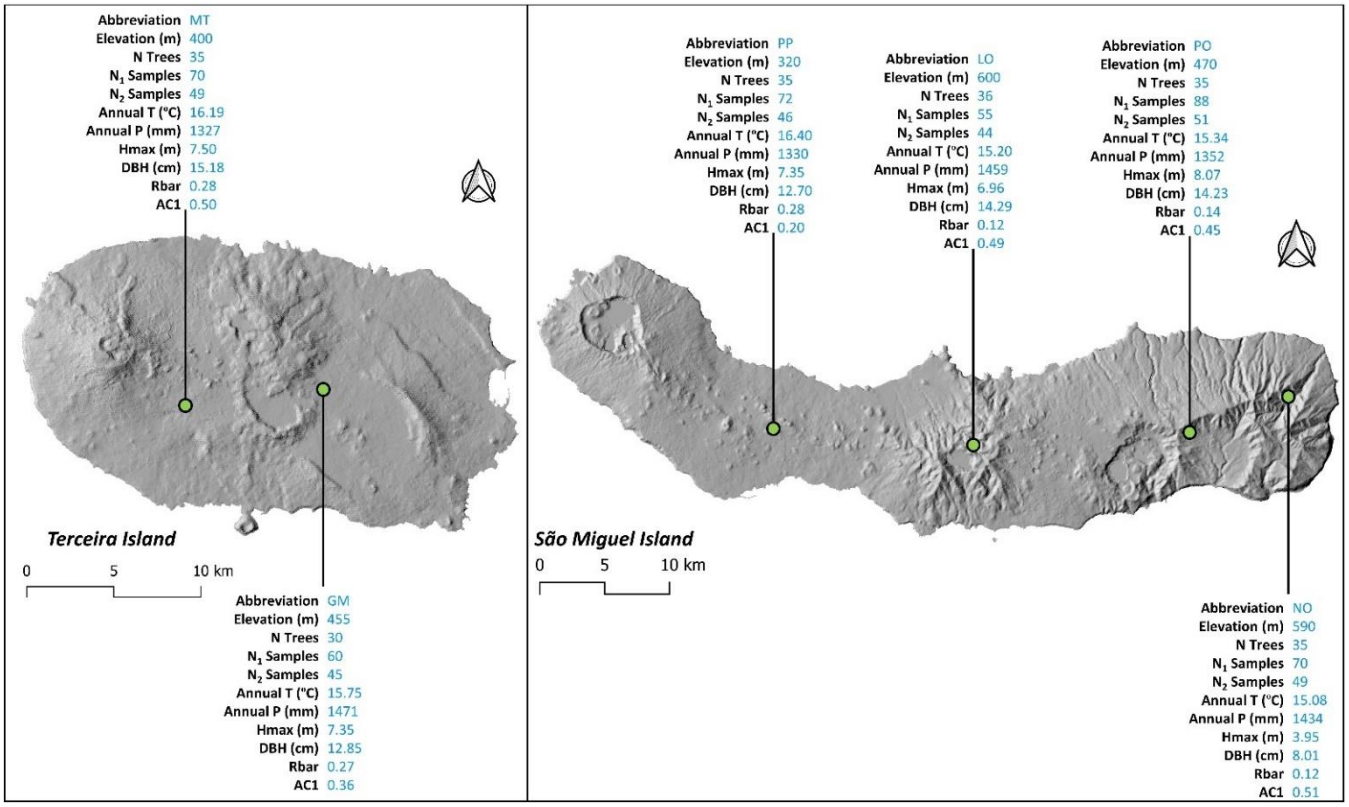


Figure 17. General characterization of the sampled sites at two Azores islands (Terceira and São Miguel), and basic parameters of the site chronologies used to study the climate-growth relationship in six *Laurus azorica* forest stands. Sampled sites are highlighted, including: locality abbreviation, elevation (m), annual mean temperature (T), annual precipitation (P), number of trees (N Trees), total number of wood cores (N1), number of wood cores used in the dendroecological analysis (N2), average maximum tree height (Hmax), average diameter at breast height (DBH), mean inter-series correlation (Rbar), and the first order autocorrelation (AC1).

3.2. Climate-growth relationships

Based on computed SSS values for each site, climate-growth models were fitted for the period 1987 to 2018 (Figure 18).

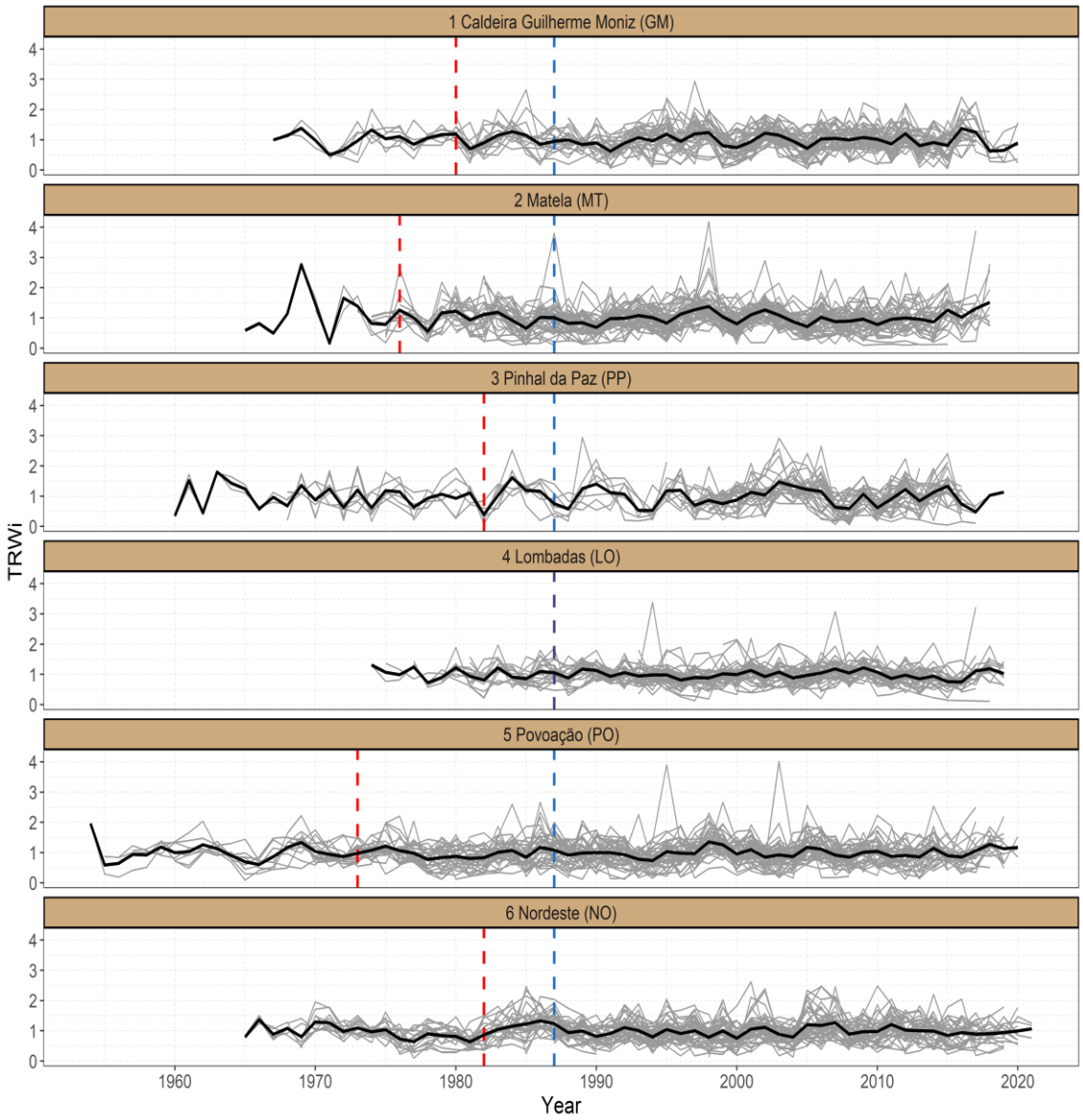


Figure 18. Spaghetti plots of *Laurus azorica* tree-ring indices for two populations at Terceira Island and four populations at São Miguel Island, Azores. Mean chronology – bold line; red dashed vertical lines – SSS≥0.85; blue dashed vertical lines – cut-off used for modelling; LO site – purple dashed vertical line with SSS≥0.85 and the cut-off used for modelling coinciding.

Considering the results from the RF analyses (see Appendices 12 and 13 for a full description), current and previous year temperatures were the main and most consistent

drivers affecting radial growth (Table 8). Spring and early summer were the most important seasonal periods according to most models, in particular the composite model. The magnitude of the spring and early summer temperature effects varied by stand and ranged from positive to negative but was positive for the composite chronology. The second step of RF originated models with percentage of explained variance ranging from 16.92% to 48.38% (Appendix 14).

Table 8. Modeling of climate-growth relationships in six *Laurus azorica* stands in two Azores islands, Terceira and São Miguel. Summary of the effects of the climatic variables retained in models both for the composite and for each individual site chronologies, after two steps of RF analysis. Direction of the effect (+ and -) was based on GLM results. Climatic variables were retained based on the respective importance value: above 10% in the first RF step; close to or above 20% in the second RF step.

ClimVar	CC	GM	MT	PP	LO	PO	NO	ClimVar	CC	GM	MT	PP	LO	PO	NO
T4		+						TminPre6				+			
T6			-		-			TminPre7						-	
T10		-						TminPre10						+	
Tmin3		+						TminPre12					+		
Tmin5	+			+				TmaxPre6	+	-					+
Tmin10	+			-				TmaxPre10						+	
Tmax3	-							P1			+				
Tmax5		-	-					P9						+	
Tmax6								Ppre4					+		
Tpre2							-	Ppre5					-		
Tpre6							+	Ppre8			+				
Tpre10				+				Ppre10						+	
TminPre2							-								

Note: + positive effect, - negative effect; T= temperature for different months (1-12); P= precipitation for different months (1-12); suffix Pre= previous year temperatures or previous year precipitation. CC, Model for the composite chronology; GM to NO, models for each individual site chronology.

The GLM results also revealed a prominent effect of current or previous year temperatures for all chronologies (except for MT). Late spring and early summer temperature effects were detected in five of the six site chronologies (Table 9 and Appendix 14). In the reduced models, possible precipitation effects were detected only in two cases: August precipitation with a positive effect on MT, and May precipitation with a negative effect on LO.

Table 9. Modeling of climate-growth relationships in six *Laurus azorica* stands in two Azores islands, Terceira and São Miguel. Performance of the reduced GLMs for the composite and for each individual chronology. Regression coefficients of each explanatory variable, AIC, AICc, Null Model AIC and adjusted R^2.

Chronology	Model	Coefficients	AIC	AICc	Null model AIC	R^2
CC	Tmin5 ***	+0.23618	317.02	317.234	349.084	0.171
	TmaxPre6 **	+0.11627				
GM	Tmax6 ***	-0.29387	15.592	17.074	27.623	0.386
	TmaxPre6 **	-0.22347				
MT	Ppre8 *	+0.002231	11.588	12.445	14.284	0.125
PP	Tmin5 ***	+0.6203	70.255	71.736	81.250	0.366
	TminPre6 *	+0.4827				
LO	T6 *	-0.0882183	-13.663	-12.182	-8.901	0.230
	Ppre5 *	-0.0008316				
PO	TminPre7 *	-0.14009	-7.3785	-5.897	7.716	0.442
	TminPre10 ***	+0.12668				
NO	Tpre6 *	+0.05826	-45.015	-43.534	-37.001	0.304
	TminPre2 **	-0.06556				

Note: + positive effect, - negative effect; *p=0.05, **p=0.01, ***p=0.001; T= temperature for different months (1-12); P= precipitation for different months (1-12); suffix Pre= previous year temperatures or previous year precipitation.

4. Discussion

4.1. Chronology evaluation

We were able to reliably and accurately delineate and crossdate annual growth patterns in all *L. azorica* tree core samples. However, the relatively low rbar values suggest that the growth of individual trees within each stand was not strongly synchronized. Similar results have also been reported for the Azorean endemic trees *Juniperus brevifolia* (Pavão et al., 2022) and *Ilex azorica* (Pavão et al., 2023), a common outcome in regions with low thermal amplitude and low seasonality (e.g., Brienen and Zuidema, 2005; Espinosa et al., 2018; Granato-Souza et al., 2018; Vasconcellos et al., 2019). Stands at Terceira Island showed higher rbar values than most of the sites at São Miguel Island, which suggest that other factors might be affecting or disturbing individual tree growth (Ford et al., 2017; Zalloni et al., 2019; Luo et al., 2020), including competition due to the presence of invasive plants that are more common in São Miguel natural forests (Elias et al., 2016; Borges Silva et al., 2022).

Chronology length differed among stands, due to the different ages of the forest stands since natural forests have been deeply disturbed in the Azores, some being secondary and not primordial forests (Elias et al., 2016). For example, most of the *Laurus* submontane forests have been replaced by pastureland, exotic woodland, or production forests (Elias et al., 2016). Likewise, developed chronologies were relatively short, with a maximum of 67 years. Considerable changes have occurred in the Azorean soil cover, starting with the human settlement and intensifying in the 1950's, which influenced the distribution and age of the extant natural forests (Costa, 1952).

4.2 Modelling constraints

Our stepwise approach to RF allowed selecting a range of explanatory climatic variables corresponding to importance values above 20% and providing a reasonable percentage of explained variance comparing to previous studies (e.g., Lopatin et al., 2006; Bhuyan et al., 2017; Babst et al., 2018). The GLM approach was also previously used in other studies from the Azores archipelago (e.g., Borges Silva et al., 2017; Matos et al., 2019; Pavão et al., 2023). Moreover, although delivering a useful estimation of the direction of the effect, the final GLMs did not show a relevant improvement in terms of model evaluation statis-tics (AICc and adjusted R^2), comparing to the climatic variables selected in the second step of RF. A possible explanation is the fact that RF is a versatile, robust, and stable analysis. Apart from being a straightforward method in terms of the simplicity of its parameters, it generates low bias and moderate variance (Arlot and Genuer, 2014; Painsky and Rosset, 2017; Piryonesi and El-Diraby, 2020). This error reduction is related to the random selection of the elements used for the induction of each tree, reducing the correlation between individual models, and providing predictions with greater stability (Fox et al., 2017; Painsky and Rosset, 2017). RF models provided an indication of the importance of specific climatic variables for tree growth (Jevšenak et al., 2018; Jevšenak and Skudnik, 2021; Li et al., 2021; Sahour et al., 2021), while GLMs provided more explicit information describing the strength and direction of these effects. However, our GLM regression analyses only considered linear additive effects and were arguably sensitive to outliers (Zheng and Agresti, 2000; Dobson and Barnett, 2018), although showing consistency with RF results. Hence, the discussion of the modelling results will consider a global evaluation based on the two complementary approaches – RF and GLM.

4.3. Climate-growth relationships – Temperature effect

The overall composite chronology (metapopulation) helped to understand similarities among sampled stands and the overall effect of the climatic variables on *L. azorica* radial growth in the Azores. The models derived for the composite chronology showed that growth-rings in *L. azorica* were predominantly sensitive to current and previous year spring temperatures. As a ring-porous species, *L. azorica* xylem vessels include distinct pits in tangential section, which allows water transport between individual vessels. Pit structure together with diffusely distributed xylem vessels may function to reduce tree susceptibility to environmental stressors, including drought (Morales et al., 2002; Matos et al., 2019). Thus, this mechanism, together with warmer temperatures in late spring and early summer, may enhance photosynthetic performance for the rest of the growing season, potentiating carbon uptake and positively affecting tree growth (e.g., Cermák et al., 2002; Tixier et al., 2019; Wong et al., 2021). Nonetheless, the role of carbon storage in the previous year is still an open question that requires experimental studies (see Körner, 2003, 2015). Additionally, submontane, and montane forests in the Azores are usually associated with high levels of occult or horizontal precipitation, intercepted by the vegetation cover (Prada et al., 2009; Dias and Melo, 2010). This ensures water availability that, together with warm temperatures, may favor radial growth (Dawadi et al., 2013; Thapa et al., 2015).

Further explanation for our results might related to an earlier onset of cambial activity and cell differentiation during relatively warm spring conditions. In fact, the flowering season in *Laurus azorica* might start as early as November or December, extending until April, followed by a fruiting season that extends into summer and autumn (Schäfer, 2005). Thus, warmer spring and early summer months might extend the length of the

growing, flowering and fruiting seasons, and, consequently, of the total period available for wood pro-duction in a given year (Zani et al., 2020).

An exception to this pattern, in some cases (Composite, GM, MT and LO), was the negative effect of high summer temperatures, particularly of maximum temperature. This suggests that extremely high temperatures might affect tree growth due to water imbalance (Dawadi et al., 2013; Thapa et al., 2015). Despite the positive impulse associated with high temperatures at the beginning of the growing season, the subsequent negative effect of extremely high summer temperatures has been reported for other broadleaved species (e.g., Babst et al., 2019; Harvey et al., 2020), and for the Azorean tree *Ilex azorica* (Pavão et al., 2023). Summer water stress has been shown to affect radial growth rate (Biondi, 2000; Weijers et al., 2018; Zhang et al., 2018). Indeed, extremely high summer temperatures increase evapotranspiration and reduce water availability, prompting stomatal closure. This will decrease photosynthetic activity, carbohydrate storage, and, consequently, reduce cambial activity (Fritts, 1966; Qaderi et al., 2019; Roig-Oliver et al., 2021). Within the Lauraceae, extensive studies at Brazil Atlantic Forest with *Nectandra* spp. reported that warmer summers suppressed tree growth due to water stress and increased evapotranspiration (Reis-Avila and Oliveira, 2017; Granato-Souza et al., 2019; Gonçalves et al., 2021).

4.4. Climate-growth relationships – Precipitation effect

Globally, no relevant effect of precipitation was found, except in MT and PO where a positive effect of late spring and summer precipitation was observed, related to the water balance required for tree growth during the drier months (Sun et al., 2021a), as previously observed in other broadleaved species (e.g., Camarero and Rubio-Cuadrado, 2020; Roibu et al., 2020; Anderson-Teixeira et al., 2022). In fact, the archipelago presents high relative

humidity and a precipitation evenly distributed throughout the year, except during the driest summer months (Azevedo, 2001; Couto, 2012).

4.5. Climate-growth relationships – Previous year effect

We found an effect of climatic variables from the previous year on growth rings, which has been previously reported for diffuse porous species (e.g., García González and Eckstein, 2003; Buttó et al., 2021). Research in boreal, temperate, and tropical forests, with a broad range of tree taxa, has also reported relationships between tree growth and previous year climatic variables (e.g., Boninsegna et al., 2009; Babst et al., 2013; Hacket-Pain et al., 2015). This so-called legacy effect is controlled by several interactions between the environment and tree physiology (Cook, 1985). It also suggests lagged physiological effects persevering longer than the current year (LaMarche and Stockton, 1974; Timofeeva et al., 2017; Xu et al., 2020). For example, non-structural carbohydrate (NSC) allocation and storage might affect tree growth on the following years (Monserud and Marshall, 2001; Liu et al., 2018; Smith et al., 2018; Szejner et al., 2018; Kannenberg et al., 2019; Xu et al., 2020). Warmer temperatures at the end of the growing season (as it happens in the Azores archipelago) can extend its length. Thereby, the NSC stock that will be available for the next growing season will be increased (e.g. Tixier et al., 2019; Wong et al., 2021). However, NSC accumulation in *L. azorica* has not been investigated.

4.6. Climate-growth relationships – Differences among sites

We obtained slightly different climate-growth relationships amongst sites that can be linked to different site conditions (i.e., elevation) existing in the archipelago (see Elias et al., 2016; Pavão et al., 2019), possible competition with other native or exotic species (e.g., Primicia et al., 2015; McCarroll et al., 2017; Lu et al., 2019; He et al., 2022),

differences between the microclimates (e.g., Moser-Reischl et al., 2019; Wang et al., 2020) and high variability within stands (low rbar values).

Regarding stand characteristics (soil type, slope, and species composition), the most abundant soil types were ferruginous andosols (present in MT, LO, PO, and NO) and shallow allophanic regosols (present in PP, PO, and NO), except for GM with a vitric andosol. Ferruginous andosols have low water infiltration capacity (Ricardo et al., 1977), which could reduce water availability for trees at four of the studied stands. Sloped terrain was mostly found at São Miguel Island stands (PP, LO, PO, and NO), while species composition was relatively homogeneous in all stands, with the presence of exotic species and, consequently, possible competition. Despite some local variation, laurel forests in the Azores generally occur in similar environmental conditions, with a considerable amount of organic matter on soils, even for very shallow regosols (see Borges Silva et al., 2022). In fact, no relevant environmental differences have been found between laurel forests in different Azores islands in previous studies, except for some local variation in plant community composition (Elias et al., 2016; Borges Silva et al., 2022). Therefore, the establishment of a direct link between differences in climate-growth relationships and stand characteristics is not possible at this stage.

Biotic factors also mediate growth responses to climate (e.g., Foster et al., 2016; Yang et al., 2020), even though our data transformations (i.e., detrending) should have removed most of these biotic effects. Nevertheless, it seems likely that there may be residual growth variance that is at-tributed to competition or age (e.g., Monserud and Marshall, 2001; Primicia et al., 2015; He et al., 2022). Matos et al. (2019) also found differences in radial growth rate between different stands of *L. azorica* at different elevations. Other studies addressing one tree species at different elevations also found distinct climate-growth relationships among sites (e.g., van der Maaten-Theunissen and

Bouriaud, 2012; Mazza et al., 2014; Rollinson et al., 2016). Moreover, different responses of tree growth to climate have also been found at intra-individual scale (e.g., Misi et al., 2019). Furthermore, different populations could have become locally adapted or acclimated. Many studies show that both local adaptation and acclimation are quite common in plant species (e.g., Misi et al., 2019; Sun et al., 2021b). However, experimental studies would be needed to confirm differentiation among *L. azorica* populations (e.g., Benito Garzón et al., 2019; Kumarathunge et al., 2019; Ren et al., 2020; Sun et al., 2021b; Wright et al., 2022).

Our results emphasize the importance of modelling under different site conditions, to better encompass the various situations and factors affecting growth ring width and its inherent variation.

5. Conclusions

Our study demonstrated the possibility to develop reliable tree-ring chronologies of a key species of the Azorean laurel forest ecosystems, showing that the relationship between tree-ring widths and climate parameters was mainly connected to temperature of the current and previous years. Hence, this work together with recent studies dealing with other important laurel forest trees (Pavão et al., 2022, 2023), contributed to build base-line climate-growth relationships in an island forest under low climatic seasonality. Furthermore, future dendrochronological studies could be applied to other relevant native or introduced species (e.g., Vieira et al., 2017; Pavão et al., 2022), or to other Macaronesian islands (e.g., Jonsson et al., 2002; Pérez-De-Lis et al., 2011; Rozas et al., 2011, 2013; Fernández de Castro et al., 2020). Nonetheless, due to the high levels of within stand variation, and to refine the climate-growth analysis, different approaches and

proxies will have to be explored in the future, including early and latewood vessel area (García-González and Fonti 2006; Souto-Herrero et al., 2018) since most native species are angiosperms. Moreover, other insights (e.g., site characteristics and physiological processes) could be tested in future works to refine the relation between climate and radial tree growth in the Azores archipelago.

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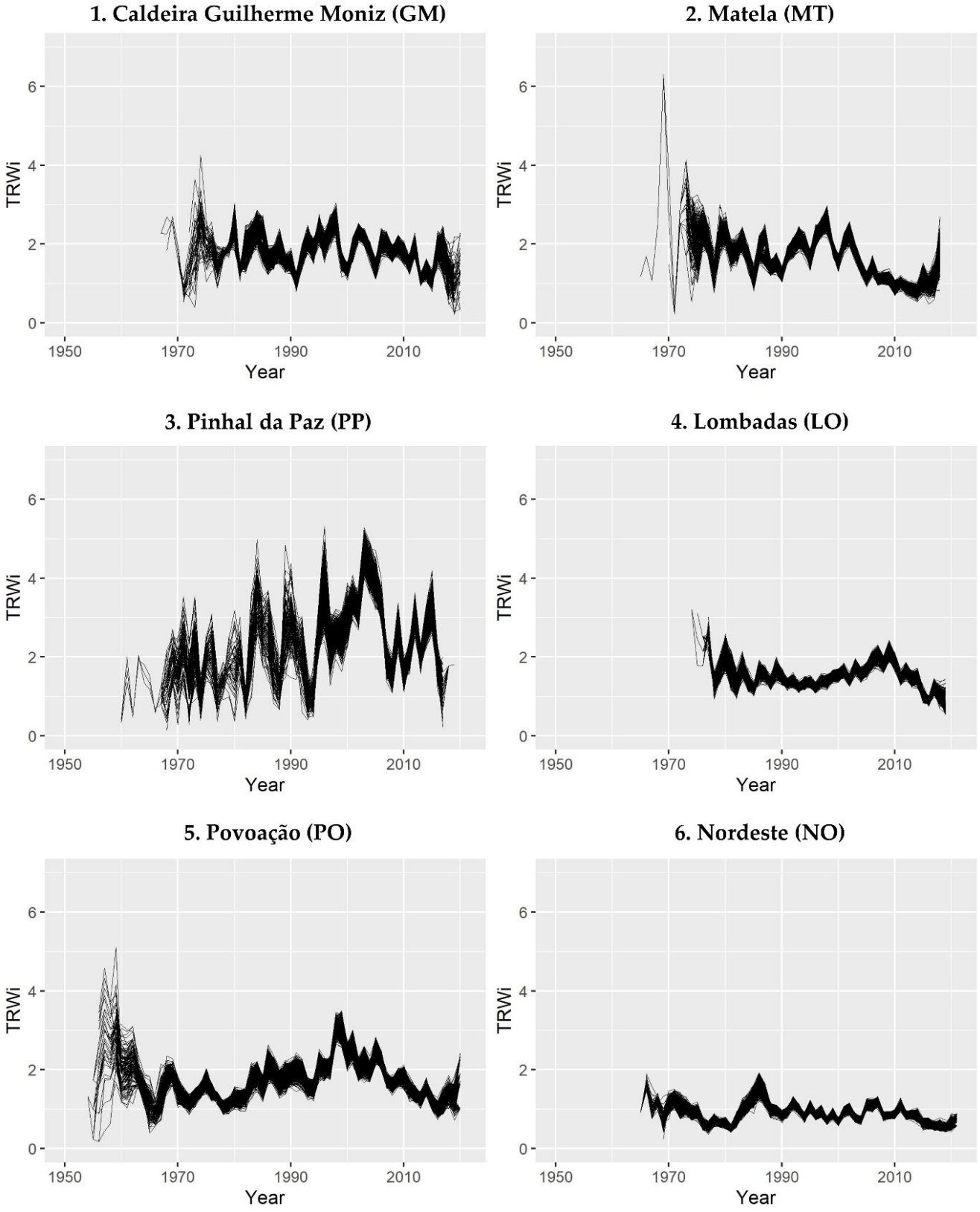
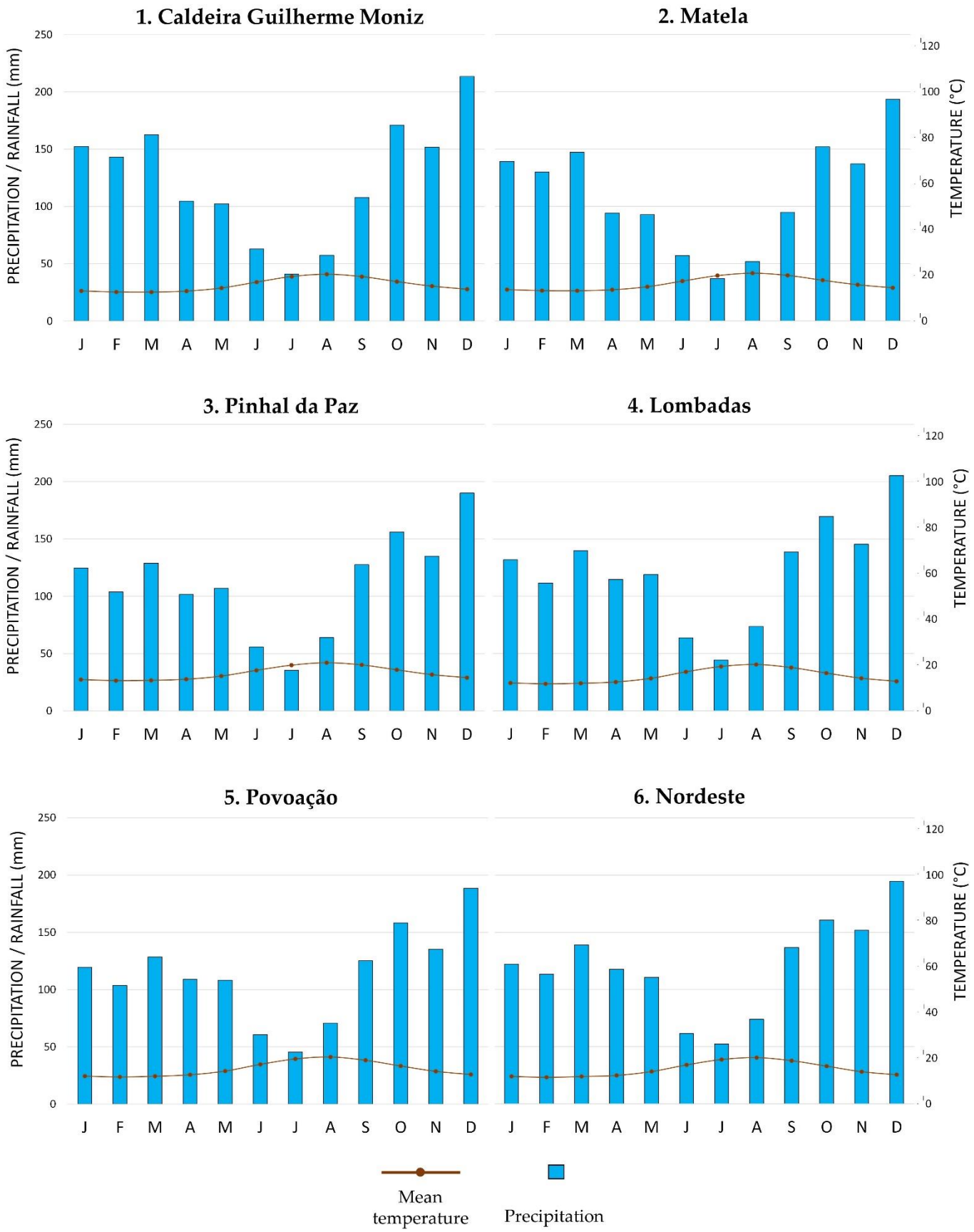
CHAPTER 4 – Supplementary Material



Appendix 10. Bootstrapped mean chronology for all studied sites. Years on x axis and tree-ring indices (TRWi) on y axis.



Appendix 11. Average temperatures (lines) and monthly precipitation (bars) for all study sites. Data was extracted from CHELSA timeseries dataset with a spatial resolution of 30-degree seconds.

Please, use the following link to download Appendix 12 (Excel Sheets): https://figshare.com/s/b290523001db055cc654

Appendix 12. Results from the first RF step (various combinations of climatic variables, i.e., temperature and precipitation from current and/or previous year) for composite and site chronologies, with the respective variable importance (%IncMSE). Those variables that were selected for the second step of RF are marked in green.

Please, use the following link to download Appendix 13 (Excel Sheets): https://figshare.com/s/fe753b0435db95ac692b

Appendix 13. Results from second RF step (based on the variables selected on the first RF step), for composite and site chronologies, with the respective variable importance (%IncMSE) and increase in node purity (IncNodePurity). Those variables that were selected for the GLM analysis are marked in green.

Please, use the following link to download Appendix 14 (Excel Sheets): https://figshare.com/s/c23807f1a507a71a4a76

Appendix 14. Performance of all RF and GLM tested models (based on the variables selected on the second RF step) for composite and site chronologies, with the respective regression coefficients for each explanatory variable, AIC, AICc, Null Model AIC, adjusted R^2, mean of squared residuals and % of explained variance.

CHAPTER 5

General discussion, conclusions, and perspectives for future studies

CHAPTER 5

General discussion, conclusions, and perspectives for future studies

1. Chapter outline

In this final chapter, a general discussion is provided, including limitations of dendrochronological studies in the Azores, a general overview of the factors that affected tree age and tree growth, and the potential application of dendrochronological methods in ecological modelling.

The general conclusions will address the implications of the dendrochronological results obtained in the study allow to foresee a relevant role of the Azorean tree species on studies regarding carbon sequestration and the impact of climate change.

Finally, perspectives for future research are presented, addressing the potential study of different species, tree-ring measurements, and statistical methods.

2. General discussion and conclusions

Limitations of dendrochronological studies in the Azores

Tree-rings in regions with low thermal amplitude, high relative humidity and low marked seasonality are often more challenging to work with (Haines et al., 2018; García-López et al., 2022). In fact, in the Azores, limitations in dendrochronology studies can occur in two ways. In one hand, the climate does not present marked seasonality and has low thermal amplitude between seasons (Azevedo, 2001; Couto, 2012), which is proven to be an obstacle in dendrochronological studies (Rozendaal and Zuidema, 2011). Also, plant families of the laurel and mountain forests of the Azores, such as the Lauraceae,

Aquifoliaceae, and Myricaceae, are still rarely cited in dendrochronological databases and literature (Zhao et al., 2019).

Results from this work show that, despite some challenges (i.e., presence of several ring anomalies), growth-ring boundaries can be identified, and mean chronologies could be built for the three species at different sites. However, low rbar values were present in several stands, meaning low correlations among growth ring patterns from individuals at the same site. Being a common outcome in regions with low thermal amplitude and low seasonality (e.g., Brienen and Zuidema, 2005; Espinosa et al., 2018; Granato-Souza et al., 2018; Vasconcellos et al., 2019), different responses of tree growth can also be found at intra-individual scale (e.g., Misi et al., 2019). Likewise, populations could have become locally adapted or acclimated, which is quite common in plant species (e.g., Benito Garzón et al., 2019; Misi et al., 2019).

To overcome this challenge, other tree species can be used in dendrochronological studies, that may be more sensitive to specific environmental conditions (i.e., climate). Therefore, species that are particularly sensitive to moisture levels would be interesting to focus, such as *Quercus* spp., since a precipitation gradient occurs with elevation in the Azores. This genus is quite studied in Europe, showing good climate-growth relationships (e.g., Kostić et al., 2022; Mészáros et al., 2022; Pasho and Alla, 2022; Solomina et al., 2022; Tsavkov et al., 2022). However, there are no native species of *Quercus* in the Azores, and those that are present are mainly represented by planted specimens. Therefore, other alternatives will have to be investigated.

Tree ages of the Azorean laurel and mountain forests

Developed chronologies in this work were relatively short for the two studied islands. Globally, the population showing the smallest chronology, from *Ilex azorica*, was located

at Sete Cidades (Chapter 3). Natural or anthropogenic disturbance is one of main factors affecting tree age in forest ecosystems (Thom et al., 2017; Assefa and Abate, 2018; Rydval et al., 2018). In this specific case, this site is a fragmented forest with high human pressure (e.g., tree cutting, plantation of exotic species) and the presence of several introduced species, potentially affecting the establishment of young trees (e.g., Caetano Andrade et al., 2019). On the other hand, *Juniperus brevifolia* population from Serra de Santa Bárbara (Chapter 2) and *Ilex azorica* population in Terra Brava (Chapter 3) both in Terceira Island, included individuals more than 100 years old. Indeed, both are two of the most well preserved patches of natural forest in the Azores (Elias et al., 2016).

Nevertheless, chronology length differed among stands for all species, due to the different ages of the forest stands. In fact, the archipelago suffered significant changes in the soil cover, starting with the human settlement and escalating in the 1950's (Costa, 1952). Those changes influenced the distribution and age of the extant natural forests.

Moreover, in many forest ecosystems, a natural process of succession and regeneration can occur, in which different species of trees and other plants establish and grow over time, leading to differing tree ages among stands (e.g., Matsuo et al., 2021). For the Azorean laurel and mountain forests, different natural processes were previously identified, wherein *J. brevifolia* is considered a pioneer species, *I. azorica* a mature species regenerating in the forest, and *Laurus azorica* a primary species forming seedling-sapling banks (Elias and Dias, 2009; Elias et al., 2011, 2016).

Climatic factors influencing tree growth

Temperature, especially from late spring and early summer, stood out as the main climatic factor affecting tree growth in the three studied species occurring in the laurel and mountain forests in the Azores, which are associated with high levels of occult or

horizontal precipitation, intercepted by the vegetation cover (Prada et al., 2009; Dias and Melo, 2010). This ensures water availability that, together with warm temperatures, favors radial growth (Dawadi et al., 2013; Thapa et al., 2015). Global results agree with previous work in Macaronesia with conifers - *Pinus canariensis* (e.g., Jonsson et al., 2002; Brito et al., 2016; López et al., 2021) - and with other broad-leaved species (e.g., García-López et al., 2022), where links between tree growth and temperature have also been found.

Despite the potential limitations imposed on dendrochronological studies by the Azorean climate, due to low thermal amplitude and high relative humidity, temperature was shown to affect tree growth in the three target species. However, slightly different climate-growth relationships were found between sites and species, which are most likely related to specific biotic and abiotic factors underlying present at each stand (e.g., Primicia et al., 2015; McCarroll et al., 2017; Lu et al., 2019; Moser-Reischl et al., 2019; Wang et al., 2020; He et al., 2022). Moreover, because there was high variability within stands (i.e., low rbar), climate response also differed due to the low strength of common patterns (Cook and Pederson, 2011). Diverse climate-growth relationships for the same species at different locations have also been found in other studies (e.g., Mazza et al., 2014; Misi et al., 2019).

Growth rates and carbon sequestration

Estimating growth rates of tree species can have different purposes, such as resource management, environmental monitoring, and silviculture (Drake, 2009; Poorter et al., 2012; Mathewos, 2017). Meanwhile, one of the main objectives of estimating growth rates of native species such as *J. brevifolia*, *I. azorica* and *L. azorica*, is to understand their role on carbon sequestration (Farrelly et al., 2013). In fact, our dendrochronological

results and the dendrometric traits retrieved can be used as predictors of carbon sequestration in aboveground biomass as done for other studies (e.g., Rieger et al., 2017).

Besides trunk diameters and tree height measurements, tree-ring measurements should be used to estimate tree ages more reliably and therefore growth rates. This has been previously done, for a widespread invasive species on the Azores archipelago (Borges Silva et al., 2017). Our results confirmed that, even in areas where tree-ring distinctness is not the best (García-López et al., 2022), dendrochronological methods can be applied, opening the possibility to create reliable tree-ring chronologies for native Azorean trees.

Thus, it will be possible to calculate growth rates for Azorean tree species, despite the challenges mainly posed by problems with tree ring-boundary delimitation and measurement). Nevertheless, with the use of anatomical analysis (Chapter 2) and other standard dendrochronological methods such as crossdating and data standardization, applied throughout the research, refined growth rates can be estimated, allowing to understand their potential as a carbon sinks (e.g., Shadman et al., 2022). Alternatives to estimate growth rates include terrestrial LiDAR and flux tower data (Karamihalaki et al., 2023) or the analysis of phloem sap and of other dendrochronological properties (Halder, 2020).

Dendrochronology in ecological modeling

Dendrochronology allows reconstructions of past climate conditions (e.g., Blake et al., 2020; Tejedor et al., 2020), which can then be used as a predictor variable in species distribution models (e.g., Zhang et al., 2022). For example, temperature signal found in our three studied species could be modelled to infer future optimum conditions (e.g., Speer et al., 2004; Chen et al., 2012).

Since the results from climate-growth relationships, using correlations GLM or RF analysis, showed relatively low levels of explained variance, as in other modeling analyses, using dendrochronology in ecological modelling can be valuable if it is coupled with field or remote sensing data validation to increase explained variance (e.g., Fois et al., 2018; Randin et al., 2020). More specifically, accurate temperature data and tree growth rates would be needed for the specific studied sites, since modelling species distribution or growth with projected climate change scenarios relies on highly site-specific factors (van der Maaten et al., 2017).

Therefore, the title of this dissertation "*Linking climate, distribution and growth in forest research: can dendrochronology improve species distribution modelling?*" has a positive answer, meaning that dendrochronology can improve species distribution modeling. This is possible by using trees responses to climate (i.e., temperature in this specific case) as predictor variables in species distribution modelling, although with site-specific data to reduce the error associated to the models.

Dendrochronology in climate change

The continuous increase of average temperature associated to climate change is already impacting productivity, forest decline and tree mortality in temperate and Mediterranean regions (Camarero et al., 2015; Neumann et al., 2017). In fact, the incidence of heat waves and droughts is currently intensifying, for example in the Macaronesia (Cropper and Hanna, 2014), although the effect on the Azorean laurel and mountain forests is yet unknown.

Nevertheless, the temperature signal found in climate-growth relationships in the three studied species, raises some concern. Summer temperatures are expected to increase

(IPCC, 2022), overriding the ecological limitations of some tree populations , which can lead to local extinctions (Guada et al., 2021).

Moreover, the dendrochronological methods used in this thesis can indeed be applied to understand the impact of climate change on tree growth (e.g., Upadhyay and Tripathi, 2019); the increased atmospheric CO_2 levels (directly related to climate change), positively affected radial tree growth (e.g., Martinelli, 2004). However, other dendrochronological studies indicated that a negative impact of high temperatures on tree growth can be present due to atmospheric warming in the last decades, overcoming the positive fertilizing effect of CO_2 (Barber et al., 2000).

3. Perspectives for future studies

Potential applications in other species

Our results suggest that other species and habitats can be focused, while working in dendrochronology in the Azores. In this study, temperature was shown to be the main climatic driver of tree growth in the selected species and study sites, probably due to a focus on middle and high elevations and, consequently, on medium to relatively lowe temperatures (*Principle of Limiting Factors*).

Therefore, to retrieve different climatic signals, other native species in low-lands or coastal habitats may be aimed in future studies. For instance, spatial distribution of *Morella faya* and *Picconia azorica* is limited to medium/low altitude areas (*Principle of Ecological Amplitude*) (Martins et al., 2013; Elias et al., 2016; Dutra Silva et al., 2017; Pavão et al., 2019). In fact, the most important ecogeographic variables for the distribution of *M. faya* was total annual precipitation and slope in Terceira and São Miguel

islands (Dutra Silva et al., 2019), which already gives indication for a potential analysis of climate-growth relationships.

In other regions, dendrochronological studies have also been applied to non-native Azorean species, such as *Cryptomeria japonica* (e.g., Jung et al., 2020; Mori et al., 2020), *Platanus* spp. (e.g., Gillner et al., 2014; Nitschke et al., 2017), *Eucalyptus globulus* (e.g., Leal et al., 2004; González-Muñoz et al., 2014) or *Ulmus* spp. (e.g., Babushkina et al., 2019; Bridge, 2020). Therefore, comparative dendrochronological studies could be done with non-native species, evaluating different methods, approaches, or even climatic responses, as done in this thesis.

Other tree-ring measurements

This work showed tree-ring distinctness is not the best in the Azorean tree species, with the presence of several indistinct ring-boundaries and ring anomalies. However, tree-ring measurements can always be refined to better retrieve a specific climatic signal. For example, Fonti and García-González (2008) found difficulties in using tree-ring widths to retrieve precipitation signal on mesic sites and concluded that the use of earlywood vessel size as a dendroclimatic proxy resulted in better outcomes.

Furthermore, additional tree-ring proxies can also be applied in future studies, such as stable carbon and oxygen ratios to provide climatic signal and atmospheric CO_2 and O_2 concentrations (Shestakova and Martínez-Sancho, 2021), wood-anatomy to provide intra-annual variations of tree growth (Arnič et al., 2021), and blue reflectance to derive a relative-density parameter of the latewood, being a highly robust climate-sensitive approach (Kaczka and Wilson, 2021).

Moreover, a focus on sub-annual tree growth would be very important, by using dendrometers or a xylogenetic approach (Poljanšek et al., 2019). Dendrometers have an

advantage of being an analysis that permits long-term assessment (e.g., Löffler et al., 2021), can allow a better assessment of the influence of temperature and precipitation on tree growth, and an accurate estimation of growth rates (Deslauriers et al., 2007).

Other statistical methods

In dendrochronological studies, different statistical approaches can be found, from detrending individual tree-ring series to climate-growth relationship analysis (Speer, 2010). In this thesis, only on the latter process different approaches were tested: Pearson's correlation on Chapter 2, Generalized Linear Models (GLM) on Chapters 3 and 4 and a machine learning approach with Random Forest (RF) on Chapter 4. In fact, creating a stepwise approach in Chapter 4, resulted into a more versatile, robust, and stable procedure by integrating both GLM and RF in the analysis (Arlot and Genuer, 2014; Painsky and Rosset, 2017; Piryonesi and El-Diraby, 2020; Barreiro et al., 2022).

The other statistical methodological adaptation undertaken along this thesis was on chronology quality assessment, where Expressed Population Signal was used on Chapter 2 but replaced by Subsample Signal Strength on the following studies, according to Buras (2017) critical analysis of both parameters.

Regarding detrending, only the response period on spline curve fitting method was used, allowing to run a more flexible approach in shorter chronologies (Fritts, 1976; Cook and Kairiukstis, 1990; Bontemps and Esper, 2011).

Though, other statistical methods could be tested and adapted depending on site conditions or chronologies characteristics. For example, Moon et al. (2020) utilized double-detrending methods, because of the high crown density and keen competition of Korean forests. At a first stage, they removed biological growing trend by applying a negative exponential curve, and then forest stand competition and disturbance was

removed by using a spline curve of 60 years of response cycle. In another study, different machine learning approaches (e.g., Artificial Neural Network, Hyperparameter Tuning) were used to reconstruct hydrometeorological records, since they can analyze incoming information and look for explicit and hidden patterns in these data (Isaev et al., 2022).

Since, in the Azores, there are some potential limitations to dendrochronological studies, methods in this research should be adapted to our stand and trees characteristics. Moreover, a future methodological analysis could be driven to test different detrending methods (e.g., from "dplR" R package) and climate-growth relationship analysis (e.g., linear and non-linear regressions or machine learning methods), and create a broad methodology suitable for the region, based on the comprehensive analysis of our native tree species data and new data regarding introduced species already studied in other regions.

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