Long-term growth and functioning of high-elevation Pinus uncinata forests and trees inferred through dendroecology

Creixement i funcionament a llarg termini de boscos i individus de Pinus uncinata inferits mitjançant dendroecologia

Juan Diego Galván Candela

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Juan Diego Galván Candela

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Memòria presentada per Juan Diego Galván Candela per optar al grau de doctor per la Universitat de Barcelona.

Programa de Doctorat de "Ecologia Fonamental i Aplicada".

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Doctorand	Director de tesi	Co-directora i tutora
J. Diego Galván Candela	J. Julio Camarero Martínez	Emilia Gutiérrez Merino

A ma mare i amiga,

Rosa

... In their highest boughs the world rustles, their roots rest in infinity, but they do not lose themselves there, they struggle with all the force of their lives for one thing only: to fulfil themselves according to their own laws, to build up their own form, to represent themselves ...

… En sus copas susurra el mundo, sus raíces descansan en lo infinito; pero no se pierden en él, sino que persiguen con toda la fuerza de su existencia una sola cosa: cumplir su propia ley, que reside en ellos, desarrollar su propia forma, representarse a sí mismos …

Wanderung: Aufzeichnungen
Hermann Hesse

Content

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General Introduction

Dendrochronology: population- *vs.* individual-based approaches

Dendrochronology is the science of dating annual growth layers (rings) in woody plants, which allows the retrospective tracking of tree growth at multiple temporal and spatial scales (Fritts 1971, 2001). Dendroclimatology and dendroecology are two of the best known dendrochronological subdisciplines. Dendroclimatology is able to reconstruct the climate history by using tree rings, and it has attained an increasing influence in paleoenvironmental studies, primarily because it not only provides annually resolved records with precise dating to the calendar year, which allows them to be compared directly with instrumental climatic records (Griggs et al. 2007), but also because it constitutes a powerful tool for developing qualitative and quantitative reconstructions of past climate on seasonal to century or longer time scales (Manrique and Fernández-Cancio 2000, Touchan et al. 2005, Hughes et al. 2011). Moreover tree-rings represent the most geographically widespread proxy records and generally possess the highest correlations with instrumental climate data in extratropical regions (Briffa et al. 1998). For its part, dendroecology is a subdiscipline that focuses in the study of past and present ecological changes of trees in their local environments (Fritts and Swetnam 1989). The main difference between dendroclimatology and dendroecology is that the former is distinguished by a sole focus on using tree-ring proxies for the reconstruction of climate history rather than to study the effects of climate on tree growth, functioning and performance. Dendroecology investigates a wide spectrum of phenomena influencing tree growth responses to diverse disturbances as insect outbreaks (Esper et al. 2007, Büntgen et al. 2009), the occurrence of severe frosts or droughts (Panayotov et al. 2013), windstorms (Čada et al. 2013), avalanches (Muntán et al. 2010), fires (Christopoulou et al. 2013), droughts (Vicente-Serrano et al. 2013) or competition interactions (Fonti et al. 2006) among other phenomena, all of them remaining reflected in the annual patterns of tree-ring variables such as ring-width (Fritts 1976), density (Fritts 2001) or isotopic composition (Leavitt and Long 1982).

Trees of the same species growing in the same site show a similar growth pattern in the aforementioned tree ring characteristics over time, which allows them to be cross-dated. This assumption holds particularly true for trees living in areas where a seasonal climate is the main constraining factor of tree-ring formation, as it is the case of old trees occurring in and around altitudinal or latitudinal distribution limits. Consequently, dendrochronologists emphasize subjective site and tree selection, as well as tree replication, to build representative mean growth series or chronologies willing to reveal common regional climatic signals, as well as to reduce unwanted non-climatic “noise” (Briffa and Melvin 2011). To achieve this, dendrochronologists average different growth series coming from different trees with supposedly high climate sensitivity that preserve a high resemblance in temporal tree-ring patterning. This population-based approach may not capture growth responses to heterogeneous environmental conditions, which are known to affect trees of different sizes, ages, species and successional trajectories, thus producing biased growth estimates (Bowman et al. 2013). That is to say, the population approach reinforces the mean climatic signal, but at the cost of losing the information contained at the individual level (Carrer 2011). Further, pooling individual-scale data brings a loss of information related to how trees tolerate environmental stressors, compete for resources and respond to extreme climatic events (Ettl and Peterson 1995, Rozas and Olano 2012). While useful for reconstructing past climate patterns, this classical dendrochronological approach does not give an accurate picture of the individual trees response to climate change, which is the result of multiple interactions between environmental inputs and the physiological responses of the tree (Fritts 2001).

Seeing the trees for the forest: individual- and site-level characteristics influencing tree growth

Tree growth and productivity in cold-limited environments such as high-latitude and mountain forests including the arctic and alpine ecotones is often limited by low temperatures and a short growing season, both constraining wood formation (Körner 2012). On the other hand, tree growth is being affected by global warming and related biogeochemical changes such as rising atmospheric CO_2 concentrations (Soulé and Knapp 2006). In Europe and North America, while broad areas of mountain conifer forests have displayed increasing rates of radial growth in the last decades (Graumlich 1991, Boisvenue and Running 2006), other studies have suggested that cold-limited boreal forests may not consistently show increased growth under warming conditions (Barber et al. 2000, Lloyd and Fastie 2002). Furthermore, a recent site-dependent loss in growth responsiveness to the temperature rise has been also noted (Briffa et al. 1998) (see chapter 3 of this thesis). These contrasting growth patterns also appear among coexisting trees and nearby forests, thus challenging our understanding of tree growth responses to climate warming (Wilmking et al. 2004). The diverse range of growth responses to climate among coexisting trees is partly due to additional non-climatic factors such as local soil water availability (Oberhuber et al. 1998), soil organic layer thickness (Porter and Pisaric 2011), competition for light (Coomes and Allen 2007), sapwood production (see chapter 1), altitude (Tardif et al. 2003; see chapter 2), topography (Bunn et al. 2005), age (Szeicz and MacDonald 1994), etc.

In the Mediterranean Basin, the complex topography (Giorgi and Lionello 2008) derives from luv-lee (e.g. Xoplaki et al. 2000, Fox and Deil 2004) and slope aspect effects (e.g. Karschon et al. 1979, Kutiel 1992) or concave-convex microtopography effects (e.g. Ruiz-Flaño et al. 1992, Ozkan 2009). Therefore, the responses of trees to climate may vary amongst co-occurring individuals and these reactions may be affected by non-climatic drivers differently acting at several spatial scales across the distribution area of a tree species (chapter 2).

At the site level, altitude and other local non-climatic drivers have been shown to control recent growth trends in mountain conifer forests (Tardif et al. 2003, Carrer et al. 2007, Littell et al. 2008). Hence, mountain forests are characterized by a high spatial variability among sites and trees in their responsiveness to climate (Bunn et al. 2005). A critical evaluation of such variability may help to disentangle the roles of local conditions such as altitude and topography in mediating recent growth trends (see chapter 1 of this thesis). At the tree level, studies performed across altitudinal gradients have shown that growth depends on changes in sapwood area (Vertessy et al. 1995) (see also chapter 1 of this thesis). Sapwood area and basal area increment (BAI) are tightly related in conifers (Sellin 1994, Knapic and Pereira 2005), and the former is closely linked to the growth efficiency of trees in terms of wood produced by needle area (Waring 1987). In *Pinus ponderosa* forests, size-related growth constraints explained the decline in growth efficiency which translated into a reduction of sapwood area (McDowell et al. 2007). The role of sapwood as a growth driver may depend on age-dependent changes in the stem hydraulic conductivity (Spicer and Gartner 2001). Consequently, sapwood area might modulate the growth responses of mountain conifer forests to recent climate warming.

The aforementioned diverse findings reveal that individuals, not forests (i.e. populations), respond to climate (Clark et al. 2012), and that we need a better understanding of the interactions between site conditions and tree characteristics at regional and local scales to disentangle how these features may modulate the individual growth responses to climate warming (see chapters 1 and 2 of this thesis).

Taking an individual-scale approach to measure or track radial growth variation among individuals allows using changes in growth as a proxy of tree performance. This approach may give a biased assessment of population vulnerability based on growth response to climate; however, the adoption of this view is fundamental for a broader understanding of long-term growth responses of forests to climate change.

Seeing the forest for the trees: diverging growth-climate relationships at the population level

As pointed out before, the population approach is useful for reconstructing past climate patterns since it reinforces the mean climatic signal happening in trees of a same species growing in a same site or region, minimizing the individual differences on growth that constitutes the unwanted non-climatic "noise" (Cook and Kairiukstis 1990). We also stressed the main growth constrain imposed by low temperatures in high-elevation forests located near the alpine treeline. However, the vast majority of mid-latitudinal mountains included in the Mediterranean Basin (MB) such as the Pyrenees are also characterized by more periodic moisture deficits, because climate in the MB may alternate between arid and humid conditions (Lionello et al. 2006). At a synoptic scale, subtropical atmospheric high pressures from the North African arid zone and westerly circulations from central-northern Europe, together with other influences (South Asian Monsoon in summer, western Russian/Siberian High Pressure System in winter) shape the complex climate of the MB (Lionello et al. 2006). In this way, several studies have revealed distinct synoptic-scale climate areas or diverse gradients in growth-climate responses in the MB ranging from north to south (Andreu et al. 2007, Carrer et al. 2010) and from east to west (Roberts et al. 2011), sometimes along gradients over ~4000-km long. This complexity at multiple scales may result in contrasting spatial responses to climate change between populations growing in different areas of the MB (Tardif et al. 2003, Carrer et al. 2010), making tree-growth inferences from regional climate trends weakly accurate. In fact, studies concerning tree growth patterns across the MB have been showing different behaviour in the tree-ring variables during the last decades of the 20th century, some of them displaying opposite trends' sign even deriving from sites being located very close (see chapter 4 of this thesis). In these Mediterranean ecosystems, daily to seasonal precipitation changes can mediate intra and inter-annual patterns of tree growth, and summer drought can be strong enough to even interrupt tracheid formation (Nicault et al. 2001, De Luis et al. 2007). If such drought-induced growth responses also occur in high-elevation forests located at mid-latitudes of the MB remains unknown. If however true, such hydroclimatic stressors would question the reliability of temperature reconstructions from MB alpine treelines (see chapter 3 of this thesis).

This high MB climatic diversity entails complex growth-climate relationships (i.e. with different influences of more than one climatic factor) (Tardif et al. 2003, Andreu et al. 2007, Carrer et al. 2010, Büntgen et al. 2012). Temporal instability in growth-climate relationships, the so-called divergence phenomena (D'Arrigo et al. 2008), may indeed be magnified by warming-induced aridification trends as those forecasted for the MB (Lebourgeois et al. 2012), which would subsequently dampen the temperature control of tree growth. Testing the hypothesis of recently more complex growth-climate relationships in Mediterranean mountain forest ecosystems is, however, complicated due to the scarcity of high-elevation sites that are only temperature-controlled (Körner 2012). The Pyrenees constitutes the only MB mountain system where relatively undisturbed temperature-driven but possible drought-affected high-elevation forests can be found south of the Alpine arc (see chapter 3 of this thesis).

Dendroecology of Iberian *Pinus uncinata* forests: from an individual- to a population-level approach

Pinus uncinata Ram. is a long-lived, slow-growing and shade-intolerant conifer which shows a large ecological amplitude regarding topography (slope, exposure, altitude) and soil type (Ceballos and Ruiz de la Torre 1979). It is found in subalpine forests from the Alps, the Pyrenees and the Iberian System, lashed by the icy winter and its roots piercing the rocky, wind-swept land. Until 2011, we carried out dendrochronological samplings of 711 trees from 30 *P. uncinata* sites of which 27 sites were located in the Pyrenees, one site was located in the Pre-Pyrenean Sierra de Guara and two southern relict populations were located in the Iberian System (Soria and Teruel provinces). Pyrenean *P. uncinata* forests are usually low-density open-canopy stands located in steep and elevated sites forming isolated patches near the alpine treeline. The macroclimate of the Pyrenees is strongly influenced by east–west and north–south gradients with increasing Mediterranean conditions (e.g. warm and dry summers) eastwards and southwards, whereas continental conditions prevail in the Central Pyrenees, which explains the high climatic heterogeneity of this area (López-Moreno et al. 2008). The relict populations of Teruel and Soria and the Prepyrenean site Guara are subjected to typically Mediterranean conditions such as warm and dry summers. Mean annual temperature and total precipitation in the studied sites ranged from 2.0 to 4.9 °C and from 1200 to 2000 mm, respectively, with January and July as the coldest (mean -2.0 °C) and warmest (mean 12.5 °C) months respectively (Camarero 1999).

Research conducted in Pyrenean alpine treelines have dealt with tree-ring structure and formation (Camarero et al. 1998), growth trends (Rolland et al. 1998), climate-growth relationship (Gutiérrez 1991, Rolland and Schueller 1995, Camarero and Gutiérrez 2004, Creus et al. 2006, Andreu et al. 2007), tree-climate-site interactions (Tardif et al. 2003), regeneration and recruitment (Camarero et al. 2005), demographic models (Wiegand et al. 2006), effects of human abandonment of land use on recolonization (Améztegui et al. 2010) or long-term changes in the isotopic composition of tree-ring wood (Esper et al. 2010). Regarding dendroclimatic reconstructions, studies from Büntgen et al. (2008, 2010), Nicault et al. (2008; focused not only in the Pyrenees but in the whole MB), and Dorado-Liñán (2012) constitute relevant studies that try to amend the traditional scarcity in research related to Pyrenean reconstructions and fill a MB gap in the worldwide tree-ring density network (Büntgen et al. 2008).

Our study represents a step ahead relative to the former studies, since:

- Our data cover the whole geographical range of the species in the Iberian Peninsula and thus capture most of the ecological variability experienced by this species (Fig. 1). This allows evaluating how species responses to climate can vary amongst coexisting individuals regarding non-climatic drivers.
- Iberian *Pinus uncinata* tree growth is here examined following different approaches (Fig. 1): an individual-level approach to assess the potential influence of site (e.g. topography, altitude) and individual (e.g. size, sapwood) characteristics on growth, and a population-based approach to evaluate the species growth-climate relationships and to test whether these relationships are stable along time.

The Iberian *P. uncinata* forests constitute a suitable and interesting ecosystem to perform our study since:

- The Pyrenees constitutes the only Mediterranean mountain system where undisturbed temperature-driven upper treelines can be found south of the Alpine arc. Hence it is a proper location to test whether growth-climate relationships in Iberian mountain forests have recently become more complex.

- The Iberian Peninsula is located in a very sensitive area regarding climate change, being subject to diverse climatic influences (Mediterranean, continental, subtropical and Atlantic) and to variable drought severities.

- The northern Iberian mountains have two ecological drawbacks to face global-change effects. First, they constitute a mountain area east-west arranged, i.e. perpendicularly to the expected northern (or upward) migratory routes. Second, they are influenced by Mediterranean climatic conditions characterized by summer drought. Hence, these mountains are more likely to be vulnerable against climate warming and drying trends than other Mediterranean and European ranges (Schröter et al. 2005). These facts make the Iberian mountains, and specially the Pyrenees, an attractive place to study growth-climate relationships and tree-growth performance to track climate change effects.

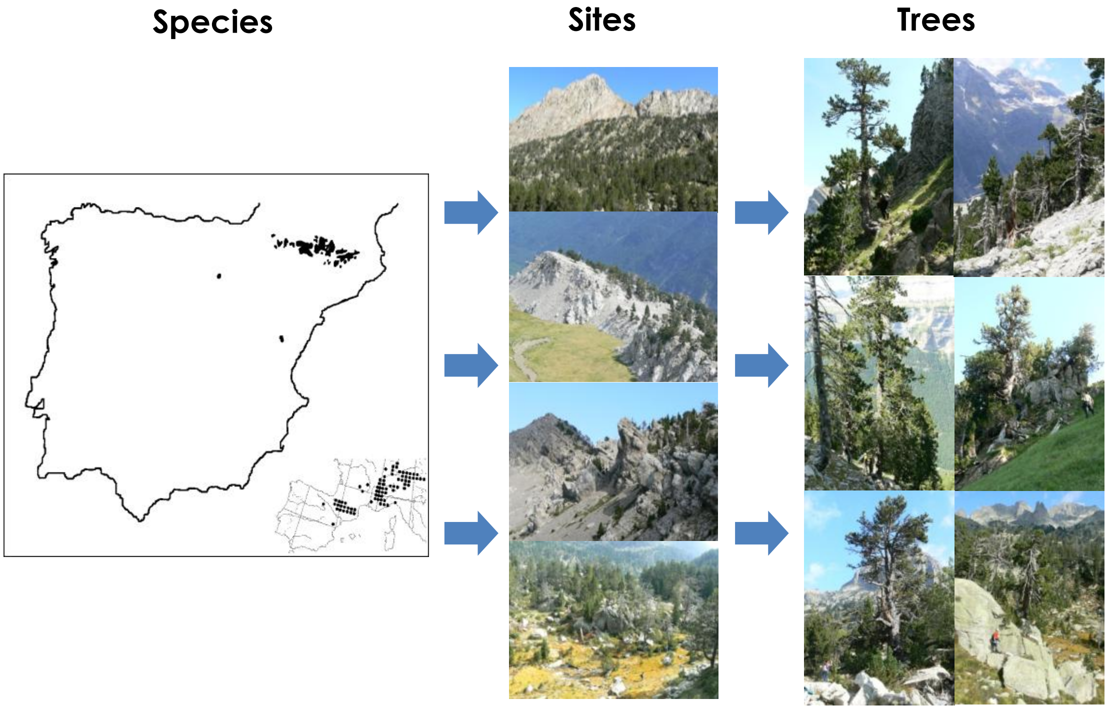

Figure 1. The study of Iberian *P. uncinata* high-elevation forests is here addressed from a species- to a tree-level approach. The map on the left shows the distribution area of the species in the Iberian Peninsula and in Europe (lower inset).

Objectives

The general objective of this thesis is to attain knowledge about Iberian *Pinus uncinata* tree-growth variability and its responses to climate at individual- and population-level scales. The specific objectives associated to the different chapters of the study are the following:

Chapter 1

- To assess the interactions between local site conditions (e.g. altitude, topography) and intrinsic tree characteristics (e.g. size, age, sapwood production) and evaluate how these factors modulated the individual growth throughout the warm 20th century.

Chapter 2

- To determine how important are those site conditions and intrinsic tree characteristics as drivers of the variability in tree-ring width indices and, in particular, in their responses to climate.

Chapter 3

- To evaluate if the growth-climate relationships changed over the last century and, if so, to test if that divergence was induced by drought even in the sampled high-elevation forests located near the alpine treeline.

Chapter 4

- To set in a Mediterranean perspective our growth trends registered in the Iberian *Pinus uncinata* distribution area by assessing spatial patterns in recent tree growth across the Mediterranean Basin.

Chapters

... When a tree is cut down and reveals its naked death-wound to the sun, one can read its whole history in the luminous, inscribed disk of its trunk; in the rings of its years, its scars, all the struggle, all the suffering, all the sickness, all the happiness and prosperity stand truly written, the narrow years and the luxurious years, the attacks withstood, the storms endured. And every young farm boy knows that the hardest and noblest wood has the narrowest rings, that high on the mountains and in continuing danger the most indestructible, the strongest, the ideal trees grow.

... Cuando se ha talado un árbol y éste muestra al mundo su herida mortal, en la clara circunferencia de su cepa y monumento puede leerse toda su historia: en los anillos y cicatrices están descritos con fidelidad todo el sufrimiento, toda la lucha, todas las enfermedades, toda la dicha y prosperidad, los años angostos y los años frondosos, los ataques superados, las tormentas sobrevividas. Y cualquier campesino joven sabe que la madera más dura y noble tiene los anillos más estrechos, que en lo alto de las montañas y en peligro constante crecen los árboles más fuertes, ejemplares e indestructibles.

Chapter 1

Sapwood area drives growth in mountain conifer forests

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Summary

It is expected that climate warming will enhance tree growth of mountain conifer forests in cold regions. However, trees have shown unstable, age-related and site-dependent growth responses to climate throughout the past century, but information on the drivers controlling such responsiveness at the site and tree scales is lacking. We evaluated whether such changing growth responses are more influenced by site features, such as altitude, or by tree features, such as size and sapwood area. We quantified the growth trends at the site and tree levels in Iberian *Pinus uncinata* forests using dendrochronology. Tree-ring width was converted to basal area increment (BAI) to assess the relationships between growth and site and tree variables over three time periods (1901–1994, 1901–1947, 1948–1994) using structural equation models. Trees were older at higher altitudes, and the amount of sapwood decreased as trees aged. BAI trends were lower in the period 1948–1994 than in the period 1901–1947, i.e. tree growth is decelerating, despite BAI values of both periods showing the reverse pattern. Sapwood area and, to a minor extent, tree age were the main positive and negative drivers, respectively, controlling BAI during the 20th century, whereas altitude played a minor role. Our results highlight the relevance of tree individual characteristics as the main drivers modulating growth responses to climate warming. We conclude that climate warming will have a lower effect on radial growth in slow-growing high elevation trees than in fast-growing low elevation trees, which produce a greater sapwood area. Trees may become relatively insensitive to climate as they age and reach a size-related functional threshold linked to reduced sapwood production.

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Introduction

Air temperatures during the late 20th century were higher than during any other period of the last 500 years and are likely to be the highest of the past 1000 years (Jones et al. 2009). In the European mountains, Diaz and Bradley (1997) reported a warming trend since the 1950s leading to some of the warmest decades of the instrumental records in the last half of the past century. The length of the growing season has also potentially increased in mountain forests of temperate and cold areas where tree growth is mainly constrained by low temperatures (Menzel and Fabian 1999, Tardif et al. 2003, Wieser et al. 2009). In these areas, regional climate models predict temperature increases by 1.4 to 5.8 °C during the 21st century (IPCC 2007). However, in a warmer scenario tree growth in mountain forests may also be affected by additional site and tree factors. In addition, potential trade-offs or relationships at the tree level between several features such as radial-growth rate, leaf and sapwood production and lifespan can explain their different individual growth responses (Loehle 1988).

Global warming and related changes such as rising atmospheric CO_2 concentrations are affecting tree growth (Soulé and Knapp 2006). Rates of radial growth are reported to have recently increased over broad areas of mountain conifer forests in Europe and North America (Graumlich 1991, Boisvenue and Running 2006). Despite these observations, other studies have suggested that warming may not consistently lead to increased growth in cold-limited forests (Lloyd and Fastie 2002, Harsch et al. 2009). Others have noted a recent site-dependent loss in growth responsiveness to the temperature rise (Briffa et al. 1998). Such contrasting growth patterns also appear among nearby forests and coexisting trees, and thus challenge our understanding of tree growth responses to climate warming (Wilmking et al. 2004). These diverse findings demand a much better understanding of the interactions between site conditions and tree characteristics at regional and local scales to disentangle how these features may modulate the individual growth responses to climate warming.

At the site level, altitude and other local conditions have been shown to control recent growth trends in mountain conifer forests (Tardif et al. 2003, Carrer et al. 2007, Littell et al. 2008). Hence, mountain forests are characterized by a high spatial variability among sites and trees in their responsiveness to climate (Bunn et al. 2005). A critical evaluation of such variability may help to disentangle the roles of local conditions such as elevation and topography (e.g. aspect) in mediating recent growth trends.

At the tree level, studies performed across altitudinal gradients have shown that growth depends on changes in sapwood area (Vertessy et al. 1995). Sapwood area and basal area increment (BAI) are tightly related in conifers (Sellin 1994, Knapic and Pereira 2005), and the former is closely linked to the growth efficiency of trees in terms of wood produced by needle area (Waring 1987). In *Pinus ponderosa* forests, size-related growth constraints explained the decline in growth efficiency which translated into a reduction of sapwood area (McDowell et al. 2007). The role of sapwood as a growth driver may depend on age-dependent changes in the stem hydraulic conductivity (Spicer and Gartner 2001). Consequently, sapwood area might modulate the growth responses of mountain conifer forests to recent climate warming.

In the case of Iberian mountain conifer forests, a rise in temperatures accompanied by an increase in climatic variability has driven trees recent growth trends (Camarero 1999, Andreu et al. 2007). In fact, the contrasting climatic conditions between the first and the second halves of the 20th century were also reflected in the radial growth patterns of *Pinus uncinata*, the dominant species in Iberian high elevation forests, which showed an increased temporal variability in growth towards the very warm last half of that century (Tardif et al. 2003). Therefore, the Iberian *P. uncinata* subalpine forests offer a valuable system to evaluate whether growth throughout the past century was modulated by local site conditions (e.g. altitude, topography) or by intrinsic tree features (e.g. size, sapwood production). In this study, we aim to evaluate these effects at the site and tree levels for three distinct periods of the 20th century (1901–1947, 1948–1994 and 1901–1994). Previously, Tardif et al. (2003) speculated on a possible warming-induced "relaxation" of the altitude-mediated control of tree growth in these forests during the 20th century. Consequently, we hypothesize that tree features, such as size and sapwood production, were the main drivers of tree growth during the 20th century in these high elevation forests and that altitude played a minor role in constraining tree growth.

Materials and methods

Study species

Pinus uncinata Ram. is a long-lived, slow-growing and shade-intolerant conifer which shows a large ecological amplitude regarding topography (slope, exposure, altitude) and soil type (Ceballos and Ruiz de la Torre 1979). Based on xylogenesis studies, spring cambial resumption in *P. uncinata* starts in May and most of the tree ring (ca. 80% of the annual width) is formed between June and July (Camarero et al. 1998). Radial growth in Pyrenean *P. uncinata* forests is enhanced by warm autumn and spring temperatures in the seasons before the growth occurs (Tardif et al. 2003).

Study sites

We sampled 27 *P. uncinata* sites located across the whole geographical range of the species in the Iberian Peninsula to capture most of the ecological variability experienced by this pine. We sampled 25 sites located in the Pyrenees and two relict populations of the Iberian System located in the Soria and Teruel provinces (Fig. 1, Table 1). Pyrenean forests are usually low density, high elevation stands with isolated trees reaching the alpine treeline (Fig. 1). The two relict populations of *P. uncinata* located in the Iberian System constitute the southern and western geographic limits of the species distribution (Ceballos and Ruiz de la Torre 1979).

The macroclimate of the Pyrenees is strongly influenced by east–west and north–south gradients with increasing Mediterranean conditions (e.g. warm and dry summers) eastwards and southwards, whereas continental conditions prevail in the Central Pyrenees (Del Barrio et al. 1990). Mean annual temperature and total precipitation in the studied sites ranged from 2.0 to 4.9 °C and from 1200 to 2000 mm respectively, with the coldest and warmest months being January (mean -2.0 °C) and July (mean 12.5 °C) (Camarero 1999). In the study region there was a rise in temperature but no significant change in precipitation during the period 1901–1994 (Supporting Information, Fig. S1).

Most of the Pyrenean sites (eighteen sites) were located within or near protected areas; therefore, these areas are not likely to have been disturbed by logging for much of the 20th century. Six sites were sampled within or near the Ordesa y Monte Perdido National Park (42° 40’ N, 00° 03’ E; established in 1918) and twelve sites were sampled in the Aigüestortes i Estany de Sant Maurici National Park area (42° 35’ N, 00° 57’ E; established in 1955) (Fig. 1).

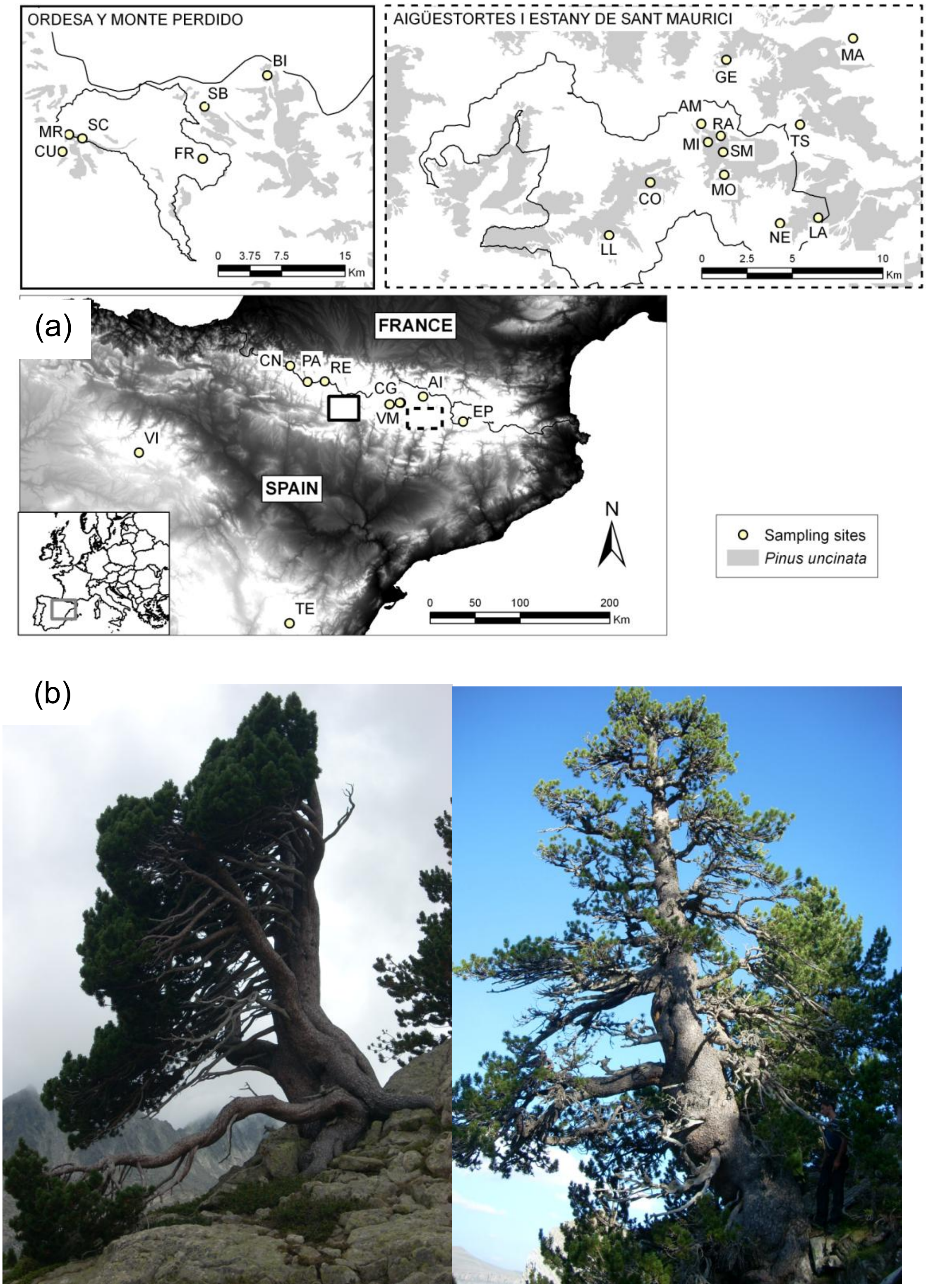

Figure 1. Sampled *Pinus uncinata* sites in the Iberian Peninsula (a, white indicates high elevation areas). The area delineated by the solid and dashed lines includes Ordesa y Monte Perdido (upper left map) and Aigüestortes i Estany de Sant Maurici National Parks (upper right map). Shaded areas in upper maps correspond to *P. uncinata* sites. The southernmost sites VI and TE are located in the Iberian System mountains. (b) Views of old *Pinus uncinata* trees in sites NE and SC (see sites codes in Table 1).

Table 1. Geographical, topographical and ecological characteristics of the sampled *P. uncinata* sites. Stands were arranged from east to west. Sites' codes are as in Figure 1. Age was determined from cores taken at 1.3 m. Values are means ± SD

Site (code)	Latitude (N)	Longitude (E / W)	Elevation (m a.s.l)	Aspect	Slope (°)	Dbh (cm)	Height (m)	Sapwood (cm)	Age (years)
Estanys de la Pera (EP)	42° 27'	1° 35' E	2360	SW	30 ± 0	65.2 ± 11.0	7.8 ± 2.0	5.5 ± 2.6	339 ± 117
Mata de València (MA)	42° 38'	1° 04' E	2019	N-NW	19 ± 10	43.2 ± 3.6	12.0 ± 3.1	5.2 ± 1.7	237 ± 72
Estany de Lladres (LA)	42° 33'	1° 03' E	2120	NW	35 ± 12	52.1 ± 9.8	8.3 ± 1.6	5.0 ± 1.9	313 ± 123
Airoto (AI)	42° 42'	1° 02' E	2300	W	47 ± 29	58.5 ± 13.5	7.4 ± 1.6	6.7 ± 2.1	288 ± 100
Tessó de Son (TS)	42° 35'	1° 02' E	2239	N-NE	42 ± 14	74.5 ± 18.8	9.3 ± 3.8	7.4 ± 4.1	346 ± 202
Estany Negre (NE)	42° 33'	1° 02' E	2451	SE	35 ± 18	71.0 ± 26.0	6.6 ± 1.9	4.4 ± 1.9	411 ± 182
Estany Gerber (GE)	42° 37'	0° 59' E	2268	W	15 ± 15	53.5 ± 14.6	6.9 ± 1.4	4.8 ± 2.2	426 ± 147
Estany d'Amitges (AM)	42° 35'	0° 59' E	2390	S-E	40 ± 21	69.0 ± 26.0	9.3 ± 3.8	5.7 ± 2.2	355 ± 106
Mirador (MI)	42° 35'	0° 59' E	2180	SE	33 ± 18	55.1 ± 25.8	7.6 ± 2.3	4.6 ± 2.0	401 ± 132
Ratera (RA)	42° 35'	0° 59' E	2170	N	40 ± 5	28.3 ± 8.1	10.4 ± 2.0	–	380 ± 146
Sant Maurici (SM)	42° 35'	0° 59' E	1933	S-SE	16 ± 15	38.2 ± 5.7	13.7 ± 1.7	4.2 ± 1.2	204 ± 23
Monestero (MO)	42° 34'	0° 59' E	2280	SE	28 ± 13	64.4 ± 16.1	9.3 ± 2.1	5.0 ± 2.4	346 ± 110
Corticelles (CO)	42° 34'	0° 56' E	2269	W-NW	24 ± 17	83.1 ± 28.8	10.7 ± 3.8	4.9 ± 2.7	509 ± 177
Barranc de Llacs (LL)	42° 32'	0° 55' E	2250	N-NW	44 ± 38	71.7 ± 20.0	10.5 ± 2.5	5.0 ± 2.5	616 ± 175
Conangles (CG)	42° 37'	0° 44' E	2106	S-SW	43 ± 15	56.0 ± 14.5	6.4 ± 2.7	4.7 ± 2.8	318 ± 117
Vall de Mulleres (VM)	42° 37'	0° 43' E	1800	N-NE	34 ± 13	69.0 ± 26.0	9.8 ± 1.8	5.2 ± 2.6	437 ± 184
Bielsa (BI)	42° 42'	0° 11' E	2000	E	88 ± 4	45.1 ± 9.4	7.7 ± 3.0	4.7 ± 1.5	270 ± 67
Sobrestivo (SB)	42° 40'	0° 06' E	2296	S	38 ± 2	61.7 ± 17.5	7.6 ± 1.7	4.1 ± 1.7	341 ± 97
Foratarruego (FR)	42° 37'	0° 06' E	2031	W	37 ± 11	49.5 ± 18.3	8.3 ± 2.9	5.5 ± 1.9	433 ± 50
Senda de Cazadores (SC)	42° 38'	0° 03' W	2247	N	49 ± 12	60.9 ± 16.5	9.4 ± 1.6	4.3 ± 2.0	337 ± 145
Mirador del Rey (MR)	42° 38'	0° 04' W	1980	SW	25 ± 10	53.3 ± 15.3	10.9 ± 4.6	–	117 ± 18
Las Cutas (CU)	42° 37'	0° 05' W	2150	S-SW	20 ± 5	33.3 ± 8.3	9.9 ± 2.5	4.4 ± 2.8	129 ± 16
Respomuso (RE)	42° 49'	0° 17' W	2350	S	70 ± 19	49.5 ± 15.1	7.6 ± 1.5	6.1 ± 4.1	280 ± 83
Pic d'Arnousse (PA)	42° 48'	0° 31' W	1940	NW	32 ± 4	65.4 ± 5.1	9.4 ± 0.7	9.0 ± 4.6	248 ± 83
Valdelinares-Teruel (TE)	40° 23'	0° 38' W	1800	SW-W	10 ± 5	63.8 ± 12.4	10.2 ± 1.8	5.8 ± 4.9	214 ± 107
Larra-La Contienda (CN)	42° 57'	0° 46' W	1750	SW	38 ± 24	46.4 ± 14.0	7.8 ± 2.2	3.8 ± 1.3	350 ± 108
Castillo de Vinuesa (VI)	42° 00'	2° 44' W	2050	W	21 ± 1	85.6 ± 23.0	9.4 ± 2.9	6.7 ± 2.4	368 ± 148

Field sampling and dendrochronological methods

From 1994 until 2010 we sampled 642 living trees following standard dendrochonological methods. At each site, from 5 to 65 dominant trees (mean ± SE = 24 ± 3 sampled trees per site) were randomly selected for sampling. The number of trees sampled per site depended on the density of trees within each sampled plot. Except for a few cases, distance between trees was sufficient to avoid capturing local effects on tree growth due to spatial autocorrelation. The geographical position of sampled trees was registered with GPS (accuracy ± 5 m).

Topographic (altitude, slope, aspect) and biometric (dbh, diameter at breast height measured at 1.3 m; tree height) variables were registered for each tree. All individuals were cored at 1.3 m using a Pressler increment borer taking two or three cores per tree (n = 1296 cores). We measured the sapwood length in the field, since the sapwood-heartwood boundary was usually evident. In some selected cores from trees of contrasting dbh and age (n = 140 cores) we checked these visual field estimates by applying bromocresol green stain on recently collected cores in the laboratory (Kutscha and Sachs 1962). Field and laboratory estimates of sapwood length were significantly related (R^2 = 0.81, $P<0.001$). The diameter, excluding bark, and the sapwood length were converted to basal area and sapwood area respectively, assuming a circular shape of the stem.

Each core was mounted and sanded with sandpapers of progressively finer grain until tree rings were clearly visible (Stokes and Smiley 1968). Then, the samples were visually cross-dated and measured to a precision of 0.01 mm using a LINTAB measuring device (Rinntech, Heidelberg, Germany). Cross-dating was evaluated using the program COFECHA, which calculates cross correlations between individual series of each core and a master chronology, obtained averaging all measured series in each site (Holmes 1983).

Tree-width series were converted to basal area increment (BAI) considering two radii per tree (inside bark) and assuming concentric circularity. BAI removes variation in growth attributable to increasing stem circumference and captures changes in growth better than linear measures such as tree-ring width (Biondi and Qeadan 2008). BAI series for dominant healthy trees usually show an early suppression phase before a rapid increase and a stable senescent phase (Duchesne et al. 2003). In the case of declining radial growth trees, BAI may show a long-term decrease before tree death (Jump et al. 2006). Sharp BAI reductions are also characteristic of stressed or dying trees (Piovesan et al. 2010). The annual BAI was calculated as follows:

$$\mathrm{BAI} = \pi\ (r_t^2 - r_{t-1}^2) \qquad (1)$$

where r_t and r_{t-1} are the stem radii in the current (year t) and previous (year t-1) years. In the cases of cores without pith, the distance to the pith was estimated by fitting a template of concentric circles with known radii to the curve of the innermost rings (Norton et al. 1987). This allowed the estimation of the missing radius length to transform it into the number of missing rings. Conversion of the radius length into rings was done using a subset of cores with pith (n = 17 cores), and considering the innermost 40 rings, by using a regression calculating the mean number of rings (*y*) for the estimated distance to the pith (x): $y = 0.0109\,x$ ($R^2 = 0.99$, $P<0.001$). In those trees in which the central core section could not be estimated because the innermost rings did not curve ($n = 250$ trees) we used the dbh of each tree to estimate the tree radius (*r*) inside bark using this formula:

$$r = (\mathrm{dbh} - (b_1 + b_2)) / 2 \tag{2}$$

where b_1 and b_2 are the widths of the bark measured in two opposite sides of the stem in the field in a subset of trees ($n = 131$). We also estimated tree age at 1.3 m for each tree based on the calculated number of missing rings and considering the core reaching the maximum number of rings for each tree. Finally, we calculated the BAI of each core and then we obtained BAI averages for each tree and site. Throughout the study we considered and compared the BAI data for three different periods to assess temporal changes. We considered mean BAI annual values (in cm^2) for the period encompassing most of the 20th century (1901–1994) or for two sub-periods of equal span including most of the first (1901–1947) and second (1948–1994) halves of the past century. We also calculated BAI trends (cm^2 yr^{-1}) based on the slopes of linear regressions between time and BAI.

Then, we examined the correlations between potential predictor variables, BAI and BAI trends, by calculating Pearson correlation coefficients between them at the site ($n = 27$) and tree ($n = 642$) levels. To summarize the relationships among topographic (altitude, aspect, slope), tree (basal area, height, tree age, sapwood area) and growth variables (BAI averages and trends for the three periods described before) we performed a Principal Component Analysis (PCA). The PCA was performed on standardized variables, and it was based on the correlation matrix among variables to avoid problems arising from different units and variances. The common within-site variability in BAI was quantified as the percentage of variance explained by the first principal component. Statistical analyses were carried out using the R package (R Development Core Team 2011).

Theoretical model of tree growth for mountain cold-constrained forests

We built a theoretical and conceptual model of tree growth based on the effects of decreasing air temperature with increasing altitude negatively affecting radial growth (Fig. 2). Such negative effects are exerted through a shortening of the growing season and a reduced rate of cambial division in cold high elevation sites (Fritts 1976, Rossi et al. 2007). Less growth, and thus reduced BAI, and decreased sapwood production are also expected as altitude increases, since stem growth is closely linked to sapwood area (Vertessy et al. 1995). Tree growth and size (basal area, height) will also be comparatively lower in high elevation stands (Yokozawa and Hara 1995, Petit et al. 2010). Several studies have also revealed that sapwood and basal area covary following allometric functions in conifers, and that sapwood area is closely linked to the total cross-sectional area of living branches and to total needle area (Sellin 1994, Longuetaud et al. 2006), despite some studies showing that growth does not only depend on the sapwood amount (Yang and Murchison 1992). In addition, BAI and sapwood area decrease as trees age (Spicer and Gartner 2001). Furthermore, the negative relationship between tree lifespan and growth efficiency reported for several species may also explain this age-related growth decline (Martínez-Vilalta et al. 2007, Black et al. 2008). Finally, we also expect a positive association between radial and height growth and hypothesize that BAI will increase as tree height augments for trees with similar age (Ryan et al. 1997).

We also assumed that topographical variables (aspect, slope) may also affect BAI and postulate that trees will grow less in northern-oriented sites with steep slopes than in southern-oriented sites with gentle slopes. Furthermore, in previous studies we found that mean tree age in *P. uncinata* stands usually increases with altitude (Camarero and Gutiérrez 1999). This positive altitude-age association may be due to a low growth rate and extended lifespan in these environmentally harsh sites (Bigler and Veblen 2009). Hence, we also speculate that growth will also be negatively affected by the increased longevity of trees at high altitudes as compared with those at low altitudes (Rossi et al. 2008).

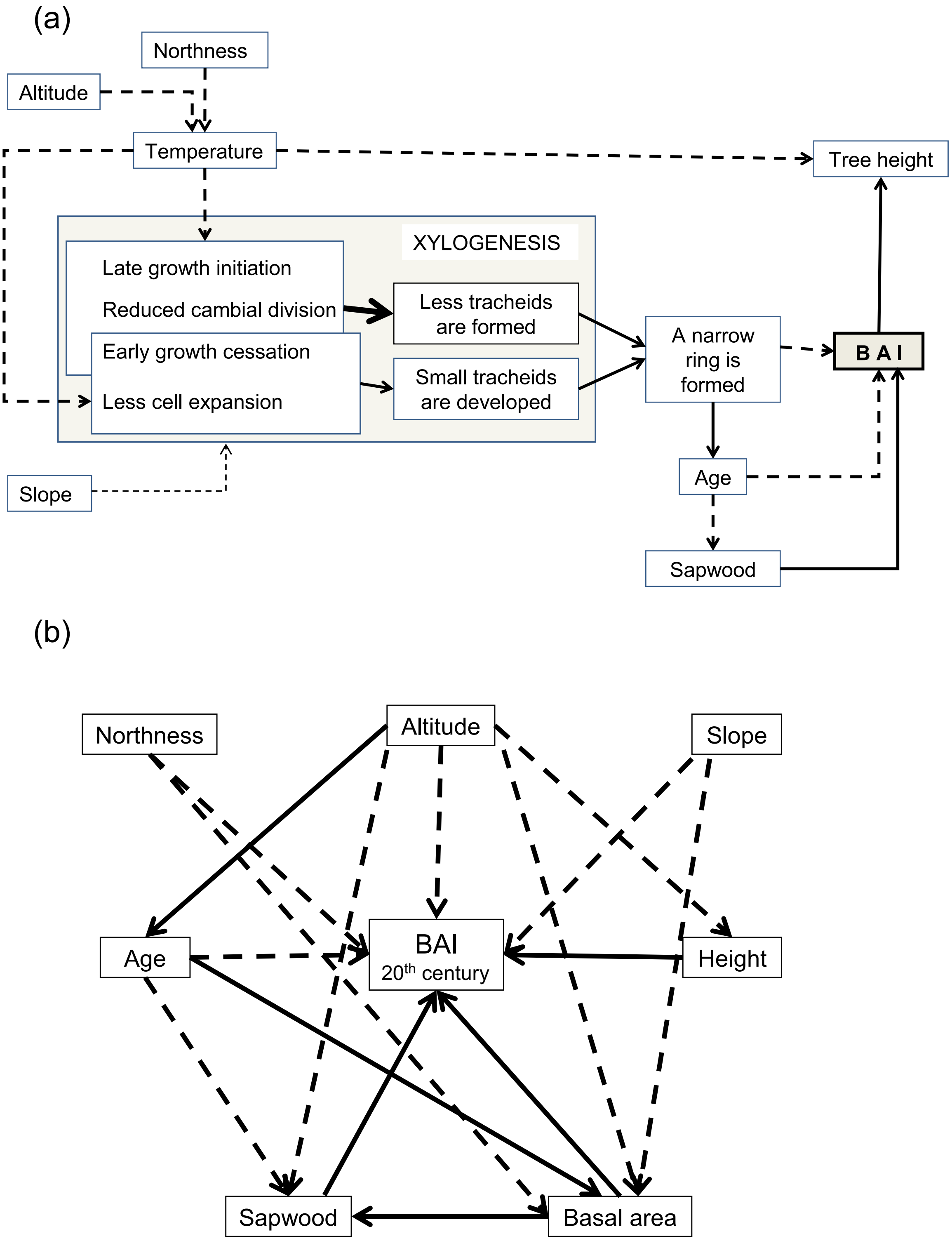

Figure 2. Proposed (a) theoretical model of basal area increment (BAI) based on hypotheses and relationships among altitude, temperature and growth and (b) conceptual model derived from it and ajusted according to previous knowledge of environment-growth relationhsips in *Pinus uncinata*. Positive and negative effects are indicated by solid and dashed lines, respectively.

Structural Equation Models

Structural Equation Models (SEM) were calculated using the program EQS (Bentler and Wu 2002) and used as multivariate tools to statistically evaluate the postulated theoretical model of tree growth, i.e. to determine the main factors potentially driving changes in BAI during the twentieth century for the three periods analysed (1901–1994, 1901–1947 and 1948–1994). First, we specified a theoretical model based on *a priori* assumed relationships among variables (Fig. 2) and on the previous knowledge and published works on growth of mountain conifer species (see the previous section). Second, we tested if the variance-covariance matrix obtained from observational data significantly differed from the matrix imposed by the hypothetical model (Grace 2006). SEMs are able to deal with the interdependence of variables and to decompose total effects in direct and indirect types, and they allow comparison of alternative models using indices of goodness of fit (Mitchell 1992). To estimate the standardised path coefficients, which quantify the strength of the associations among variables, we used a robust Maximum Likelihood method since all variables excepting BAI deviated from normality even after log-transformation (Bentler and Wu 2002).

The use of several indices to evaluate the model fitness provides a robust assessment of the fitted SEM (Jöreskog 1993). Hence, the models were evaluated using the chi-square (χ^2) test and its related probability level (*P*), as well as several complementary goodness-of-fit indices (AGFI, Adjusted Goodness-of-Fit Index; RMSEA, Root Mean Square Error of Approximation; AIC, the Akaike Information Criterion). Values close to zero for the χ^2 and RMSEA statistics and values close to one of the AGFI index would indicate that the evaluated models are consistent with the observed data. Lower AIC values correspond to more parsimonious models. In relative terms, models with low AIC and high *P* values associated with χ^2 correspond to better fits than models with the reverse characteristics. In contrast to traditional significance testing, it is usually preferable to obtain non-significant χ^2 values which indicate that the predicted model is congruent with the observed data. We also displayed the proportion of observed variance of dependent variables (R^2) and the measurement errors of tree variables.

Results

BAI patterns and trends at the site and tree levels

All sampled living trees were established before the 20th century, with maximum ages reaching 741 years in site GE. The mean BAI per tree for the period 1948–1994 (mean ± SE: 10.7 ± 0.4 cm^2) was significantly higher (F = 4.56, P = 0.03) than the mean value for the period 1901–1947 (10.0 ± 0.3 cm^2) (Table 2). However, the BAI trends of both sub-periods showed the reverse pattern and differed among periods being significantly (F = 39.2, P < 0.001) lower in 1948–1994 (mean ± SE: -0.05 ± 0.01 cm^2 yr^{-1}) than in 1901–1947 (0.02 ± 0.01 cm^2 yr^{-1}) (Table 2).

Table 2. Basal-area increment values and trends at the three level for three selected periods of the 20th century. Values are means ± SD

Site	No. trees / radii	Basal area increment (cm^2)			Trends in basal area increment (cm^2 yr^{-1})		
		1901–1994	1901–1947	1948–1994	1901–1994	1901–1947	1948–1994
EP	20 / 39	13.4 ± 7.8	12.2 ± 7.6	14.5 ± 8.4	0.04 ± 0.07	-0.03 ± 0.10	0.02 ± 0.11
MA	10 / 20	7.6 ± 2.1	7.4 ± 1.9	7.8 ± 3.3	-0.01 ± 0.06	-0.01 ± 0.10	-0.13 ± 0.13
LA	36 / 74	10.3 ± 5.5	10.2 ± 6.2	10.4 ± 5.4	-0.02 ± 0.08	-0.01 ± 0.13	-0.12 ± 0.19
AI	16 / 31	21.5 ± 10.3	19.7 ± 9.7	23.3 ± 11.6	0.06 ± 0.11	0.16 ± 0.17	-0.11 ± 0.19
TS	10 / 17	13.7 ± 11.2	13.8 ± 10.7	13.6 ± 12.5	-0.02 ± 0.11	-0.03 ± 0.19	-0.12 ± 0.15
NE	46 / 86	10.3 ± 7.5	9.8 ± 7.8	10.7 ± 7.5	0.01 ± 0.09	0.05 ± 0.14	-0.07 ± 0.24
GE	41 / 79	7.0 ± 4.1	6.5 ± 4.5	7.4 ± 3.9	0.01 ± 0.05	0.03 ± 0.08	-0.02 ± 0.09
AM	25 / 56	10.7 ± 7.0	10.4 ± 7.3	11.1 ± 6.8	0.01 ± 0.06	0.02 ± 0.11	-0.06 ± 0.15
MI	33 / 85	8.2 ± 7.0	8.4 ± 7.1	8.0 ± 7.1	-0.01 ± 0.05	0.02± 0.07	-0.06± 0.10
RA	5 / 13	6.3 ± 3.1	7.2 ± 4.5	5.4 ± 2.7	-0.05 ± 0.07	-0.06 ±0.14	-0.07 ± 0.06
SM	20 / 40	5.9 ± 2.7	6.8 ± 3.2	5.0 ± 2.4	-0.04 ± 0.03	-0.06 ± 0.05	-0.05 ± 0.08
MO	30 / 76	16.1 ± 9.9	16.2 ± 9.8	16.0 ± 10.6	-0.01 ± 0.10	0.04 ± 0.19	-0.08 ± 0.25
CO	25 / 43	11.1 ± 7.6	10.8 ± 6.9	11.4 ± 8.8	0.01 ± 0.07	-0.01 ± 0.08	-0.04 ± 0.12
LL	17 / 17	11.1 ± 7.8	10.9 ± 8.0	11.5 ± 8.1	0.01 ± 0.08	0.03 ± 0.15	-0.11 ± 0.20
CG	25 / 54	12.1 ± 7.5	10.5 ± 6.7	13.7 ± 8.9	0.06 ± 0.10	0.02± 0.18	0.05 ± 0.21
VM	12 / 23	11.6 ± 9.9	11.6 ± 10.1	11.7 ± 10.0	-0.01 ± 0.05	-0.02 ± 0.07	-0.06 ± 0.13
BI	11 / 20	7.3 ± 4.2	6.9 ± 4.2	7.5 ± 4.4	0.01 ± 0.04	-0.05 ± 0.12	-0.02 ± 0.07
SB	53 / 95	11.1 ± 7.4	12.2 ± 9.5	10.0 ± 6.0	-0.05 ± 0.11	-0.02 ± 0.16	-0.10 ± 0.12
FR[1]	12 / 25	–	5.5 ± 2.4	–	–	-0.06 ± 0.08	–
SC	65 / 119	10.0 ± 5.7	10.4 ± 5.9	9.6 ± 5.8	-0.03 ± 0.06	-0.03 ± 0.16	-0.09 ± 0.12
MR	17 / 34	3.8 ± 2.3	2.2 ± 1.2	5.3 ± 3.8	0.06 ± 0.06	0.03 ± 0.04	0.05 ± 0.11
CU	10 / 20	10.2 ± 3.5	6.4 ± 2.9	13.2 ± 4.8	0.15 ± 0.09	0.19 ± 0.08	0.04 ± 0.13
RE	20 / 47	8.9 ± 5.1	8.4 ± 4.9	9.4 ± 5.4	0.01 ± 0.03	-0.02 ± 0.06	0.01 ± 0.08
PA	8 / 16	14.4 ± 6.4	13.2 ± 6.3	15.1 ± 7.0	0.06 ± 0.14	0.04 ± 0.40	0.19 ± 0.14
TE	35 / 68	14.3 ± 6.5	11.5 ± 5.6	15.8 ± 8.1	0.05 ± 0.11	0.19 ± 0.46	-0.11 ± 0.21
CN	25 / 57	5.7 ± 2.4	5.5 ± 2.6	5.6 ± 2.7	0.01 ± 0.04	-0.02 ± 0.05	0.08 ± 0.08
VI	24 / 42	11.7 ± 5.2	11.4 ± 5.3	12.0 ± 5.5	0.01 ± 0.07	-0.06 ± 0.14	0.02 ± 0.18

[1] Site FR had only 3 living trees covering the period 1901–1994 and it was excluded in further analyses.

At the site level, three sites showed positive and significant (*P*<0.05) BAI trends in the 1901–1947 sub-period and one site in the 1948–1994 sub-period, and most sites (38%) showed negative BAI trends in both analysed sub-periods. Approximately 32% of sites showed positive BAI trends followed by negative ones for the 1901–1947 and 1948–1994 sub-periods, respectively, whereas 15% of sites showed the reverse pattern and the remaining 15% of sites showed positive trends for these sub-periods. At the tree level, 28% of the individuals presented negative BAI trends in the 1901–1947 and 1948–1994 sub-periods, whereas 36% showed positive and negative BAI trends in these sub-periods, in that order. At the individual level, 11% of all trends were negative and significant in the 1901–1947 sub-period and 22% in the 1948–1994 sub-period, while 12% and 8% were positive and significant for the aforementioned intervals. Lastly, 18% of trees presented negative trends followed by positive ones and 18% of trees showed positive trends throughout the 20th century.

The distribution of BAI values at the tree level did not differ among sub-periods but their trends were mostly higher in 1901–1947, when 53% of trees had positive BAI trends, than in 1948–1994 when only 36% of trees presented positive BAI trends (Fig. 3a). Only in one site with relatively young trees (site CU) did we find a trend towards showing more positive BAI values in the later half compared to the early half 20th century, whereas in seven sites the distributions of BAI trends differed between both sub-periods (Fig. S2). The BAI values of the two studied sub-periods were significant and positively related at the tree level (r = 0.85, P<0.001), whereas the BAI trends were inversely related (r = -0.28, P<0.001) (Fig. S3).

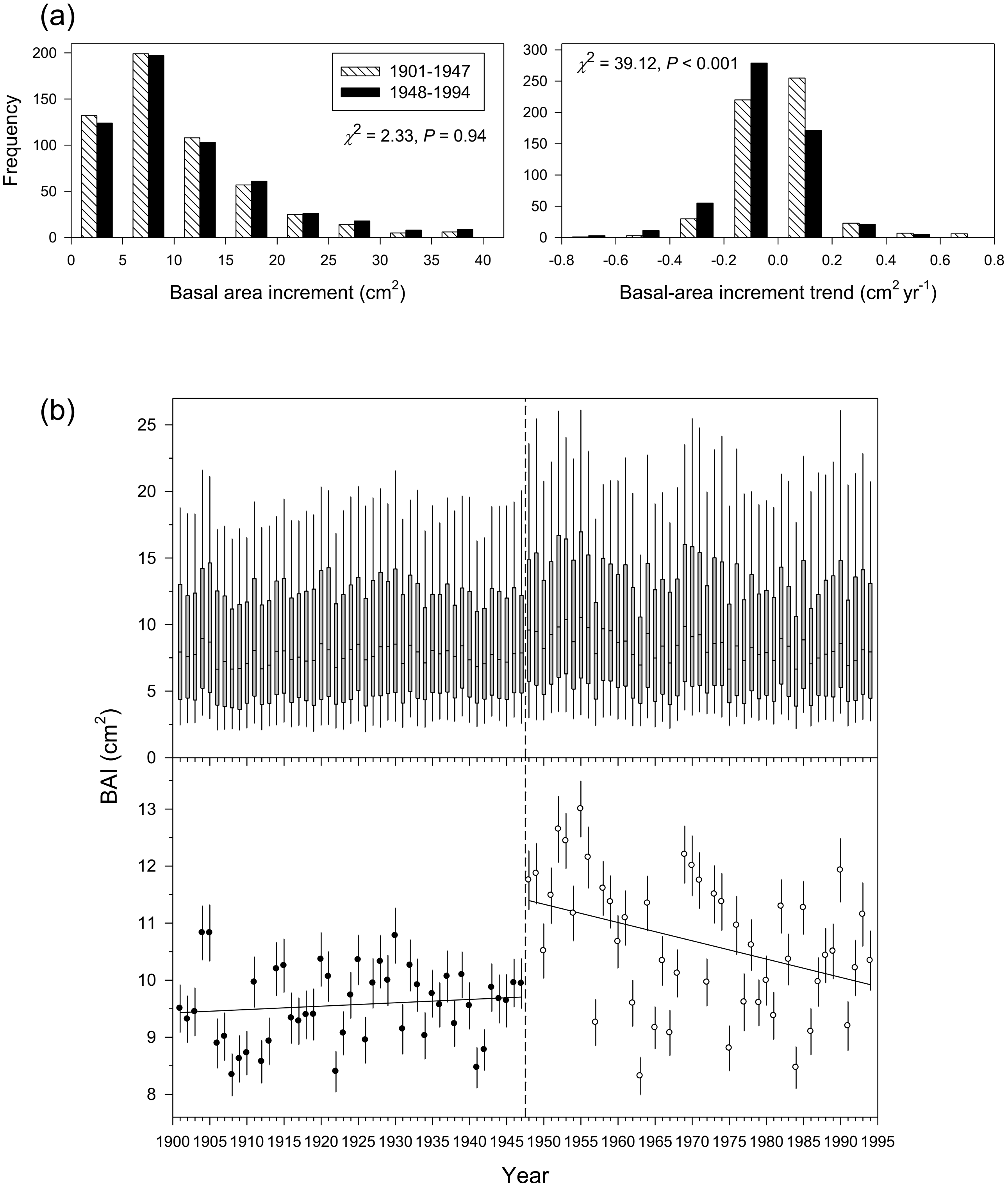

Figure 3. Comparisons and related statistics (X^2, *P*) between the frequency of basal area increment and its linear trends for the sub-periods 1901–1947 and 1948–1994 (*n* = 642 trees) (a) and temporal changes in BAI during the study period (1901–1994, box plots of annual BAI vales) and the two sub-periods (lower graphs, mean annual BAI values and corresponding linear trends) (b).

We found that the variability of BAI at the site level, assessed as the mean percentage of variance accounted for by the first principal component (PC1) of BAI of trees living within each site, has significantly (Mann-Whitney U = 120.0, P = 0.012) increased in 1948–1994 (mean 42%) compared with 1901–1947 (mean 36%), and such an increase was observed in 81% of all sites (Supporting Information, Table S1). Exceptions to such rising trend were observed in sites dominated by relatively young trees (e.g. site MR), the two southernmost sites located in the Iberian System mountains (sites TE and VI) and two Pyrenean sites (sites BI and RE) (Table S1). Furthermore, this common BAI variability was positively related with sapwood area at the site level (Fig. 4a). Such positive association between sapwood area and BAI was also observed at the tree level for all sites (Fig. 4b).

Drivers of BAI at the site and tree levels

At the site level, BAI was positively related to sapwood and basal areas, while altitude affected negatively and significantly BAI trends in the period 1948–1994 (Table S2). No variable satisfactorily explained the different BAI trends among sites (results not shown). At the tree level, BAI for any period was strongly and positively related to sapwood and basal area and tree height, whereas age had a significant negative effect on BAI only in 1948–1994 (Table S2). Contrastingly, age negatively influenced BAI trends in the period 1901–1947, while sapwood area exerted a positive influence on BAI trends in the same period. The linear regressions fitted to BAI-sapwood area relationships for both sub-periods presented confidence intervals which did not overlap (1901–1947, mean ± SD: 0.0088 ± 0.0005; 1948–1994, 0.010 ± 0.0005). This indicates that, despite the declining BAI trends of the late 20th century, the BAI increase as a function of sapwood area increment was proportionally higher in 1948–1994 than in 1901–1947 at tree level (Supporting Information, Fig. S4). The first and second principal components of the PCA explained 30.3% and 14.9% of the total variability among trees, and they were mainly related to changes in BAI, basal and sapwood areas (PC1) and to BAI trends (PC2), respectively. Hence, the PCA confirmed the positive links between BAI and the basal and sapwood areas.

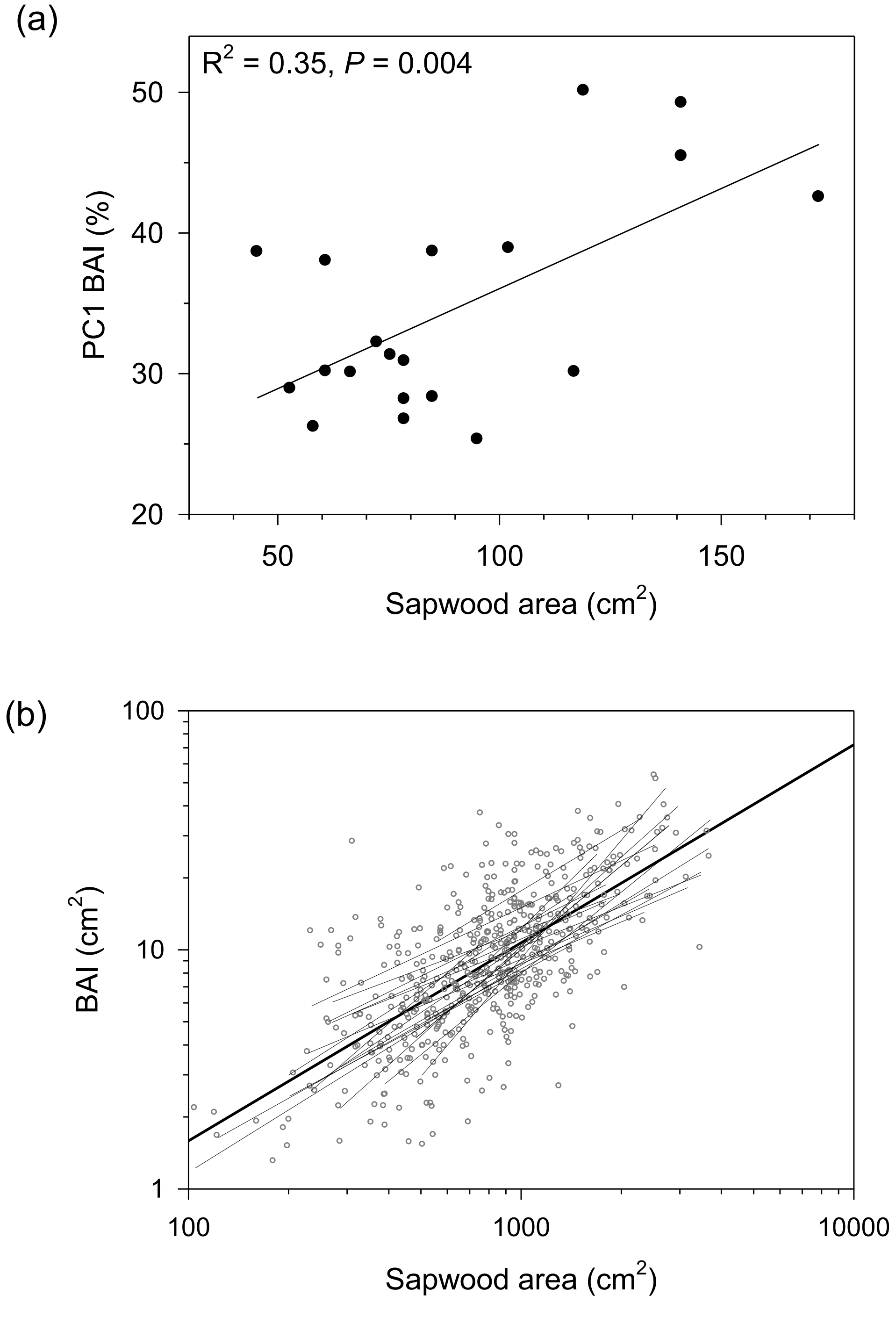

Figure 4. Sapwood is the main driver of variability in basal area increment among (a) and within sites (b), i.e. among trees. The common within-site BAI variability was quantified as the percentage of variance accounted for by the first principal component (PC1, upper graph). The lowermost graph shows all individual tree values (symbols), the linear regression for all trees (thick line) and the site regressions (thin lines). Note the log-log scale in the lowermost graph.

Structural equation models of BAI

The accepted SEMs show that BAI was predominantly positively related to the sapwood area and, to a minor extent, negatively influenced by age. Whereas the associations of BAI with altitude and height were weak (Fig. 5). Sapwood area was mainly controlled by changes in basal area and, secondarily, in a negative way, by tree age. Basal area was mainly driven by tree age. The accepted SEMs for the two sub-periods also showed satisfactory goodness-of-fit indices, as did the model for the 1901–1994 period (1901–1947, X^2 = 4.05, *P* = 0.26, AGFI = 0.98, AIC = 40.05, RMSEA = 0.02; 1948–1994, X^2 = 3.46, *P* = 0.33, AGFI = 0.99, AIC = 39.46, RMSEA = 0.02). The percentage of BAI variability explained increased from 40% in 1901–1947 to 47% in 1948–1994 because the positive influence of sapwood area on BAI was higher in the second than in the first analysed sub-periods, whereas the negative effect of age on BAI also became more important (Table 3).

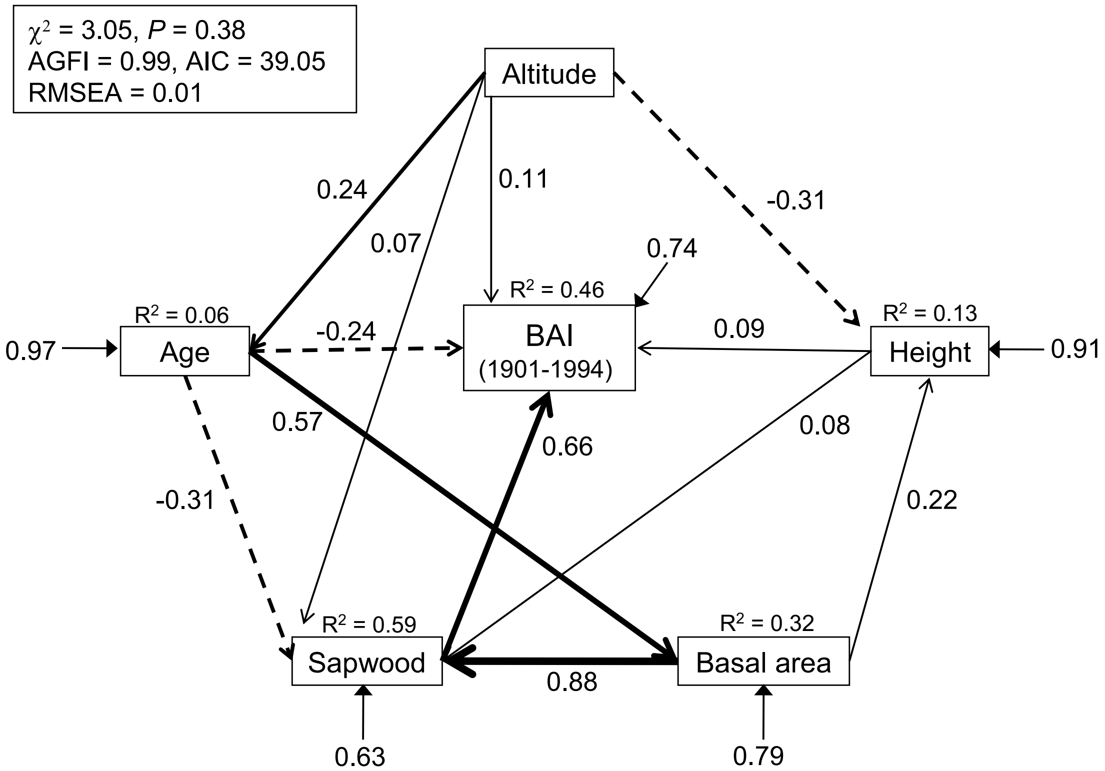

Figure 5. Selected structural equation model of basal area increment (BAI) as a function of several variables at the tree level and for the period 1901–1994. Goodness of fit statistics appear in the upper part. A non-significant (*P*>0.05) χ^2 value indicates that the predicted model is congruent with the observed data. Positive and negative effects are indicated by solid and discontinuous lines respectively. Arrow widths are proportional to the absolute value of standardized path coefficients (numbers near arrows) which measure how strongly a variable is related another one. Only significant (*P*<0.05) coefficients are displayed. R^2 is the observed variances of dependent variables explained by the model. The numbers located before the tree variables (age, height, sapwood area, basal area) are the measurement errors.

Table 3. Standardized path coefficients affecting basal area increment (BAI) for the structural equation models fitted to the sub-periods 1901–1947 and 1948–1994 (see also Fig. 5). The amount of explained variance (R^2) of BAI is presented in the lowermost line. All coefficients were significant (P<0.05)

Variables	Period	
	1901–1947	1948–1994
Sapwood area	0.59	0.68
Height	0.15	0.04
Altitude	0.14	0.09
Age	-0.18	-0.27
R^2 (%)	0.40	0.47

Discussion

Sapwood area was the main driver of recent decelerating growth trends in Iberian mountain *P. uncinata* forests. Trees which produced more sapwood area also showed a higher BAI. Furthermore, this association between sapwood and wood production has increased in the last decades of the past century. In Iberian *P. uncinata* forests BAI increased at higher rates in the first than in the second half of the 20th century, despite mean BAI being higher in the later sub-period. Such deceleration in BAI is not consistent with a widespread warming-related enhancement of growth during the late 20th century in mountain conifer forests (Graumlich 1991, Boisvenue and Running 2006). The reduction in the growth rates may be caused by the fact that trees reach the senescent phase when BAI stabilizes (Duchesne et al. 2003). The inverse relationship between age and growth rate has been widely documented in several tree species (Johnson and Abrams 2009). However, despite declining radial-growth rates with age, trunk volume or whole-crown mass augment as trees get older (Sillett et al. 2010). The effects of tree age on BAI were negative in both analysed sub-periods of the 20th century. This agrees with numerous studies demonstrating how sapwood area decreases as trees age (Hazenberg and Yang 1991, Sellin 1994, Spicer and Gartner 2001). Nevertheless, the negative influence of age on BAI is becoming stronger based on our SEMs. The increasing influence of age on BAI can be mediated by changes in sapwood area, i.e. older trees produced proportionately less sapwood area than younger ones in the late 20th century. Since trees whose ages were estimated using cores without pith were at least 30% of all sampled individuals, further research is on course to get better estimations of tree age, which would provide a more robust test of our ideas.

Why is radial growth becoming increasingly linked to sapwood area and tree age than before? The increasing length of the hydraulic pathway as trees age and accumulate biomass may be one of the answers, despite the fact that any potential loss in conductivity may be partially offset by decreased leaf-to-sapwood area ratios (Magnani et al. 2000, Zaehle 2005). Indeed, trees with different sapwood areas may also modulate their sapwood hydraulic conductivity and growth rates by keeping relatively stable values of water transport efficiency (Medhurst and Beadle 2002). However, the ageing of conductive structures and the alteration of hydraulic networks of old trees and big stems (Martínez-Vilalta et al. 2007, McCulloh et al. 2010), and the harsh climatic conditions imposed by high altitudes may also contribute to explain a sharp decrease in hydraulic conductivity and sapwood production as trees grow and age, thus leading to sapwood-mediated declining growth trends. The harsh environmental conditions in high-elevation forests (low air and soil temperatures, frequent freeze-thaw events, elevated radiation and high wind speed; see Barry 2008) are consistent with the finding that trees tend to be older at higher elevations plausibly because of a reduction in radial growth rates and increased longevity (Bigler and Veblen 2009).

A biophysical explanation of our results may also be found in the fact that as altitude increases, air and stem temperatures decrease, producing an increment in water viscosity and hence in the sap flux resistance (Grace 1983). This, together with the windy conditions in high altitude forests leading to drying effects, may cause an enhanced sapwood area to compensate this hindered sap flux in high altitude forests (Gates 1980, Gutiérrez et al. 1991). Therefore, rising temperatures along the 20th century may have induced a decrease in water viscosity, leading to enhanced sap flux and a reduction in sapwood production leading to slowing down growth rates in the second half of the century. Mechanistic approaches based on physiological measures such as long-term estimates of water-use efficiency should further test this idea. For instance, the increasing atmospheric CO_2 concentration may stimulate tree growth through enhanced water use efficiency (Körner et al. 2007). However, rising CO_2 does not imply enhanced BAI as has been observed in many sites where regional climatic factors (e.g. rising temperatures) and tree features (e.g. vigour) were the major drivers of growth (Peñuelas et al. 2010, Linares and Camarero 2011).

Our findings suggest that any potential climate-induced change of BAI will be mainly driven by sapwood production, which is mediated by tree age and, in a lower extent, by altitude. Since slow-growing high elevation trees get older than fast-growing low elevation trees we expect differential age-mediated BAI responses along the altitudinal gradient. Both xylogenesis studies and dendrochronological assessments of growth-climate relationships indicate that wood formation and growth responsiveness to climate are age-dependent (Carrer and Urbinati 2004, Rossi et al. 2008) and modulated by site conditions (Tardif et al. 2003 and chapter 2). Photosynthetic rates can also decrease as trees age (Yoder et al. 1994). Therefore, an increasing size-mediated constraint of xylogenesis, photosynthesis and hydraulic conductivity in old trees, usually located at high altitudes, would cause a more intense reduction of their growth and sapwood production than in low elevation younger trees. Hence, high elevation trees with intrinsically low growth rates will produce less sapwood and will live longer than the fast-growing trees that dominate downslope localities. Furthermore, forest density cannot explain this pattern as in the open, high elevation stands most sampled trees were old and isolated individuals. Thus, we expect a minor effect of tree-to-tree competition on growth trends of these subalpine forests. Concurrently, in similar *Pinus ponderosa* forests size-related growth constraints explained the decline in growth efficiency assessed either as stemwood production per unit basal area or as sapwood area (McDowell et al. 2007).

The tight association between BAI and sapwood area suggests that climate is the main driver of changes in growth and in sapwood amount in the uppermost treeline (Paulsen et al. 2000, Ettinger et al. 2011). Some studies indicate that climate warming is responsible for an observed growth enhancement of high-elevation trees in the last decades (Wieser et al. 2009). Others have projected more pronounced growth reductions for high than for low elevation conifer populations in mesic areas (Chen et *al*. 2010). Tardif et al. (2003) suggested that the rising temperatures of the past century will “relax” the altitude-mediated temperature constrains on growth, which will become more dependent on local factors. Overall, our data suggests that a more realistic projection of future growth and productivity responses of mountain forests to climate warming will be strongly affected by individual tree features (e.g. sapwood area) and secondarily by local factors (e.g. topography) modulating or buffering the regional effects of climate stress on growth (Case and Pederson 2005).

Our work complements other studies performed across altitudinal gradients in hardwood tree species showing that growth depends on changes in sapwood area (Vertessy et al. 1995). In contrast to previous research highlighting the intensity of competition for light as a main driver of tree growth along altitudinal gradients (Coomes and Allen 2007) our mainly low density stands rule this out as a factor. Finally, our findings indicate that once trees reach a maximum age- or size-related functional threshold linked to a stagnant sapwood production they will become relatively insensitive to climate variability (Voelker 2011).

We found that age-related changes in sapwood area were the main drivers of BAI in mountain *P. uncinata* forests. This finding and the temporal instability detected when comparing BAI values along the 20th century confirms that ecological research on climate–growth relationships should always involve detailed information at the individual level. Our results indicate that actively growing trees producing more sapwood area, and probably presenting a low leaf-to-sapwood area ratio, will show the highest growth response in the forecasted warmer climatic conditions in cold mountain conifer forests.

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Supporting Information

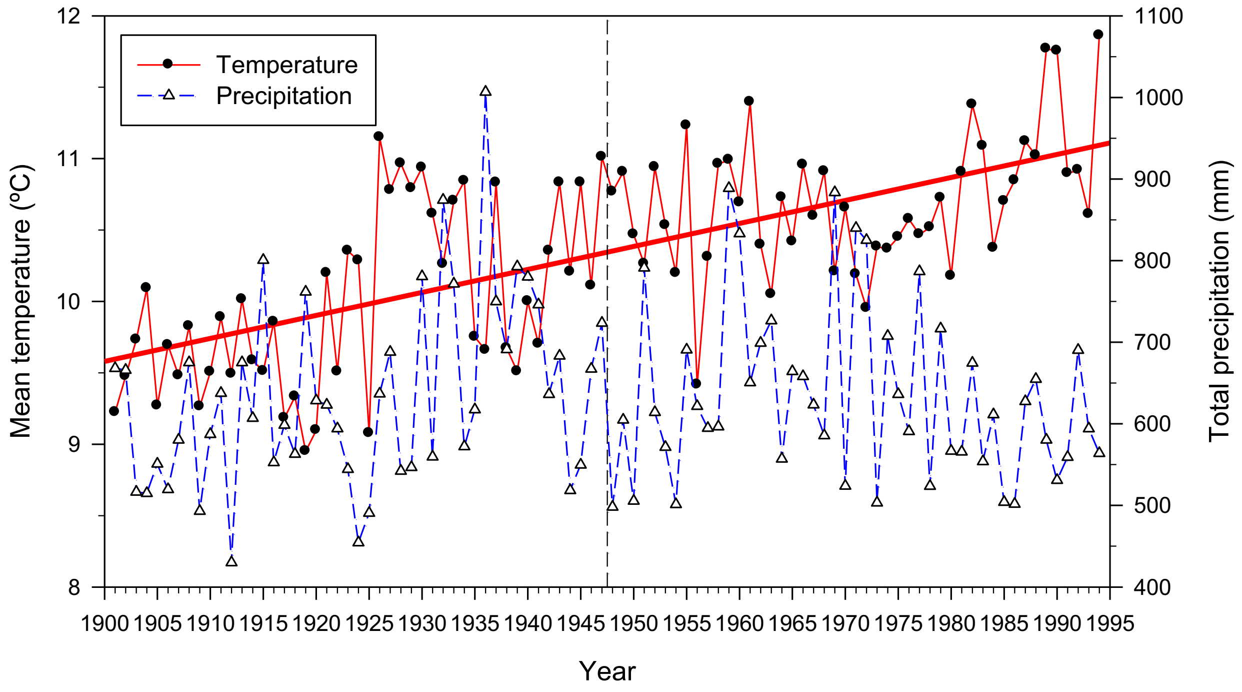

Figure S1. Trends in annual mean temperature and total precipitation in the study area for the period 1901–1994. The positive trend of temperature (thick line) was statistically significant ($R^2 = 0.45$, $P < 0.001$), whereas precipitation did not show any significant trend ($R^2 = 0.003$, $P = 0.61$). The dashed vertical line separated the two studied sub-periods based on BAI data (1901–1947 and 1948–1994). Climatic data were based on homogeneous datasets of gridded (0.5° resolution) climatic data (only grids encompassing the study sites) produced by the Climate Research Unit (CRU 2008).

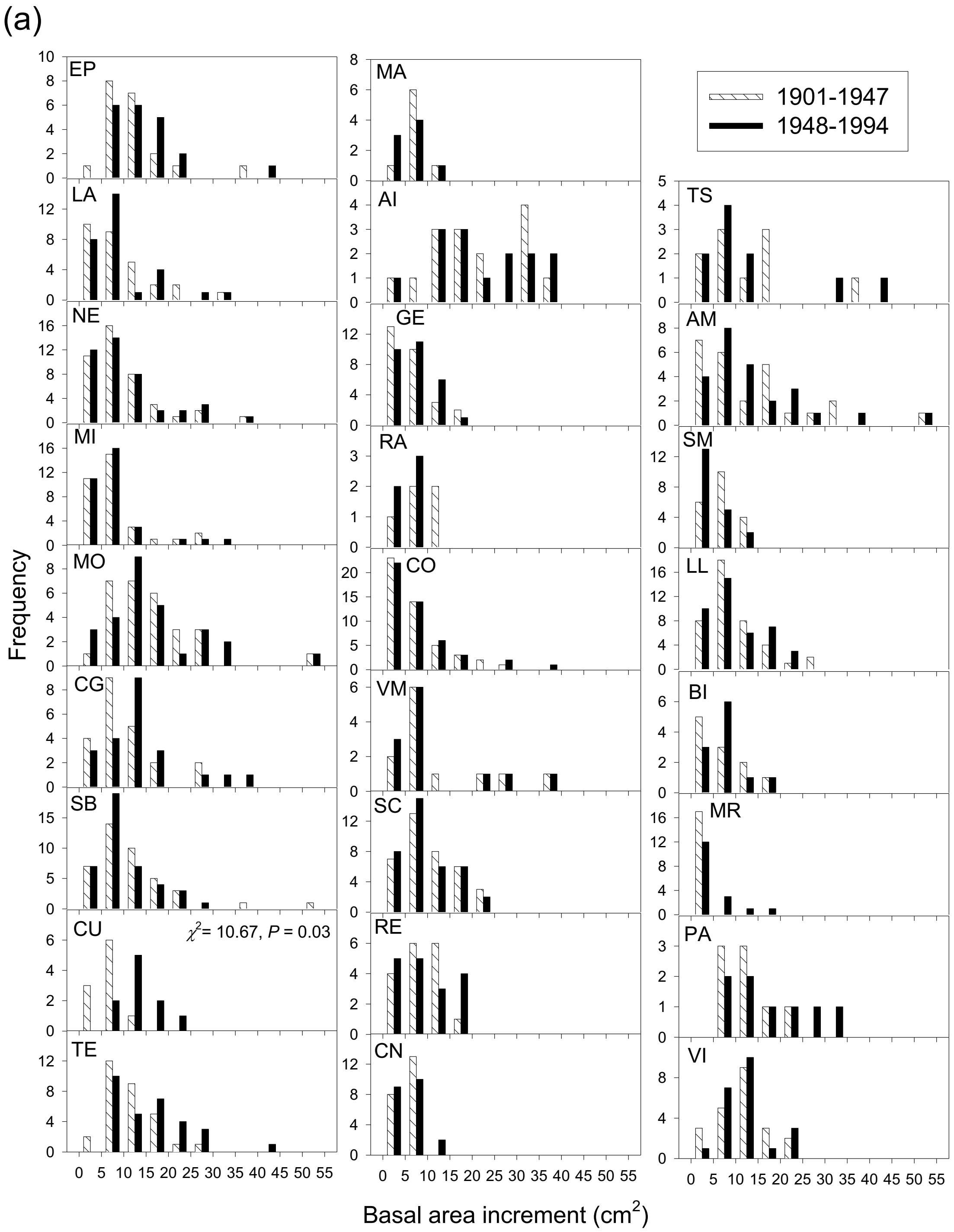

Figure S2 (legend in next page).

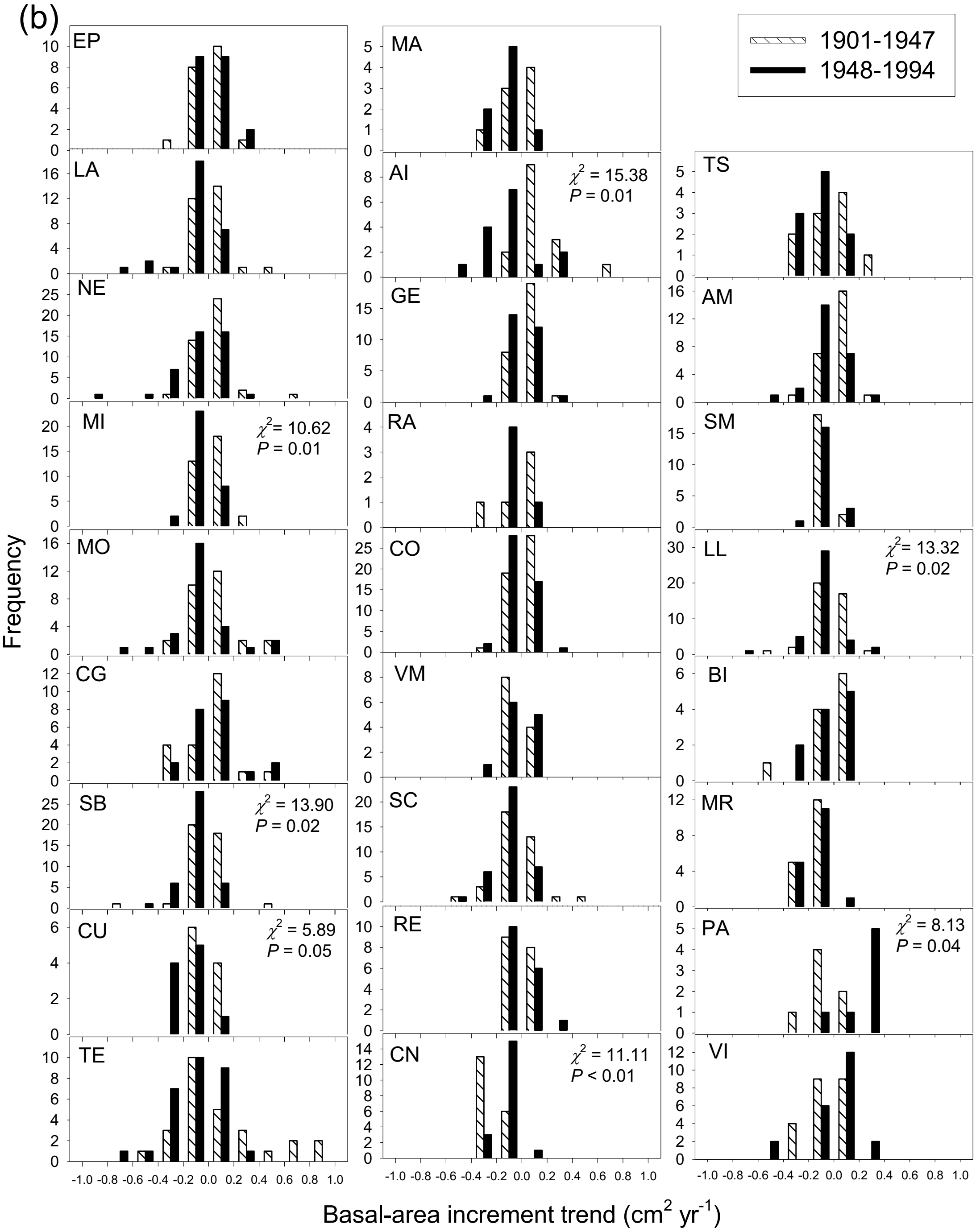

Figure S2. Comparisons for all sampled sites and related statistics (χ^2, *P*) between the frequency of basal area increment (a) and its linear trends (b) for the sub-periods 1901–1947 and 1948–1994. Statistics are displayed only in sites with significant (P < 0.05) differences between both sub-periods. Site FR was excluded in these analyses because all trees sampled there died before 1994. See sites' codes in Table 1.

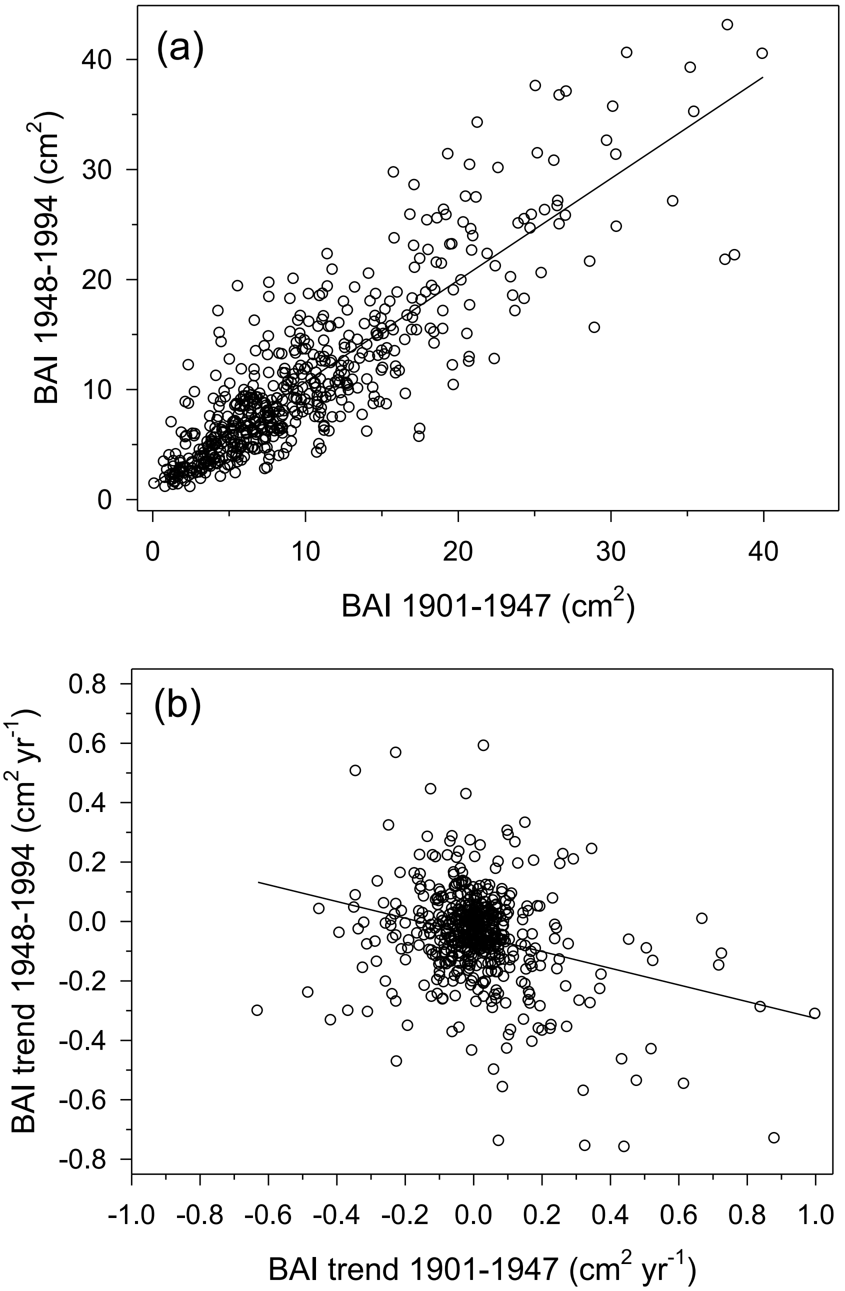

Figure S3. Relationships between mean basal area increment (BAI) (a) and its trends (b) at the tree level for the sub-periods 1901–1947 and 1948–1994.

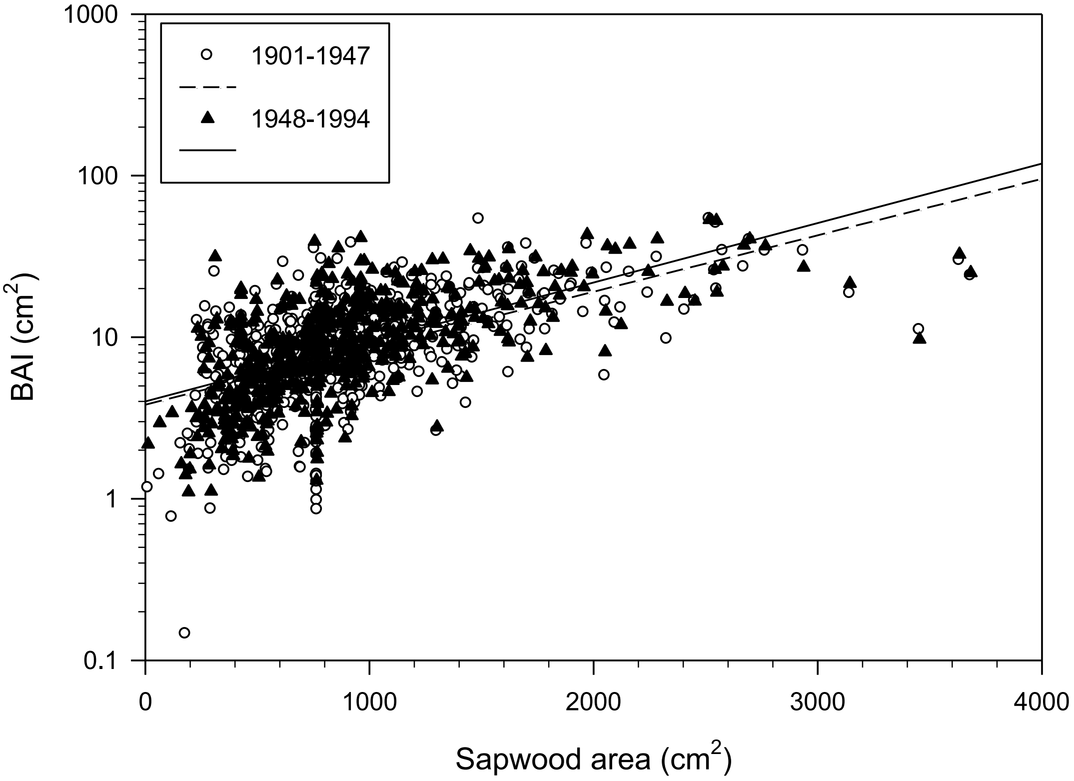

Figure S4. Associations between basal area increment (BAI) and sapwood area for the two analysed sub-periods: 1901–1947 ($R^2 = 0.36$, $P < 0.001$) and 1948–1994 ($R^2 = 0.41$, $P < 0.001$). Linear regressions were fitted to each dataset.

Table S1. Common within-site variability of basal area increment at the tree level considering three time periods (1901–1994, 1901–1947 and 1948–1994). The common variability was quantified as the percentage of variance accounted for by the first principal component (PC1) of a Principal Component Analysis.

Site	Basal area increment – PC1 (%)		
	1901–1994	1901–1947	1948–1994
EP	39.23	25.33	42.23
MA	41.29	38.69	58.22
LA	26.86	26.76	39.94
AI	46.01	49.25	50.41
TS	37.53	42.56	49.13
NE	31.14	38.03	39.73
GE	39.32	32.23	34.19
AM	40.12	38.93	48.01
MI	28.79	30.09	43.49
RA	35.60	35.80	45.00
SM	36.00	37.00	44.35
MO	29.17	30.90	46.56
CO	31.04	31.33	32.66
LL	31.02	28.19	43.66
CG	35.22	34.60	44.11
VM	26.00	28.34	37.47
BI	36.92	50.12	33.73
SB	36.59	28.94	40.36
SC	35.40	26.22	43.85
MR	60.09	55.84	36.88
CU	27.81	30.17	42.68
RE	26.80	30.13	27.73
PA	35.40	34.98	42.01
TE	39.80	42.13	39.12
CN	38.22	38.66	48.64
VI	38.77	45.47	38.23

Table S2. Pearson correlation coefficients of basal area increment (BAI) and trends for the three studied periods as related to explanatory variables calculated at the tree and site levels. Aspect was cosine-transformed into a new variable called Northness.

	BAI 1901–1994	BAI 1901–1947	BAI 1948–1994	BAI trend 1901–1994	BAI trend 1901–1947	BAI trend 1948–1994
Site (*n* = 27)						
Age	0.11#	0.23#	0.02#	-0.28#	-0.24#	-0.20#
Altitude	0.28#	0.33#	0.26#	-0.09#	0.02#	-0.31*
Basal area	0.51**	0.55**	0.46*	-0.05#	-0.01#	-0.09#
Height	-0.22#	-0.20#	-0.21#	-0.13#	-0.08#	-0.18#
Northness	0.01#	0.10#	-0.06#	-0.37*	-0.27#	-0.32#
Sapwood area	0.42***	0.43***	0.37**	0.10#	0.09#	0.15*
Slope	-0.01#	0.06#	-0.04#	-0.15#	-0.29#	0.01#
Tree (*n* = 642)						
Age	-0.07#	-0.02#	-0.10*	-0.11**	-0.12**	-0.01#
Altitude	0.07#	0.09#	0.06#	-0.01#	-0.01#	-0.03#
Basal area	0.36***	0.37***	0.33***	-0.08#	0.01#	-0.17***
Height	0.21***	0.24***	0.17***	-0.17***	-0.07#	-0.19***
Northness	0.01#	0.04#	-0.01#	-0.11#	-0.07#	-0.12#
Sapwood area	0.64***	0.60***	0.63***	0.09#	0.13***	-0.15#
Slope	-0.04#	-0.03#	-0.03#	0.01#	-0.11#	0.05#

Probability values: ***$P<0.001$; **$P<0.01$; *$P<0.05$; #$P>0.05$.

... Trees are sanctuaries. Whoever knows how to speak with them, whoever knows how to listen to them can learn the truth. They do not preach learning and precepts, they preach, undeterred by particulars, the ancient law of life.

... Los árboles son santuarios. Quien sabe hablar con ellos, quien sabe escucharles, aprende la verdad. No predican doctrinas ni preceptos; predican, indiferentes al detalle, la ley primitiva de la vida.

Chapter 2

Drivers of individual growth responses to climate in mountain forests: seeing the trees for the forest

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Summary

Individual trees, not forests, respond to climate. Following a dendroecological framework, we adopt an individual view to retrospectively assess tree sensitivity to climate warming, and to evaluate the potential drivers of tree growth responses to climate acting at both site and individual scales. We obtained tree-ring width series from 642 *Pinus uncinata* individuals from 29 forests. The tree growth responses to climate were assessed using linear-mixed effects models. Beta-regression models were applied to assess the potential drivers of tree growth responses to climate. Warmer maximum November temperatures during the year prior to tree-ring formation enhanced tree growth mainly in mid-elevation sites, whereas at higher elevation growth was more positively dependent on warmer May temperatures during the year of tree-ring formation. June precipitation enhanced growth in sites prone to water deficit, and southern and low-altitude sites were more negatively affected by warm and dry summer conditions. Altitude was the main factor controlling how much growth variability is explained by climate at the site and tree scales. Both (i) a tree-scale approach to quantify growth-index responses to climate and (ii) a detailed characterization of the potential drivers of those individual tree responses are requisites for applying an individual-based framework in dendroecology.

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Introduction

The proper quantification of tree species vulnerability to stressing factors such as climate change must recognise that individuals, not forests, respond to climate (Clark *et al.*, 2012). Taking an individual-scale approach to prospectively measure, or retrospectively track, radial growth variation among individuals allows using changes in growth as a proxy of tree performance. This approach may give a biased assessment of population vulnerability based on growth responses to climate; however, the adoption of this view is fundamental to understand long-term growth responses of forests to climate change.

The retrospective tracking of growth at multiple spatial scales can be done using dendrochronology (Fritts 2001). Trees of the same species growing in the same site show a similar growth pattern which allows them to be cross-dated. This assumption holds particularly true for trees living in areas where climate is the main constraining factor of tree-ring formation, e.g. altitudinal or latitudinal distribution limits. Consequently, dendrochronologists emphasize subjective site and tree selection, as well as tree replication, to build representative mean growth series or chronologies in an attempt to reveal common regional climatic signals, as well as to reduce unwanted non-climatic "noise" (Briffa and Melvin 2011). To achieve this, dendrochronologists average different growth series that retain a high resemblance in temporal patterning, coming from different trees with supposedly high climate sensitivity.

This population-based approach reinforces the mean climatic signal, but at the cost of losing the information given at the level of individuals (Carrer 2011) and related to how trees of different sizes, ages, species and successional trajectories tolerate environmental stressors, compete for resources and respond to extreme climatic events (Ettl and Peterson 1995, Rozas and Olano 2013), thus producing biased growth estimates (Bowman et al. 2013). While useful for reconstructing past climate patterns, the classical dendrochronological approach does not give an accurate picture of how individual trees respond to climate change. In this study we adopt an individual-scale approach to quantify, in retrospect, the growth tracking of climate and compare it to the site (population) scale; this individual-based approach allow us to evaluate how trees respond to climate.

Tree growth and productivity at high altitudes is often limited by low temperatures due to the brevity of the growing season (Körner 2012). Tree populations facing the influence of a main climate driver during their lifetime, such as cold-limited high-elevation forests, will still contain individuals that show enhanced or diminished growth in response to rising temperatures, since they are also influenced by additional factors such as soil water availability (Oberhuber et al. 1998), soil organic layer thickness (Porter and Pisaric 2011), competition for light (Coomes and Allen 2007), altitude (Tardif et al. 2003), topography (Bunn et al. 2005), age (Szeicz and MacDonald 1994), sapwood production (chapter 1), etc. Climate warming, which has been particularly intense in European mountains during the second half of the 20th century (Diaz and Bradley 1997) may change tree growth at high elevations (Soulé and Knapp 2006). Moreover, warmer conditions could "relax" the stress imposed by low temperatures in high-elevation areas an alter tree responses to climate over time (Tardif et al. 2003). Therefore, the responses of trees to climate may vary amongst coexisting individuals and these reactions may be affected by non-climatic drivers differently acting at several spatial scales across the distribution area of a tree species.

In this study, we aim to determine how important are factors acting at the site- (location, altitude) and individual- (topography, size, age, sapwood production) scales for driving the variability in tree growth indices and, in particular, its response to climate. Further, which are the most influential drivers of individual tree responses? To answer these questions we analyzed a wide network of Iberian high-elevation *Pinus uncinata* forests encompassing broad ecological and biogeographical gradients. We perform these analyses at the site- (by comparing trees coexisting within the same stand) and tree- (by comparing coexisting individuals) levels. We hypothesize that high-elevation old trees growing under harsh environmental conditions, usually selected for reconstructing past temperatures, will show a climate sensitivity greatly conditioned by site- and tree-related non-climatic factors such as location, altitude and topography. Characterizing the main drivers that control individual tree growth might help us to better understand why trees from colder high latitude and high elevation areas tend to show either a positive or negative response to climate warming (Wilmking et al. 2004), and, furthermore, why a loss of thermal response in tree growth has occurred recently in such areas.

Materials and methods

Study species and sites

Pinus uncinata Ram. is a mountain, long-lived (usually up to 800 years old) and shade-intolerant conifer with a wide ecological tolerance regarding topography (slope, exposure, altitude) and soil type (Camarero 1999). It is found in subalpine forests from the Alps, the Pyrenees and the Iberian System. Its spring cambial resumption starts at the end of May and ca. 80% of the tree ring annual width is formed from May to July (Camarero et al. 1998). Radial growth in Pyrenean *P. uncinata* forests is enhanced by warm autumn and spring temperatures before and during tree-ring formation, respectively (Tardif et al. 2003).

We sampled 29 *P. uncinata* forests located throughout NE Spain (Table S1, Fig. 1), covering the whole geographic distribution of the species in the Iberian Peninsula. These sites included the southernmost (site TE) and the westernmost (site VI) limits of distribution of the species, which are located in the Iberian System (Fig. 1). We encompassed the maximum ecological amplitude of the species by including forests growing under sub-Mediterranean conditions in the pre-Pyrenees (site GU) and others forming alpine treelines (e.g. sites CU and EP). Most of the sampled sites (26 out of 29) were located in the Pyrenees, where the species is dominant at elevations from 1800 to 2500 m a.s.l. usually forming low-density stands and growing as isolated individuals near the treeline. Most sites were also located within the two main Pyrenean National Parks: seven sites were selected in “Ordesa y Monte Perdido” Park and surroundings (hereafter abbreviated as PNOMP, 42° 40’ N, 00° 03’ E; established in 1918) and twelve sites in “Aigüestortes i Estany de Sant Maurici” Park and surroundings (hereafter abbreviated as PNASM, 42° 35’ N, 00° 57’ E; established in 1955). Sampling sites inside these protected areas guaranties that trees have been less exposed to local perturbations (logging, fire) than in non-protected areas. The mean altitude and slope of the sampled sites are 2118 m and 35° (Table S1). The mean diameter at breast height (dbh) and age of sampled trees are 56.7 cm and 334 years (Table S1).

Climate in the Pyrenees is characterized by E-W and N-S gradients, which bring about warmer and drier conditions southwards and eastwards, as well as descending in altitude, meanwhile continental conditions prevail in higher-altitude areas of the Central Pyrenees (Del Barrio et al. 1990). In the studied sites, mean annual temperature and total annual precipitation range between 2.0 and 4.9 °C and between 1200 and 2000 mm, respectively.

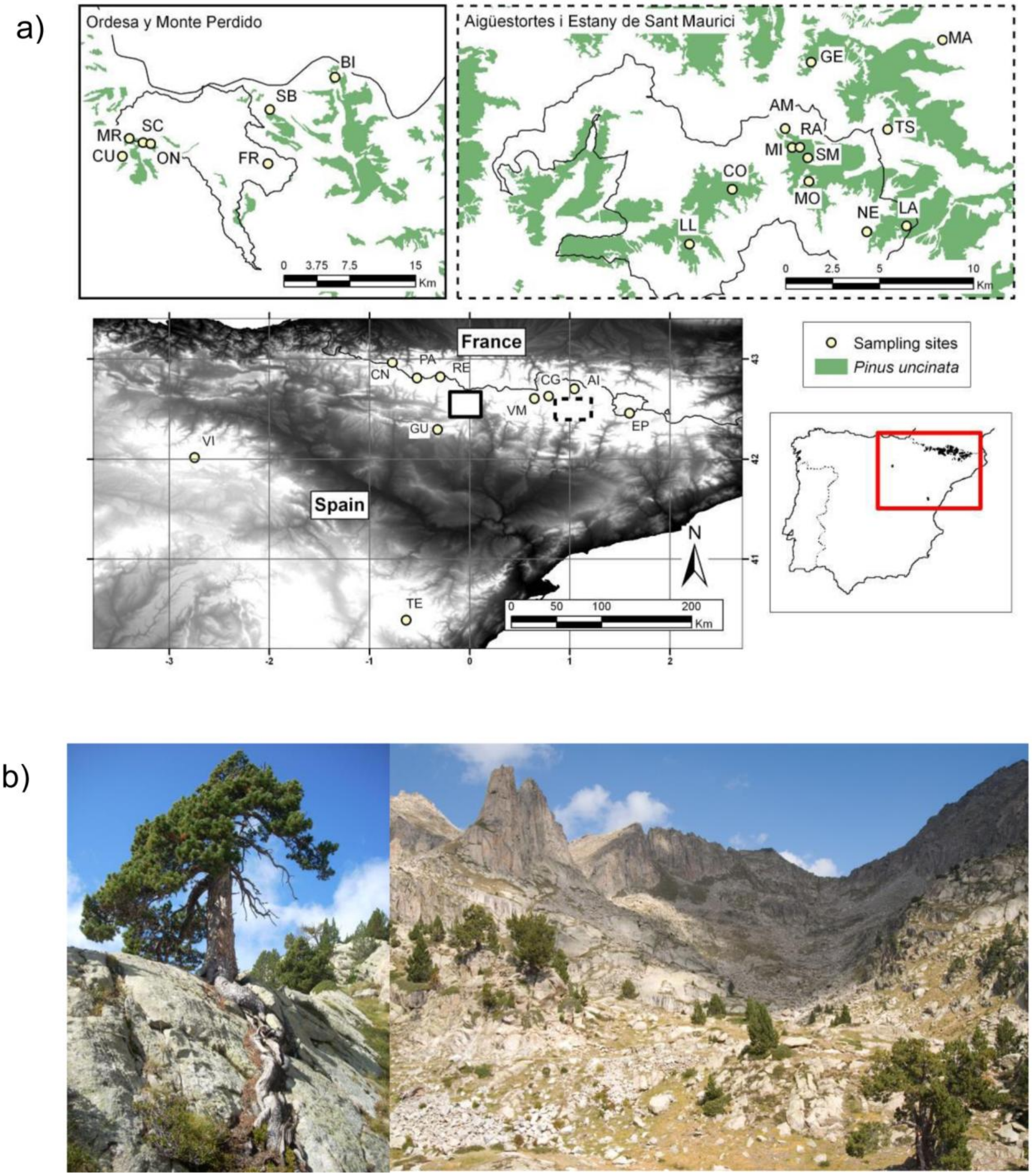

Figure 1. (a) Sampled *P. uncinata* forests (circles) located within or near the two Spanish Pyrenean National Parks: "Ordesa y Monte Perdido" (area surrounded by a continuous line; abbreviated as PNOMP) and "Aigüestortes i Estany de Sant Maurici" (area surrounded by a dashed line; abbreviated as PNASM) and additional sites sampled within the *P. uncinata* distribution area (sites VI and TE of the Iberian System range). Sites codes are explained in the Table S1. Shaded areas in the upper maps correspond to *P. uncinata* forests and the right inset shows the distribution area of the species in Spain. (b) Representative open *P. uncinata* study stands located on rocky slopes (left, Negre site, PNASM; right, Amitges site, PNASM).

January (-2.0 °C mean) and July (12.5 °C mean) are the coldest and warmest months respectively (Camarero 1999). According to homogenized and averaged data in a 0.5°-resolution grid produced by the Climate Research Unit (CRU 2008), annual temperature in the study area increased by +0.02 °C year^{-1} and +0.01 °C year^{-1} during the first and second halves of the 20th century, respectively. We estimated the temporal trends of the annual mean temperature and annual total precipitation for the study period (1901-1994) and two equal sub-periods (1901-1947, 1948-1994) considering the 0.5° grids covering the Pyrenees and the Iberian System sites using the non-parametric Mann–Kendall test. We used this non-parametric trend because linear trends cannot be assumed in the case of rainfall data. The null hypothesis of this analysis assumes that the trend of the time series is zero, and the sign of the Mann–Kendall statistic indicates whether the trend is positive or negative (Legendre and Legendre 1998). Annual temperature showed significant rises in the study area during the period 1901-1994. This warming was stronger in the sub-period 1901-1947 than in the sub-period 1948-1994, particularly over the central Pyrenees (Table 1). Significant declines in rainfall were detected in some site from the Iberian System range, whereas rainfall increased in some Pyrenean sites during the early half of the 20th century. Similar trends were observed when using local climate data (e.g., Bücher and Dessens 1991).

Field sampling and dendrochronological methods

Between 1994 and 2010 we sampled 642 living *P. uncinata* trees. In each sampled site we randomly selected from 5 to 65 dominant individuals of different sizes and ages (on average 24 trees were sampled per site), registering topographic (altitude, slope, and aspect) and biometric (dbh, diameter at breast height measured at 1.3 m, and tree height) variables for each individual. We calculated northness as the cosine of the aspect. The distance between sampled trees was usually more than 10 m in order to minimize the within site spatial correlation in growth among neighbouring trees. Note however that most sites are low-density stands or open areas with isolated trees (see Fig. 1b). Density and basal area values were within the 121-167 stems ha^{-1}and 7.3-19.2 m^{2} ha^{-1} ranges, respectively, which are much lower than values observed in subalpine low-elevation stands (475 stems ha^{-1}and 48.0 m^{2} ha^{-1}; see Bosch and Gutiérrez 1999).

We took two or three cores from each tree at 1.3 m height with Pressler increment borers gathering a total of 1296 samples (Table 2). We also measured the sapwood length of the cores (see more details in chapter 1). The diameter, excluding bark, and the sapwood length were converted to basal area and sapwood area, respectively, assuming a circular shape of the stem.

Wood samples were processed to obtain cross-dated tree-ring width (TRW) series following standard dendrochronological methods as described in the chapter 1. We standardized the TRW series to remove age or size trends and their temporal autocorrelation (Briffa and Melvin 2011), adjusting negative exponential functions and 20-year long splines to the TRW series. These relatively short splines remove growth trends in periods longer than decades, withholding the high-frequency (mainly annual) growth variability. We applied autoregressive models in order to model and eliminate the temporal (usually first-order) autocorrelation. Finally, we obtained the residual growth-index series by division, and we averaged them following a hierarchical approach from tree to site (chronology) level. These growth series were built using the program ARSTAN (Cook 1985).

To characterize the growth series at the site level we calculated several dendrochronological statistics either considering raw data (AC, first-order autocorrelation which measures the serial persistence of growth) or residual growth indices (ms_x, mean sensitivity, a measure of year-to-year growth variability; r_{bt}, mean correlation between trees which evaluates the similarity in growth variability among trees; E1, variance explained by the first principal component) (Fritts 2001). The reliable time span was defined as the period with EPS > 0.85, where the EPS (Expressed Population Signal) is a population-based measure of the statistical quality or reliability of the site chronology as compared with a perfect infinitely replicated chronology (Wigley et al. 1984).

In mountain *P. uncinata* forests individuals take (mean ± SD) 20 ± 5 years on average to reach a height of 1.3 m (Camarero 1999). Therefore we added 20 years to the estimated age at 1.3 m in order to estimate the age in the base of the trunk. In samples without pith we estimated tree age calculating the distance to the theoretical pith by means of a geometrical method based on a pith locator, and transforming this distance into a number of missing inner rings (see chapter 1).

Table 1. Temporal trends of the annual mean temperature and total precipitation calculated for the sub-periods 1901-1947 and 1948-1994, and for the period 1901-1994 considering different study sites and areas. Sites (abbreviated by uppercase letters and corresponding to the 0.5°-wide grids encompassing the site) and Pyrenean 0.5°-grids (abbreviated by lowercase letters) are indicated in Appendix S1 and Fig. 1. Trends were estimated using Mann–Kendall tests. Significant (*P*<0.05) slope values are indicated in bold.

Variable	Area	Site / grid	MK statistic			*P* value (two-sided)			Slope (°C or mm year^{-1})			Median (°C or mm)		
			1901-1947	1948-1994	1901-1994	1901-1947	1948-1994	1901-1994	1901-1947	1948-1994	1901-1994	1901-1947	1948-1994	1901-1994
Temperature	Iberian System	VI	391	215	2319	**0.0003**	**0.049**	**<0.0001**	**0.019**	**0.011**	**0.017**	9.54	10.44	10.04
		TE	308	218	2371	**0.005**	**0.046**	**<0.0001**	**0.019**	**0.008**	**0.019**	10.97	12.01	11.69
	Pyrenees	a	352	188	1839	**0.001**	0.085	**<0.0001**	**0.023**	0.008	**0.015**	11.20	11.99	11.69
		b	333	209	1996	**0.002**	0.055	**<0.0001**	**0.023**	0.010	**0.016**	9.76	10.68	10.39
		c	339	233	1953	**0.002**	**0.033**	**<0.0001**	**0.022**	**0.011**	**0.016**	5.49	6.29	6.03
		d	369	171	1707	**0.0007**	**0.117**	**<0.0001**	**0.025**	**0.0087**	**0.014**	9.37	10.07	9.83
		e	371	113	1528	**0.0007**	**0.300**	**<0.0001**	**0.026**	**0.006**	**0.013**	8.53	9.16	8.97
Precipitation	Iberian System	VI	-31	-267	-721	0.776	**0.014**	**0.018**	-0.460	**-2.589**	**-0.918**	591.49	563.80	581.80
		TE	-25	-45	191	0.819	0.679	0.533	-0.400	-0.688	0.335	479.30	495.30	488.15
	Pyrenees	a	229	-93	319	**0.036**	0.394	0.297	**2.550**	-0.929	0.500	643.10	643.30	643.20
		b	277	-113	361	**0.011**	0.300	0.238	**4.127**	-1.599	0.654	685.89	691.89	686.35
		c	257	-51	477	**0.018**	0.640	0.119	**4.365**	-1.095	1.002	975.70	980.40	978.75
		d	137	-63	255	0.209	0.563	0.405	2.209	-0.826	0.463	752.69	764.20	760.50
		e	23	-21	283	0.833	0.847	0.355	0.542	-0.567	-0.555	796.80	824.19	799.65

Table 2. Statistical characteristics for each site chronology. Variables of raw tree-ring series for the time span analyzed: SD, standard deviation; AC, first-order autocorrelation. Variables of residual chronologies: ms_x, mean sensitivity, a measure of year-to-year growth variability; r_{bt}, mean correlation between trees which evaluates the similarity in growth among trees; E1, variance explained by the first principal component. The reliable time span was defined as the period with EPS > 0.85, where the EPS (Expressed Population Signal) is a measure of the statistical quality of the mean site chronology as compared with a perfect infinitely replicated chronology (Wigley et al. 1984). The mean length was calculated for the time span, while tree-ring width, AC, ms_x, r_{bt} and E1 are calculated from 1901 to 1994.

Site	No. trees / radii	Time span	Mean length (years)	Raw data		Residual chronology (growth indices)			
				Tree-ring width ± SD (mm)	AC	Reliable time span (EPS > 0.85)	ms_x	r_{bt}	E1 (%)
EP	20 / 39	1586-1997	198	0.95 ± 0.36	0.77	1775-1997	0.15	0.35	37.84
MA	10 / 20	1668-1997	175	0.92 ± 0.51	0.85	1785-1997	0.18	0.40	47.19
LA	36 / 74	1390-2009	243	0.80 ± 0.40	0.85	1390-2009	0.13	0.27	32.34
AI	16 / 31	1651-1996	194	1.02 ± 0.35	0.77	1748-1996	0.14	0.45	49.00
TS	10 / 17	1537-1995	252	0.88 ± 0.38	0.84	1773-1995	0.12	0.32	38.43
NE	46 / 86	1393-2009	242	0.74 ± 0.33	0.79	1652-2009	0.14	0.36	38.34
GE	41 / 79	1270-2010	278	0.59 ± 0.26	0.81	1423-2010	0.12	0.43	50.06
AM	25 / 56	1592-2009	229	0.83 ± 0.33	0.77	1665-2009	0.15	0.48	51.79
MI	33 / 85	1390-2009	252	0.59 ± 0.32	0.83	1596-2009	0.16	0.34	37.25
RA	5 / 13	1818-2009	192	1.07 ± 0.70	0.88	1856-2009	0.17	0.40	50.36
SM	20 / 40	1811-1996	164	0.94 ± 0.68	0.89	1819-1996	0.18	0.48	50.57
MO	30 / 76	1481-2009	246	0.92 ± 0.50	0.87	1691-2009	0.12	0.31	34.24
CO	25 / 43	1509-1995	274	0.64 ± 0.25	0.78	1594-1995	0.14	0.34	37.51
LL	17 / 17	1338-1997	435	0.59 ± 0.29	0.88	1548-1997	0.11	0.33	38.51
CG	25 / 54	1510-1994	215	0.82 ± 0.36	0.82	1700-1994	0.15	0.26	30.37
VM	12 / 23	1476-1994	234	0.77 ± 0.37	0.83	1816-1994	0.14	0.29	34.34
BI	11 / 20	1707-1996	196	0.80 ± 0.53	0.82	1766-1996	0.21	0.40	46.27
SB	53 / 95	1512-2009	285	0.84 ± 0.51	0.85	1617-2009	0.15	0.30	32.1
FR§	12 / 25	1438-1947	305	0.50 ± 0.29	0.82	1582-1947	0.16	0.30	47.41
SC	65 / 119	1421-2010	256	0.72 ± 0.41	0.85	1571-2010	0.12	0.28	29.51
ON	14 / 27	1531-1998	234	0.76 ± 0.36	0.81	1716-1998	0.21	0.28	33.43
MR	17 / 34	1795-1998	156	0.77 ± 0.44	0.86	1836-1998	0.15	0.31	34.39
CU	10 / 20	1871-1997	98	1.71 ± 0.65	0.74	1892-1997	0.22	0.39	47.56
GU	27 42	1800-2011	122	1.85 ± 1.00	0.81	1873-2011	0.23	0.39	42.26
RE	20 / 47	1572-2010	202	0.84 ± 0.42	0.81	1742-2010	0.15	0.26	31.40
PA	8 / 16	1755-1994	170	1.14 ± 0.62	0.84	1778-1994	0.18	0.32	40.58
TE	35 / 68	1730-2008	157	1.33 ± 0.74	0.83	1741-2008	0.14	0.41	46.57
CN	25 / 57	1364-2010	252	0.68 ± 0.42	0.82	1670-2010	0.16	0.33	36.93
VI	24 / 42	1561-2010	238	0.99 ± 0.49	0.81	1731-2010	0.18	0.31	42.10

Statistical analyses

We summarized the growth variability amongst the 29 sampled sites performing a Principal Components Analysis (PCA) based on the covariance matrix of the residual growth-index chronologies of the 29 sites considering their common period (1901-1994). We assessed the growth-climate relationships calculating Pearson correlations between mean maximum temperature (TMx), mean minimum temperature (TMi) and precipitation (P) as related to: (1) the mean residual growth indices of each site and tree, and (2) the first principal component derived from the PCA (see also Tardif et al. 2003). Monthly climate data were interpolated for those 0.5° grids including each sampled site and these data corresponded to the CRU TS 3.1 data set produced for the period 1901-2009 (CRU 2008). Climatic data were obtained from the Royal Netherlands Meteorological Institute "Climate Explorer" web page (http://climexp.knmi.nl). The growth indices were compared with climatic data for the period 1901-1994 and considering the temporal window from October previous to the tree-ring formation to current September. This window was selected based on previous analyses on *P. uncinata* tree-ring formation (Camarero et al. 1998).

Evaluation of individual growth responses based on linear mixed-effects models

We evaluated the relationships between tree growth indices and climate by means of linear mixed-effects models, considering the growth index of each tree for the period 1901-1994 as the response variable, and a series of monthly climatic variables and their combinations as predictors. The model can be formulated as follows:

$$y_i = a + X_i\beta + b_i + \varepsilon_i \qquad (1)$$

where y_i represents the vector including the values of growth index for tree i, a is the intercept, X_i is the fixed-effects (i.e. climate variables) matrix, β is the vector of parameters associated to the fixed effects, b_i is the matrix including the vectors of random effects (i.e. trees) and ε_i is the within group error vector (Zuur et al. 2009). To estimate fixed effects and to test their significance we used random slope models since this allows slopes to climate parameters (responses) to vary among trees. We considered trees as random effects to take into account differences in individual tree growth-index responses to climate within each site and also considering the whole data set (Ettinger et al. 2011).

We adjusted 36 candidate models per site with different combinations of climatic variables, focusing on those assumed to be more relevant for tree growth such as the combined effects of warm conditions in the winter prior to growth and the spring of tree-ring formation (Table S2). The 37th model was a null model which did not include any climatic variable. Specifically, the climatic variables used as predictors were: mean previous November maximum temperature (abbreviated as pTMx11); mean May minimum temperature (TMi5); previous December precipitation (pP12); mean March minimum temperature (TMi3) and current June precipitation (P6). The choice of these climatic variables and no others was based on climate-growth relationship analyses performed in this study as well as on previous research (Gutiérrez 1991, Camarero 1999, Tardif et al. 2003). These climatic variables were previously standardized. They did not show significant relationships between them thus avoiding collinearity problems. The standardization method did not affect the final model performance since the main climatic variables controlling growth indices were the same ones regardless of the spline length selected (results not presented).

We ranked the obtained models using information methods based on the Akaike Information Criterion (AIC) value, which penalizes complex models (the smaller the AIC value, the more parsimonious the model). We also used the difference between the AIC value for each model and the AIC value of the best fitted model (Δ_i) (Burnham and Anderson 2002). The models were estimated by means of maximum likelihood (ML) and restricted maximum likelihood (REML) estimations (Zuur et al. 2009). First, we determined the optimal random effects structure by using REML including all explanatory variables, as well as combinations of random effects (random intercepts, random slopes, or both random intercepts and random slopes). Second, we determined the optimal fixed effects structure by fitting models with all possible fixed effects and their combinations using ML but based on the optimal random effects structure obtained in the first step. Third, we refit models using REML with the random and fixed effects structures selected in the first and second steps, respectively. In the three steps we selected the best-fitting model by choosing the model with the lowest AIC or the model with the fewest parameters when AIC values of the lowest AIC model and other parsimonious models differed by less than 2 AIC units (Burnham and Anderson 2002). We also calculated the relative probability of the selected candidate model being the best for the observed data (W_i). The marginal variance explained (R^2) by fixed factors was calculated following Nakagawa and Schielzeth (2013). Lastly, we show the best fitted model in each site and the parameters associated to the intercept and to the climatic variables evaluated. We assumed that model errors were independent because models accounting for spatial autocorrelation in the model residuals detected no spatial dependence (this was to be expected from the characteristics of the *P. uncinata* stands, as pointed out before) and produced higher AIC values than models not considering the spatial correlation structure of the residuals (results not presented). Linear mixed-effects models were performed with the *nlme* package (Pinheiro et al. 2012) of the R language version 2.11.1 (R Development Core Team 2013).

Evaluation of drivers affecting individual tree responses to climate

To analyze how climate effects on growth indices are related to additional drivers we performed bivariate tests. We chose this simple statistical framework, instead of using a multivariate approach, because some of the evaluated drivers (northness, altitude and slope) did not change through time as growth indices did. In addition, the other evaluated drivers (sapwood area, basal area, tree height, tree age) changed through time as trees grew (chapter 1), but we assumed these covarying factors would not affect the trees' responses to climate over the past century since standardization of growth indices removed part of the ontogenetic trends affecting those factors (Briffa and Melvin 2011). We assessed the relationships between site and tree drivers and the amount of growth-index variance explained by climate (R^2). We calculated beta regression models to test the relative importance of drivers (northness, altitude, slope, sapwood area, basal area, tree height, tree age) on growth-index responses to climate (R^2). Beta regression models deal with dependent variables (R^2 in this case) which are continuous and restricted to the unit interval (Cribari-Neto and Zeileis 2010). The analyses were performed for the two identical sub-periods (1901-1947 and 1948-1994) to evaluate if the influence of these drivers on growth-index response to climate changed through time. We used the coefficients adjusted by beta regression models and their probability values were adjusted using a Bonferroni procedure (P_B) to limit the likelihood of spurious correlations (Legendre and Legendre 1998). Beta regression models were calculated using the *betareg* package in the R language (R Development Core Team 2013).

Results

Growth characteristics at the site level

The mean length of the growth-index series was 224 years (Table 2), which means that around 288,000 tree-rings were measured. The longest growth-index series was in site GE with 741 years covering the period 1270-2010, whereas the shortest one was in site CU with 127 years covering the period 1871-1997. The mean annual TRW was 0.79 mm for the period common to all series (1901-1994). During that period, sites dominated by young trees (e.g., CU and GU) showed the highest mean sensitivity, which measures the year-to-year variability of growth indices. The site mean sensitivity decreased as western longitude (r = -0.40; P=0.032), elevation (r = -0.41; P=0.033), and dbh (r = -0.44; P=0.016) increased. If the latter two sites were excluded, mean TRW at the site level was positively related to sapwood width (r = 0.48; P=0.008). Mean TRW was negatively related to mean age (r = -0.68; P<0.001) and altitude (r = -0.65; P=0.001) since these two variables were positively related (r = 0.39; P=0.037), i.e. old trees were more abundant upwards.

Growth response to climate at species and site levels

The first principal component (PC1) of the PCA considering all sites explained 54.11% of the whole site growth-index variability, while the second component (PC2) explained the much smaller percentage of 7.14% (Fig. 2). The scores of the species distribution limits (e.g., sites TE, CN and VI), expanding alpine treelines (site CU) and young forests (site MR) were located apart from most PNASM high-elevation sites across the PCA diagram. Site SM constituted also a remarkable outlier since it is a relatively young, low-elevation forest with high growth levels. The PC1 site scores were related to altitude (r = 0.64; P <0.001), whereas the PC2 scores were negatively related to longitude (r = -0.81; P <0.001), i.e. western sites showed higher PC2 scores.

Considering the PC1 as a summary of the common growth-index variability of the tree species across the study area, *P. uncinata* formed wider rings in response to warm previous November temperatures and high mean May minimum temperatures (Fig. 3). Wet summers were also related to higher growth indices. Finally, the *P. uncinata* PC2 showed a significant negative relationship with previous December mean minimum temperature (results not shown).

At the site level, *P. uncinata* growth index was again positively related to the mean maximum and minimum previous November temperature and to the mean minimum May temperature, as well as with precipitations of June, July and previous December. Note that the effects of summer rainfall on growth-index detected at some specific sites were not so evident when considering the whole species response as represented by the PC1. This was also observed in the negative growth-index response to minimum March temperature (Fig. 3).

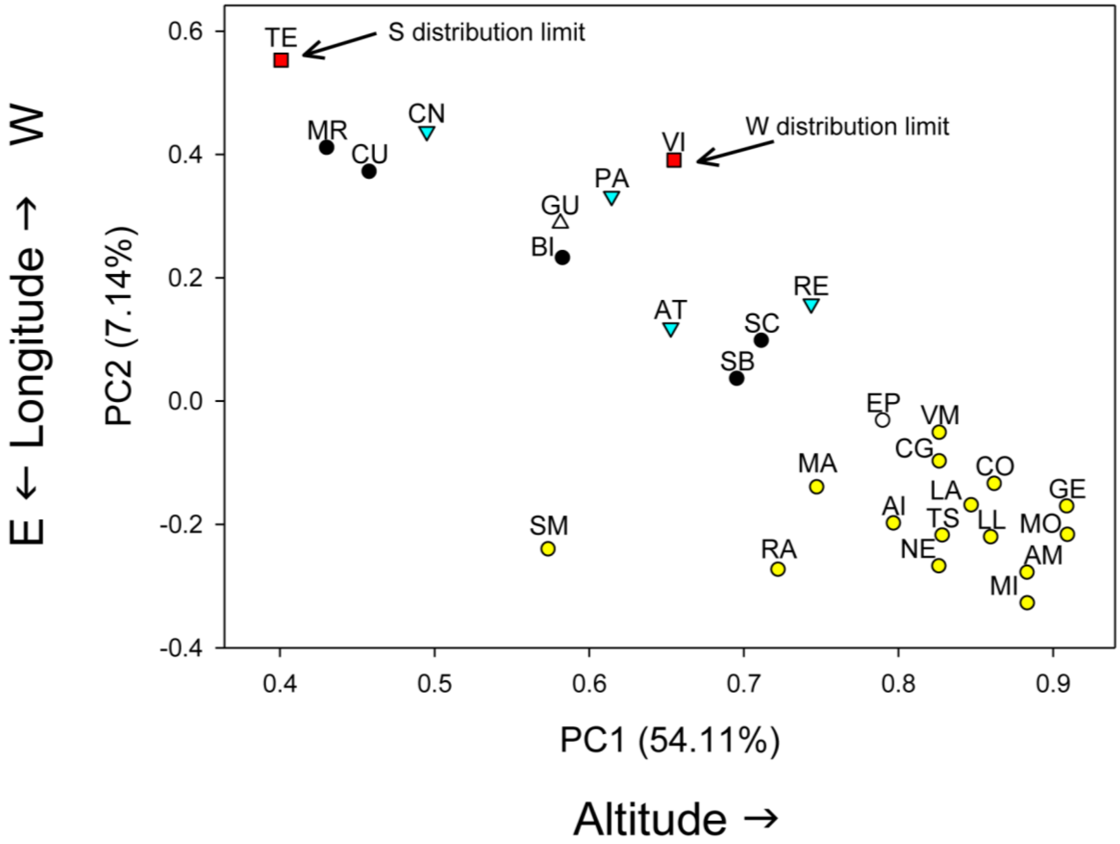

Figure 2. Principal Components Analysis diagram showing the scores of the site tree-ring width chronologies for the first two principal components PC1 and PC2 (sites codes are as in the Table S1). The arrows indicate how the scores of the first (PC1) and second (PC2) components change as a function of altitude and longitude, respectively. Stands located near the distribution limit of the species are indicated and different symbols correspond to sites from different geographical areas (PNOMP, black circles; PNASM, yellow circles; western and central Pyrenees, downward blue triangle; Iberian System, red square; eastern Pyrenees, white circle; Pre-Pyrenees, upward white triangle).

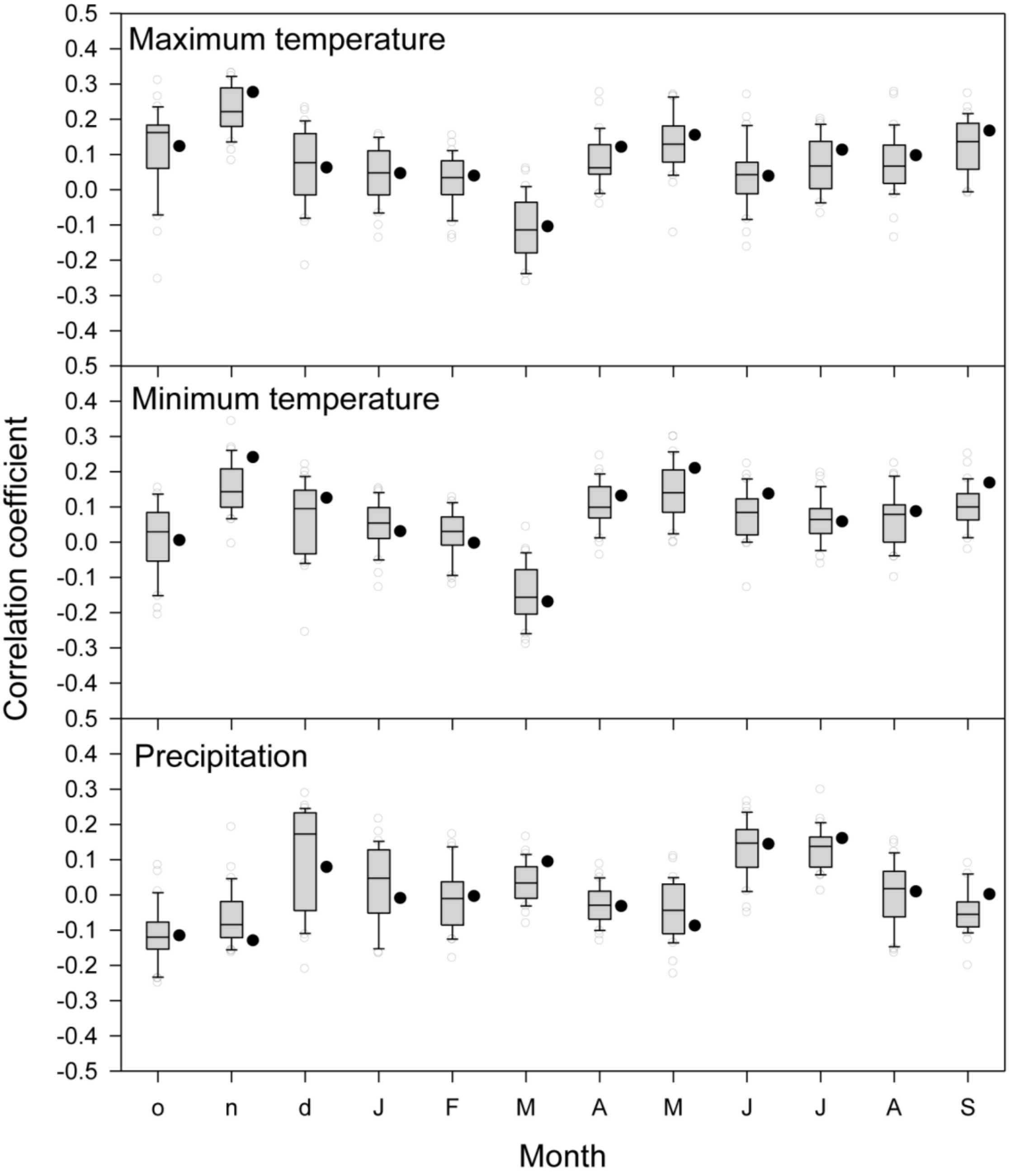

Figure 3. Pearson correlation coefficients calculated between the growth indices expressed at the species (filled symbols) and site (box plots) levels and mean maximum and minimum temperatures and total precipitation. The species level was expressed as the PC1 considering the growth series of all sampled sites for *P. uncinata*, whereas the site level was quantified as the mean of all individual growth-index of trees located within each sampled site (*n*=29 sites). For the site level, each box shows the 25th and 75th percentiles of correlations (lower and upper edges of boxes, respectively), and the median (thin line) values of the correlations. The outliers located below and above the 5th and 95th percentiles are also displayed. The analysed temporal window spans from previous October up to current September. Months are abbreviated with lowercase and uppercase letters for the previous and current year of growth, respectively.

Individual tree growth-index responses to climate

At the tree scale, 33% of all individuals showed significant enhanced growth-index responses to warmer maximum temperatures during the previous November, and 16% responded significantly and positively to warmer minimum temperatures during the current May. High March minimum temperatures were associated to significantly lower growth index in 14% of all trees. Wet conditions during the previous December and the current June were related to significantly improved growth-index of 16% and 18% of trees, respectively (Fig. 4). Overall, most trees did not show significant growth-index responses to climate at the tree level.

Linear-mixed effects models confirmed the dominant role of maximum temperatures during the previous November as the main climatic driver of *P. uncinata* growth-index at the tree scale (Table 3). Considering each site separately, this variable also showed a significant positive effect on tree growth-index in all sites. This effect on growth-index was stronger than the rest of climatic variables in 15 out of 28 sites (mainly in mid to low-elevation sites), whereas minimum May temperatures during the year of tree-ring formation was the dominant climate driver in 7 sites, particularly in high-elevation ones (e.g., sites NE, AM). Previous December precipitation was the major climate driver in two sites showing opposite effects on growth-index. Remarkably, current June precipitation was the most important climatic variable influencing positively growth-index in the southernmost limit of the species distribution area (site TE), in the sub-Mediterranean Pre-Pyrenees (site GU), in the site with the steepest slopes (site BI) and in a low-elevation site (site SM).

At the tree level climatic factors explained a mean growth-index variance of 16.2% with the lowest variance values observed in the humid western Pyrenees (3.5%-6.3%) and the highest variance values detected in high- and mid-elevation sites from the PNASM in the Central Pyrenees (27.0%-32.6%) (Table 3).

Over time, we observed an increase in growth-index variability in the sub-period 1948-1994 (Fig. S1). In fact, during the sub-period 1948-1994 more growth-index variability at the tree level was explained by climatic factors than during the first one (Fig. S2). On avereage, growth-index variability explained by climate at the site scale rose from 11% in the sub-period 1901-1947 to 33% in the sub-period 1948-1994 (Table S3). Considering the whole dataset of trees, the growth-index variance explained by climate increased from 14% in 1901-1947 to 42% in 1948-1994. Such shift in the relevance of climate as driver of growth index was due to the overwhelming role played by previous November maximum temperatures during the late 20th century.

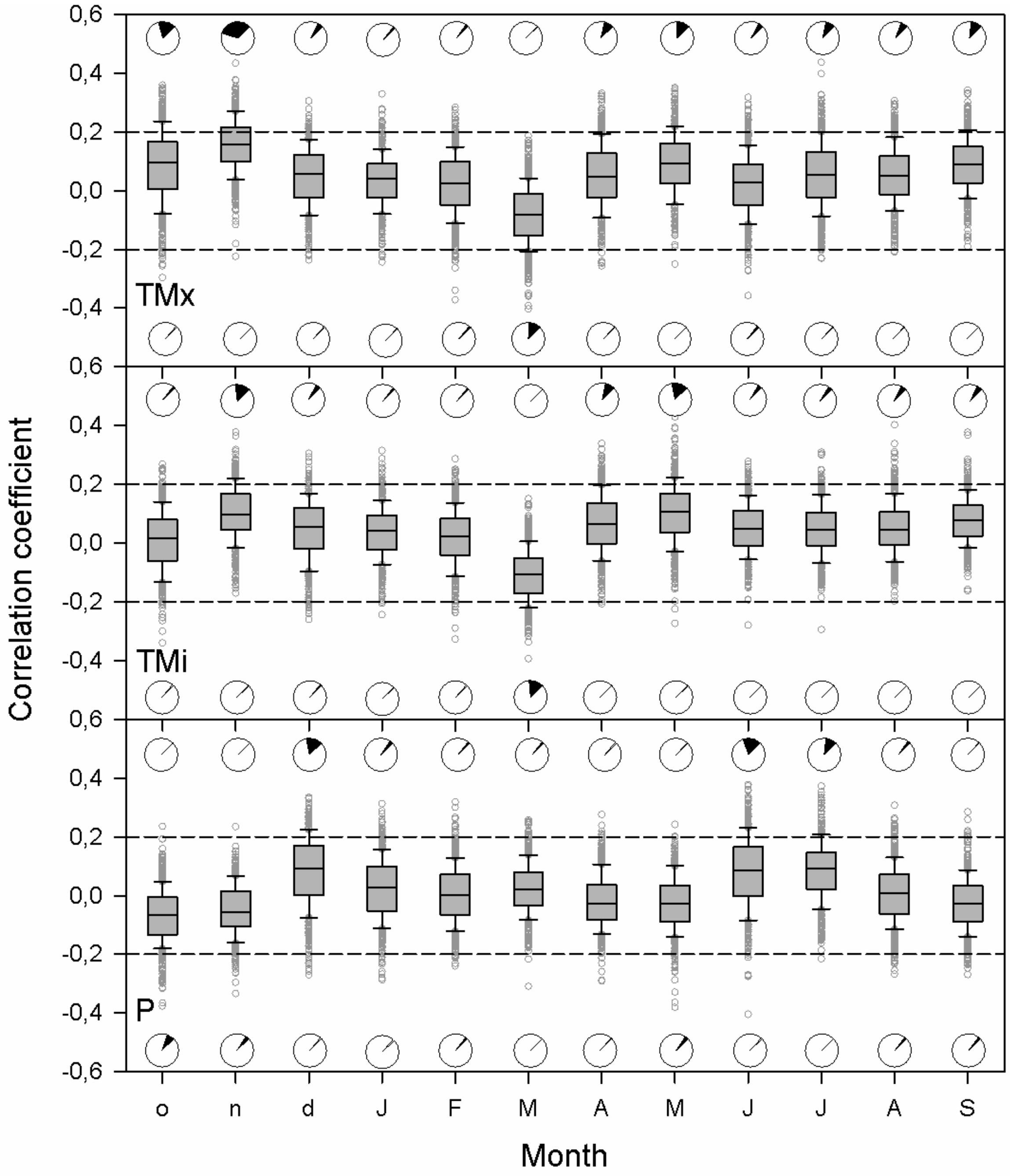

Figure 4. Pearson correlation coefficients calculated between growth indices of sampled trees (*n*=642) for *P. uncinata,* and monthly mean maximum and minimum temperatures and total precipitation. Explanations are as in Fig. 3. The pie charts displayed above and under the boxplots represent in dark the percentage of trees that shows significant positive (above) or negative (below) correlation with the corresponding climatic variable.

Table 3. Statistical parameters of the selected linear mixed-effects climatic models fitted to growth indices. Sites are arranged in decreasing value of altitude and within each sampled region. Monthly climatic predictors are abbreviated as follows: pTMx11, mean maximum temperatures of the previous November; TMi5, mean minimum temperatures of current May; pP12, precipitation of the previous December; TMi3, mean minimum temperatures of current March; P6, current June precipitation. Statistics: W_i, relative probability that the selected model is the best one; R^2, percentage of growth-indices variance explained by the model. The most important climatic variable for each site is indicated in bold characters.

Area	Site	No. trees	Coefficients						*Wi*	R^2 (%)
			Intercept	pTMx11	TMi5	TMi3	pP12	P6		
All sites	–	582	1.0011	**0.0253**	0.0086	-0.0176	0.0107	0.0121	1.00	24.48
Eastern Pyrenees	EP	20	1.0023	0.0293	**0.0351**	-0.0277			0.76	25.60
Central Pyrenees	AI	14	1.0034	0.0182	**0.0241**	-0.0195	0.0224		0.99	17.80
PNASM (Central Pyrenees)	NE	42	1.0033	0.0239	**0.0313**	-0.0256	0.0270		0.99	27.19
	AM	24	1.0048	0.0236	**0.0364**	-0.0183	0.0241	0.0194	0.99	29.46
	MO	25	1.0052	**0.0308**	0.0214	-0.0244	0.0164	0.0139	0.99	27.05
	CO	19	1.0030	**0.0281**	0.0133	-0.0244	0.0194		0.62	24.42
	GE	39	0.9998	**0.0279**	0.0221	-0.0169	0.0240	0.0153	0.99	26.80
	LL	45	1.0016	**0.0253**	0.0112	-0.0171	0.0171		0.98	23.81
	TS	10	1.0005	**0.0248**	0.0162	-0.0189			0.32	14.73
	MI	31	1.0025	0.0280	0.0272	-0.0226	**0.0283**	0.0214	0.99	32.61
	LA	21	1.0021	**0.0284**	0.0186	-0.0255	0.0164		0.98	27.46
	MA	8	1.0024	**0.0393**	0.0258			0.0270	0.55	14.70
	SM	20	0.9960	0.0198			0.0242	**0.0323**	0.64	10.97
Central Pyrenees	CG	15	1.0010	**0.0283**		-0.0210			0.44	13.20
	VM	12	1.0009	**0.0211**		-0.0164		0.0174	0.51	11.94
	BI	9	1.0054	0.0269				**0.0446**	0.66	9.89
PNOMP (Central Pyrenees)	SB	26	1.0049	0.0139	**0.0167**	-0.0170			0.94	8.49
	SC	38	1.0035	**0.0292**		-0.0186			0.99	12.46
	ON	11	1.0011	**0.0304**					0.96	7.41
	CU	8	1.0019	**0.0486**			-0.0419		0.94	18.15
	MR	17	1.0018	0.0185			**-0.0212**	0.0170	0.47	5.98
Western-central Pyrenees	RE	16	1.0032	0.0253	**0.0289**	-0.0157			0.83	19.77
	PA	7	0.9998	**0.0290**					0.71	4.96
Western Pyrenees	AT	15	1.0021	**0.0199**					0.50	3.47
	CN	20	1.0020	**0.0322**		-0.0179			0.54	6.30
Pre-Pyrenees	GU	22	1.0002	0.0269				**0.0285**	0.82	8.57
Iberian System	TE	26	1.0071	0.0170	0.0237			**0.0320**	0.87	11.41
	VI	22	1.0092	0.0171	**0.0182**			0.0147	0.94	8.74

Drivers of the individual tree growth-index responses to climate

The main positive drivers of the tree growth-index variability explained by climate variables were altitude and sapwood area, particularly in the sub-period 1948-1994, whereas slope was the main negative driver (Table 4). Altitude conditioned the tree growth responses to climate since the relevance of previous November temperatures for tree growth-index increased downslope, as well as that of current March temperatures, whereas current May temperatures were more important upwards (Table S4). A negative and a positive effects were observed for current June and previous December rainfall, respectively. Age conditioned the growth-index response to four of these five significant climatic variables. Those trees more responsive to March (May) temperatures usually formed less (more) sapwood and had bigger basal area. Growth index of older trees responded more to wet previous December conditions, while growth index of younger trees was more sensitive to winter-spring temperatures and June precipitation. Northness, slope and tree height did not condition the growth-index responses to climate of the whole data set of trees.

At the site level we detected noticeable biogeographical gradients in the mean stand growth-index response to climate which increased from west to east and from north to south (Fig. 5). Such relationship was significant if extreme sites were excluded, namely the westernmost and southernmost limits of the species distribution area and also sites located outside the Pyrenees and subjected to Mediterranean and drier conditions. Altitude played a dominant role among the evaluated drivers of growth-index responses to climate at both site and tree levels (Fig. 5). Such association was not detected when considering the relationships between altitude and the growth-index responses to climate within each site.

The prevailing influence of altitude on growth-index variability at the two considered spatial scales (i.e. site and tree), was also observed when evaluating changes through time along the 20th century (Fig. 6.). Altitude was significantly correlated with the growth-index variability explained by climatic linear-mixed effects models at the site and tree levels for the sub-period 1948-1994 but not for the sub-period 1901-1947 (Table 4, Fig. 6). In other words, during the first half of the 20th century growth-index responses to climate at the site and individuals levels were not related to the stand and tree altitudes.

Table 4. Environmental and tree variables affect the amount of growth-index variance explained by climate (R^2) at the tree level. The importance of each variable was assessed by means of beta-regression models fitted for three different periods (1901-1994, 1901-1947 and 1948-1994). Bold significance *P* values are Bonferroni-corrected (P_B) values which correspond to $P \leq 0.0024$.

Variable	Period	Coefficient estimate	*P*
Northness	1901-1994	-0.0082	0.0832
	1901-1947	-0.0003	0.5035
	1948-1994	-0.0067	0.2027
Altitude	1901-1994	0.0016	**<0.0001**
	1901-1947	0.0002	0.4729
	1948-1994	0.0018	**<0.0001**
Slope	1901-1994	-0.0008	0.0110
	1901-1947	-0.0007	0.0123
	1948-1994	-0.0009	0.0104
Sapwood area	1901-1994	0.0010	**0.0001**
	1901-1947	0.0001	0.5376
	1948-1994	0.0011	**0.0001**
Basal area	1901-1994	-0.0004	0.0289
	1901-1947	-0.0002	0.5831
	1948-1994	-0.0003	0.1048
Tree height	1901-1994	0.0004	0.1724
	1901-1947	-0.0006	0.0756
	1948-1994	0.0007	0.0177
Tree age	1901-1994	0.0003	0.2648
	1901-1947	0.0004	0.3009
	1948-1994	0.0001	0.8039

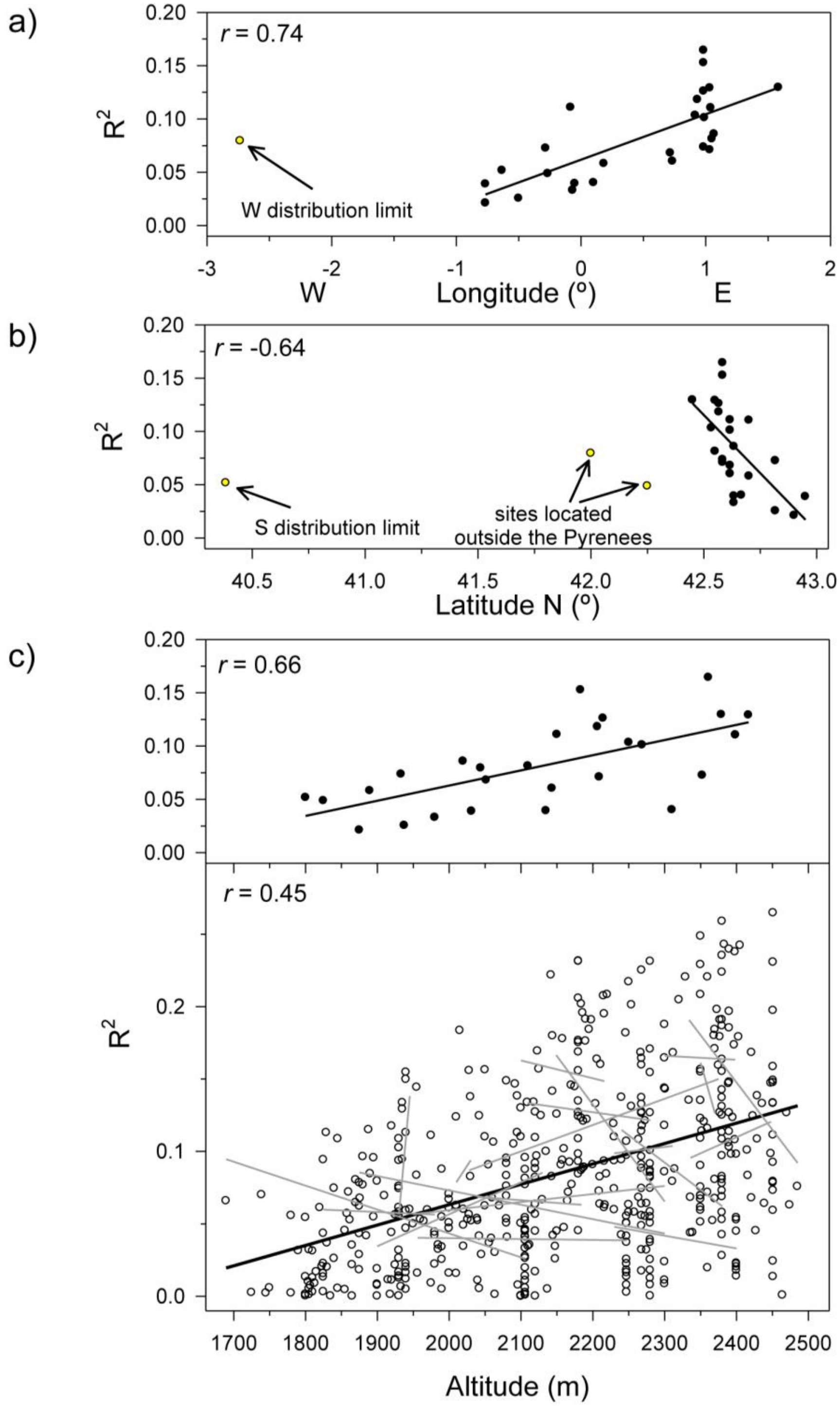

Figure 5. Significant ($P<0.0001$) correlations between the growth-index variance explained by linear mixed-effect models based on climatic variables (R^2) and site variables: (a) longitude (linear regression fitted excluding the westernmost distribution limit), (b) latitude (linear regression fitted excluding sites located outside the Pyrenees), and (c) altitude. Upper and lower graphs in (c) compare the associations between R^2 and altitude at the site and tree scales, in that order, whereas thin and thick lines correspond to the R^2 *vs.* altitude relationships for each site and for the whole dataset of trees, respectively.

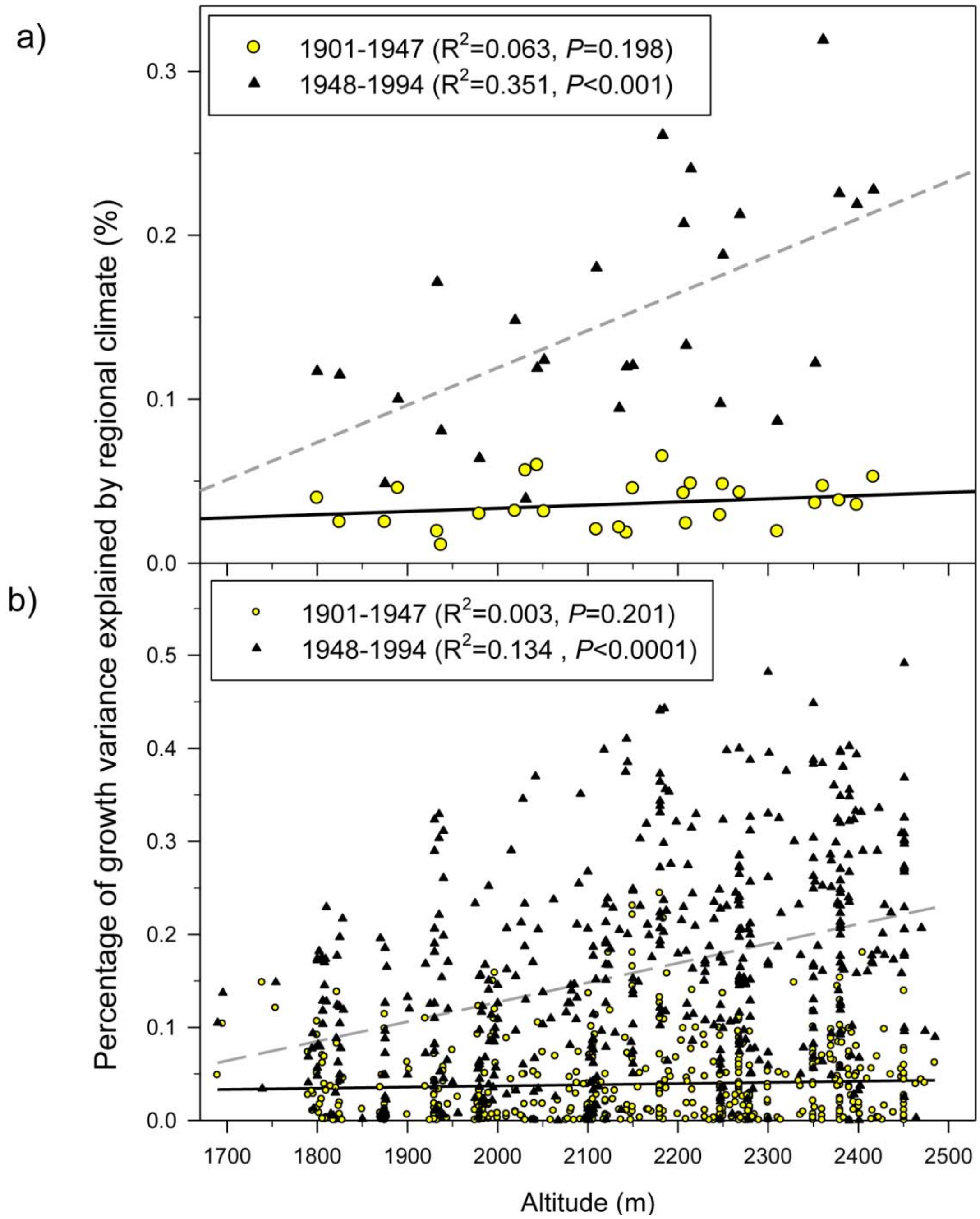

Figure 6. Growth-index variance explained by climatic linear mixed-effects models (R^2) at the site (a) and tree (b) levels, and its relationship with altitude considering two sub-periods of the 20th century (1901-1947, continuous lines; 1948-1994, dashed lines).

Discussion

Advantages and recommended uses of the individual-scale approach

Pooling individual growth-index series of trees coexisting in a site into a mean local chronology is one of the main tenets in dendrochronology when the main purpose is to reconstruct past climate (Fritts 2001). We argue that dendroecology should employ individual-based approaches since the tree is the level of interest for understanding tree species reactions to climate, and consequently for predicting their vulnerability against climate warming (Clark et al. 2012). Carrer (2011) advocated increased focus on individual tree response and our analysis supports the importance of this suggestion. Taking this paradigm shift would allow reducing some of the uncertainty of tree-ring data by sampling coexisting trees of different sizes, ages or historical trajectories (Bowman et al. 2013). We do not argue that the individual tree scale approach is necessary for every dendroecological study but for those forests where a high variability in growth responses to climate is expected. Furthermore, this individual approach may reveal why trees coexisting within the same site show opposing growth-climate responses or growth-climate divergence (Porter and Pisaric 2011). Such varied responses are manifested at different spatial (region, forest, stand, tree) and temporal scales.

Biogeographical patterns in growth-index responses are apparent at the site level

Biogeographical patterns in growth-index responses to climate were noticeable both at the site and tree scales. This is probably the result of sampling across most of the species distribution area and including multiple ecological conditions. The first two principal components of the analyzed growth-index series corresponded to altitude and longitude, respectively. These results confirm that analyses at the site scale allow detecting the idiosyncratic growth responses to climate of populations located near the margin of the species distribution area (Linares et al. 2009).

Eastern and southern sites are more affected by Mediterranean conditions than western and northern ones, which are more humid and subjected to Atlantic influence. Hence summer drought is a more important climatic constrain of growth index in the former sites (see also Büntgen et al. 2010). Carrer et al. (2010) detected similar geographical gradients dominated by latitude (Alpine *vs.* Mediterranean modes) and longitude (eastern *vs.* western Alps) by analysing a wide network of silver fir (*Abies alba*) chronologies across Italian mountains. Our results suggest that east-west dipoles may be characteristic biogeographical patterns affecting growth indices at the region and site scales in mid latitudinal drought-prone areas such as the Mediterranean Basin (Pasho et al. 2011). Nevertheless, this should be tested in the case of *P. uncinata* by sampling additional eastern Pyrenean or Alpine sites.

Unexpected individual growth-index responses to climate in P. uncinata

Following the individual-based approach we observed that the growth-index responses to climate at the species and site scales differed from those detected at the individual tree scale. At the species and site levels the growth-index of *P. uncinata* is enhanced by warm conditions during the previous late fall and during late spring of the year of tree-ring formation, which confirms that the main climatic constrain of growth indices in these forests is low temperature. High temperatures during the previous fall, when most aboveground growth is finished, probably contribute to enhanced photosynthesis and the production and storage of non-structural carbohydrates to be used for earlywood formation during the next year (von Felten et al. 2007). Contrastingly, warmer spring conditions directly affect cambial activity and may trigger earlier growth resumption after winter dormancy and enhance wood production (Camarero et al. 2010).

At the individual scale, most trees formed more wood in response to warmer maximum temperatures during the previous November, but some of them also reacted positively to wet conditions during early summer when radial-growth rates are usually the highest throughout the year (Camarero et al. 1998). The latter finding is to some degree unexpected since most sampled stands correspond to high-elevation subalpine forests where cold conditions constrain growth. However, the consideration of such ample network of sites allowed finding that summer water availability drives *P. uncinata* growth-index mainly in the most xeric sites subjected to Mediterranean influences, i.e. warmer and drier summer conditions. This implies that these trees are probably adapted to dry summers but if climate warming leads to even more arid conditions, *P. uncinata* forests located in marginal locations (Pre-Pyrenees, southern Iberian System) could respond to drying by showing growth decline and die-back as has been observed in other xeric edges of distribution (Linares et al. 2009). Our findings at the tree scale suggest that individuals better performing under these dry Mediterranean conditions have already been selected and these individuals constitute *in situ* reservoirs of drought-resistant genotypes and phenotypes. We expect that climate warming could induce an upward expansion of these xeric populations by reducing cold limitation if this is not accompanied by a severe drought moisture stress during the growing season which limits establishment up to the treeline (Moyes et al. 2013).

An individual approach would allow detecting those trees and site conditions responding more to global-change drivers like warming-induced stress. These sensitive individuals may be particularly abundant in declining tree populations or near the distributional or climatic limits of the species, including uppermost treelines, southern relict populations or drought-prone low-elevation stands.

Our research emphasizes that in a restricted geographical range where trees might be expected to experience similar regional climate, topographical differences related to changing elevation can lead to local variations in the climatic conditions experienced by mountain trees. In mountains, topographical factors such as slope or aspect can enhance or buffer climatic differences observed over large altitudinal gradients (Körner 2012). Nevertheless, we did not find any common topographic variable driving tree growth-index responses for the whole studied region. Tree density and increased competition for light (Coomes and Allen 2007) and water (Linares et al. 2009) also affect growth along altitudinal gradients, but since most *P. uncinata* sampled stands were quite open we expect tree-to-tree competition to be a secondary driver of growth index.

The low variance amount (3-33%) accounted for by linear-mixed effects models using climatic predictors of *P. uncinata* growth-index at the individual scale may be explained by several reasons. First, linear-mixed effects models were fitted to growth indices and not to TRW or basal area increment data. Second, we report the marginal variance explained by fixed factors and not the total variance explained by fixed and random factors. Third, pooling individual series into a population mean magnifies the climatic signal and eliminates variability among trees (Carrer 2011). Overall, we evidence that climate plays a secondary role in controlling growth-index variability among coexisting trees even in harsh environments. Consequently, we must consider individual tree features as drivers of growth responses to climate. In addition, individual trees with significant growth responses to climate, which may represent a small proportion of the whole population, should be carefully monitored using ecophysiological methods to properly understand the mechanisms driving tree responses to climate warming.

Altitude is related to tree growth responses to climate

Altitude plays a major role affecting *P. uncinata* growth-index responses to climate at the site and tree scales in agreement with previous works (Tardif et al. 2003) and with research in widely distributed conifers as Douglas fir (Chen et al. 2010). This suggests that the altitude-mediated decrease in air temperatures is the major driver of growth index at both the site and tree levels determining the maximum elevation of the tree growth form (Ettinger et al. 2011).

Trees growing at higher altitudes showed more growth-index variance explained by climate. This implies that elevation- and age-stratified sampling schemes would be useful to separate different growth-index responses to climate and would allow improving the robustness of paleoclimate reconstructions. Altitude seems to modulate the effects of spring temperatures on growth. Contrastingly, altitude is negatively related to how growth responds to climatic conditions during previous months (before tree-ring formation starts) when carbohydrates synthesis and storage affect subsequent growth. We do not have a satisfactory explanation for these contrasting influences but they suggest a primary effect of the altitudinal thermal gradient on cambium dynamics and tracheid differentiation during the growing season. Xylogenesis studies have evidenced that temperature determines the onset of growth whereas the maximum growth rate and growth cessation are also rather controlled by photoperiod (Moser et al. 2010). Sapwood area exerts a similar effect on spring temperatures affecting the beginning of growth while sapwood and basal areas and tree age diminish the effect of November and March temperatures on wood production before cambial resumption. Similarly, altitude, basal area and tree age enhance growth responses to previous-winter wet conditions but decrease the sensitivity to June precipitation when growth rates are very high (Camarero et al. 1998). This indicates that low-elevation, smaller and younger trees would be the most responsive to summer precipitation.

We also observe an increase in climate-driven *P. uncinata* growth-index variability in the second half of the 20th century. These findings support other studies performed also in the Pyrenees for the same species showing the same trend towards the last decades (Tardif et al. 2003). The improved explanatory power of climatic models was not due to more reliable climate data being recorded in the late 20th century than in previous decades since CRU and long-term local temperature records were tightly related throughout most of that century (Bücher and Dessens 1991). Changes in stand structure and social status of trees could be also the reason for the shift in growth-climate associations but this is not plausible given the slow successional dynamics and the open structure of these high-elevation forests.

A similar instability in the growth-climate relationships was found by Andreu et al. (2007) and related to changing climate conditions. We offer an alternative environmental explanation for this unstable behaviour. Warming has rapidly intensified over north-eastern Spain during the first half of the past century which could have partially ameliorated the coldness constrains on growth indices imposed by the altitudinal gradient. Our findings do support the "relaxation" of the altitudinal gradient due to rapid climate warming postulated by Tardif et al. (2003) particularly for the first half of the past century. Altitude may have become a less important driver of the growth responsiveness to temperature during the period 1901-1947 because of the rapid and intense warming. Later on, altitude was the main driver of temperature-mediated growth in mountain *P. uncinata* forests despite warming continued but at a rate lower than in the mid 20th century. Indeed, during the early half of the 20th century mountain *P. uncinata* trees responded less to climate than later and such responses did not depend on tree elevation. Shifts in the growth-climate associations could also indicate non-linear relationships between growth and climatic drivers. The loss of thermal responses in cold areas could be linked to alterations in carbon allocation and intra-annual growth patterns (Seo et al. 2011). Anyway, our findings emphasize the need to consider warming rates as major drivers of growth responses in forests.

We conclude that both (i) a tree-scale approach to quantify growth-index responses to climate and (ii) a detailed characterization of the potential drivers of those individual tree responses are requisites for applying an individual-based framework in dendroecology. Such increased focus on individual tree responses would improve the ecological knowledge of the individuals' vulnerability against climatic stressors.

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Supporting information

Table S1. Geographical, topographical and ecological characteristics of the sampled *P. uncinata* sites. Stands were arranged from East to West. Sites' codes are as in Figure 1. The 0.5° grids with climate data (produced by the Climate Research Unit, 2008) and covering the Pyrenees are as follows: a: 0–0.5° E, 42–42.5° N; b: 0–0.5° W, 42–42.5° N; c: 0.5°–1.0° W, 42.5–43° N; d: 0.5–1° E, 42–42.5° N; e: 1–1.5° E, 42–42.5° N. Values are means ± SD.

Site (code)	Latitude (N)	Longitude (E / W)	Grid	Altitude (m a.s.l)	Aspect	Slope (°)	Dbh (cm)	Height (m)	Sapwood (cm)	Age at 1.3 m (years)
Estanys de la Pera (EP)	42° 27'	1° 35' E	e	2360	SW	30 ± 0	65.2 ± 11.0	7.8 ± 2.0	5.5 ± 2.6	339 ± 117
Mata de València (MA)	42° 38'	1° 04' E	e	2019	N-NW	19 ± 10	43.2 ± 3.6	12.0 ± 3.1	5.2 ± 1.7	237 ± 72
Estany de Lladres (LA)	42° 33'	1° 03' E	e	2120	NW	35 ± 12	52.1 ± 9.8	8.3 ± 1.6	5.0 ± 1.9	313 ± 123
Airoto (AI)	42° 42'	1° 02' E	e	2300	W	37 ± 29	58.5 ± 13.5	7.4 ± 1.6	6.7 ± 2.1	288 ± 100
Tessó de Son (TS)	42° 35'	1° 02' E	e	2239	N-NE	42 ± 14	74.5 ± 18.8	9.3 ± 3.8	7.4 ± 4.1	346 ± 202
Estany Negre (NE)	42° 33'	1° 02' E	e	2451	SE	35 ± 18	71.0 ± 26.0	6.6 ± 1.9	4.4 ± 1.9	411 ± 182
Estany Gerber (GE)	42° 37'	0° 59' E	d	2268	W	15 ± 15	53.5 ± 14.6	6.9 ± 1.4	4.8 ± 2.2	426 ± 147
Estany d'Amitges (AM)	42° 35'	0° 59' E	d	2390	S-E	40 ± 21	69.0 ± 26.0	9.3 ± 3.8	5.7 ± 2.2	355 ± 106
Mirador (MI)	42° 35'	0° 59' E	d	2180	SE	33 ± 18	55.1 ± 25.8	7.6 ± 2.3	4.6 ± 2.0	401 ± 132
Ratera (RA)	42° 35'	0° 59' E	d	2170	N	40 ± 5	28.3 ± 8.1	10.4 ± 2.0	–	380 ± 146
Sant Maurici (SM)	42° 35'	0° 59' E	d	1933	S-SE	16 ± 15	38.2 ± 5.7	11.5 ± 1.7	4.2 ± 1.2	204 ± 23
Monestero (MO)	42° 34'	0° 59' E	d	2280	SE	28 ± 13	64.4 ± 16.1	9.3 ± 2.1	5.0 ± 2.4	346 ± 110
Corticelles (CO)	42° 34'	0° 56' E	d	2269	W-NW	24 ± 17	83.1 ± 28.8	10.7 ± 3.8	4.9 ± 2.7	509 ± 177
Barranc de Llacs (LL)	42° 32'	0° 55' E	d	2250	N-NW	44 ± 38	71.7 ± 20.0	10.5 ± 2.5	5.0 ± 2.5	616 ± 175
Conangles (CG)	42° 37'	0° 44' E	a	2106	S-SW	43 ± 15	56.0 ± 14.5	6.4 ± 2.7	4.7 ± 2.8	318 ± 117
Vall de Mulleres (VM)	42° 37'	0° 43' E	a	1800	N-NE	34 ± 13	69.0 ± 26.0	9.8 ± 1.8	5.2 ± 2.6	437 ± 184
Bielsa (BI)	42° 42'	0° 11' E	a	2100	E	60 ± 4	45.1 ± 9.4	7.7 ± 3.0	4.7 ± 1.5	270 ± 67
Sobrestivo (SB)	42° 40'	0° 06' E	a	2296	S	38 ± 2	61.7 ± 17.5	7.6 ± 1.7	4.1 ± 1.7	341 ± 97
Foratarruego (FR)	42° 37'	0° 06' E	a	2031	W	37 ± 11	49.5 ± 18.3	8.3 ± 2.9	5.5 ± 1.9	433 ± 50
Ordesa-Cara Norte (ON)	42° 38'	0° 03' W	b	2270	N	40 ± 12	50.2 ± 12.5	9.8 ± 1.7	4.0 ± 1.7	311 ± 45
Senda de Cazadores (SC)	42° 38'	0° 03' W	b	2247	N	39 ± 12	60.9 ± 16.5	9.4 ± 1.6	4.3 ± 2.0	357 ± 145
Mirador del Rey (MR)	42° 38'	0° 04' W	b	1980	SW	25 ± 10	53.3 ± 15.3	10.9 ± 4.6	–	117 ± 18
Las Cutas (CU)	42° 37'	0° 05' W	b	2150	S-SW	20 ± 5	33.3 ± 8.3	9.9 ± 2.5	4.4 ± 2.8	129 ± 16
Guara (GU)	42° 17'	0° 15' W	b	1790	N-NW	35 ± 5	44.5 ± 8.1	9.0 ± 1.7	5.9 ± 2.0	149 ± 36
Respomuso (RE)	42° 49'	0° 17' W	b	2350	S	30 ± 19	49.5 ± 15.1	7.6 ± 1.5	6.1 ± 4.1	280 ± 83
Pic d'Arnousse (PA)	42° 48'	0° 31' W	b	1940	NW	32 ± 4	65.4 ± 5.1	9.4 ± 0.7	9.0 ± 4.6	248 ± 83
Valdelinares-Teruel (TE)	40° 23'	0° 38' W	–	1800	SW-W	10 ± 5	63.8 ± 12.4	10.2 ± 1.8	5.8 ± 4.9	214 ± 107
Larra-La Contienda (CN)	42° 57'	0° 46' W	c	1750	SW	38 ± 24	46.4 ± 14.0	7.8 ± 2.2	3.8 ± 1.3	350 ± 108
Castillo de Vinuesa (VI)	42° 00'	2° 44' W	–	2050	W	21 ± 1	85.6 ± 23.0	9.4 ± 2.9	6.7 ± 2.4	368 ± 148

Table S2. List of the 36 assessed linear mixed-effects models of tree-ring width index (RWI), as a function of climatic variables. All are random intercept models considering trees as random factors. Models with asterisks between explanatory variables include the interaction term. Abbreviations of the explanatory variables: Pp6: current June precipitation; TMM3: current March mean temperature; TMMx3: current March mean maximum temperature; TMMxp11: previous November mean maximum temperature.

Null Model: RWI ~ 1 (intercept only)
Model 1: RWI ~ Pp12
Model 2: RWI ~ Pp6
Model 3: RWI ~ Pp12 + Pp6
Model 4: RWI ~ Pp12 * Pp6
Model 5: RWI ~ TMM3
Model 6: RWI ~ TMM5
Model 7: RWI ~ TMMxp11
Model 8: RWI ~ TMM3 + TMM5
Model 9: RWI ~ TMM3 + TMMxp11
Model 10: RWI ~ TMM5 + TMMxp11
Model 11: RWI ~ TMM3 + TMM5 + TMMxp11
Model 12: RWI ~ TMM3 * TMM5
Model 13: RWI ~ TMM3 * TMMxp11
Model 14: RWI ~ TMM5 * TMMxp11
Model 15: RWI ~ TMM3 * TMM5 * TMMxp11
Model 16: RWI ~ Pp12 + TMM3
Model 17: RWI ~ Pp12 + TMM5
Model 18: RWI ~ Pp12 + TMMxp11
Model 19: RWI ~ Pp12 + TMM3 + TMM5
Model 20: RWI ~ Pp12 + TMM3 + TMMxp11
Model 21: RWI ~ Pp12 + TMM5 + TMMxp11
Model 22: RWI ~ Pp12 + TMM3 + TMM5 + TMMxp11
Model 23: RWI ~ Pp6 + TMM3
Model 24: RWI ~ Pp6 + TMM5
Model 25: RWI ~ Pp6 + TMMxp11
Model 26: RWI ~ Pp6 + TMM3 + TMM5
Model 27: RWI ~ Pp6 + TMM3 + TMMxp11
Model 28: RWI ~ Pp6 + TMM5 + TMMxp11
Model 29: RWI ~ Pp6 + TMM3 + TMM5 + TMMxp11
Model 30: RWI ~ TMM3 + Pp6 + Pp12
Model 31: RWI ~ TMM5 + Pp6 + Pp12
Model 32: RWI ~ TMMxp11 + Pp6 + Pp12
Model 33: RWI ~ TMM3 + TMM5 + Pp6 + Pp12
Model 34: RWI ~ TMM3 + TMMxp11 + Pp6 + Pp12
Model 35: RWI ~ TMM5 + TMMxp11 + Pp6 + Pp12
Model 36: RWI ~ TMM3 + TMM5 + TMMxp11 + Pp6 + Pp12

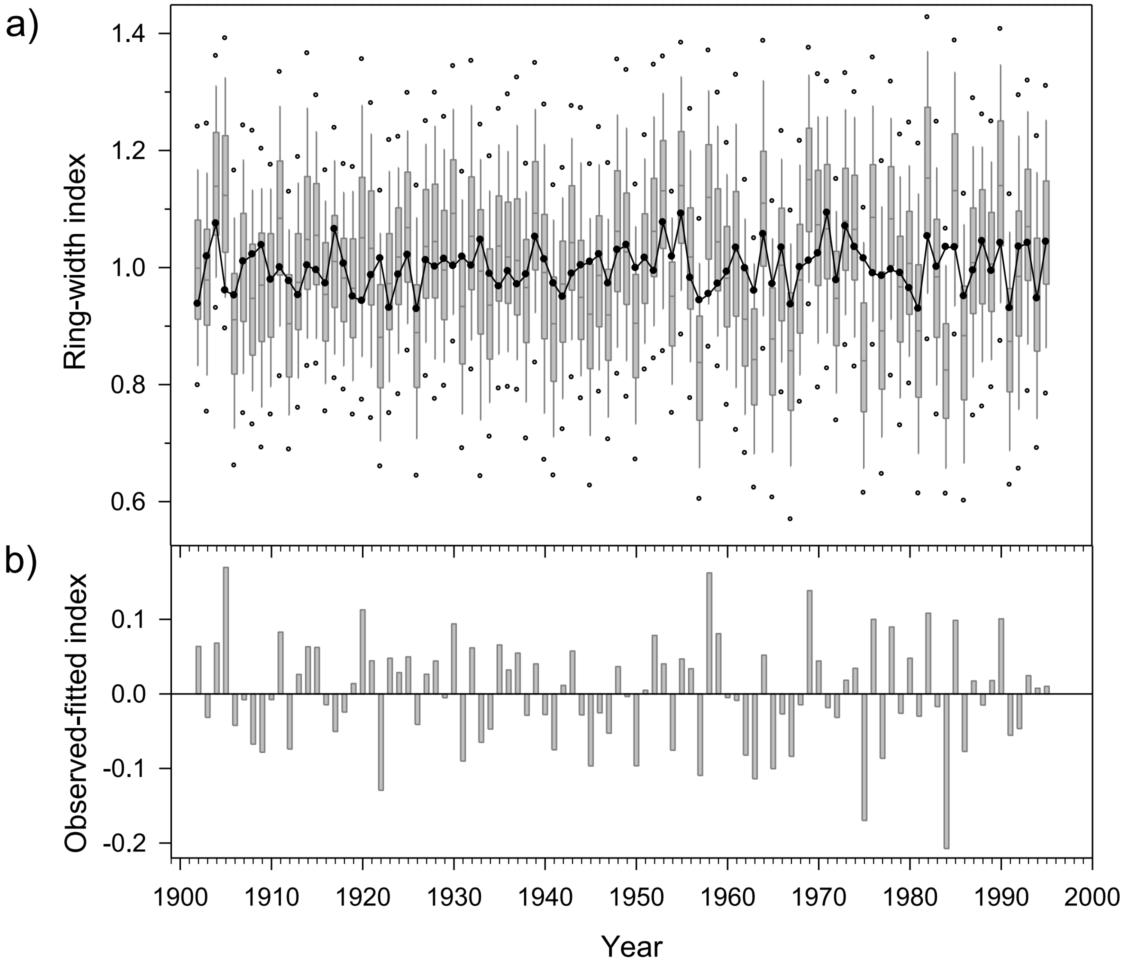

Figure S1. Linear mixed models fitted to mean growth (residual indices) series of Iberian *P. uncinata* forests during the 20th century. The observed (bars with median and 10th, 25th, 75th and 90th percentiles) and fitted (black symbols) growth data (a) are displayed and compared with residuals (b), i.e. the difference between observed and fitted data.

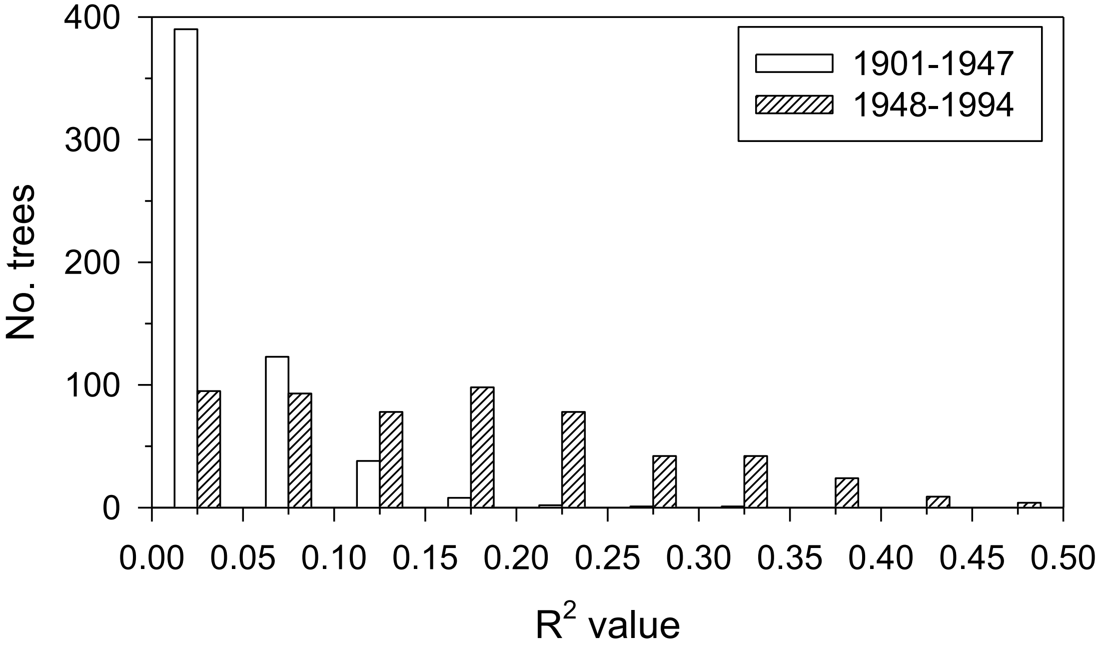

Figure S2. Frequency of trees for two studied periods (1901-1947 and 1948-1994) grouped as a function of the percentage of the variance in tree-ring growth indices (R^2) explained by linear mixed-effects models using climate variables as predictors.

Table S3. Statistical parameters of the selected linear mixed-effects climatic models fitted to residual ring-width indices for all trees and for each studied site and considering the sub-periods 1901-1947 and 1948-1994. Sites are arranged in decreasing value of altitude and within each sampled region including the two Pyrenean National Parks. Growth predictors are monthly climatic variables abbreviated as follows: pTMx11, mean maximum temperatures of the previous November; TMi5, mean minimum temperatures of current May; pP12, precipitation of the previous December; TMi3, mean minimum temperatures of current March; P6, current June precipitation. Climatic variables separated by the ":" symbol are interacting. We fitted 36 mixed-effects models including additive climatic terms and a null model (only intercept) and considering individual trees as random factors (see Table S2). Statistics: *W*ᵢ, relative probability that the selected model is the best one; R^2, percentage of growth variance explained by the model. The most important climatic variable for each site is indicated in bold characters. In those cases where the null model, i.e. the one including only the intercept and the random effects, is the selected model the R^2 was not assessed.

Sub-period 1901-1947

Area	Site	No. trees	Coefficients of climatic variables								*Wi*	R^2 (%)
			Intercept	pTMx11	TMi5	TMi3	pP12	P6	TMi3:pTMx11	TMi5:pTMx11		
All sites	–	582	1.0100	0.0171		-0.0157			**-0.0197**		0.99	14.05
Eastern Pyrenees	EP	20	0.9945			**-0.0187**					0.52	3.84
Central Pyrenees	AI	14	1.0028	0.0206		**-0.0293**					0.81	9.09
PNASM (Central Pyrenees)	NE	42	1.0024	0.0259		**-0.0379**					0.66	16.68
	AM	24	1.0139	**0.0278**		-0.0251			-0.0231		0.90	11.55
	MO	25	1.0022				0.0200	**0.0210**			0.61	16.01
	CO	19	1.0098	0.0261		-0.0304			**-0.0305**		0.99	16.24
	GE	39	1.0127	0.0298		-0.0213			**-0.0324**		0.99	15.17
	LL	45	0.9979		-0.0127		**0.0147**				0.40	8.24
	TS	10	0.9971								0.92	——
	MI	31	1.0155	0.0294		-0.0294			**-0.0323**		0.96	16.33
	LA	21	1.0055	**0.0206**							0.27	6.91
	MA	8	0.9979								0.63	——
	SM	20	1.0182	0.0093		-0.0101			**-0.0725**		0.72	14.96

Central Pyrenees	CG	15	0.9953								0.64	——
	VM	12	0.9965								0.76	——
	BI	9	1.0094					**0.0504**			0.87	7.03
PNOMP (Central Pyrenees)	SB	26	1.0019								0.42	——
	SC	38	1.0062					**0.0190**			0.81	5.28
	ON	11	1.0004					**0.0260**			0.75	7.97
	CU	8	1.0226	0.0528			**-0.0677**				0.96	23.48
	MR	17	1.0010		**-0.0262**		-0.0243	0.0230			0.37	10.36
Western-central Pyrenees	RE	16	0.9988								0.49	——
	PA	7	0.9998								0.88	——
Western Pyrenees	AT	15	0.9945								0.87	——
	CN	20	1.0082	**0.0418**		-0.0389		0.0298			0.90	14.71
Pre-Pyrenees	GU	22	1.0011					0.0211			0.68	2.63
Iberian System	TE	26	0.9975					**0.0284**			0.94	6.12
	VI	22	1.0254	0.0353	0.0289					**0.0414**	0.86	12.05

Sub-period 1948-1994

All sites	–	582	0.9888	**0.0443**	0.0134	-0.0134	0.0274	0.0111			0.99	42.32
Eastern Pyrenees	EP	20	1.0179	0.0378	**0.0511**	-0.0327			0.0419	-0.0082	0.96	51.26
Central Pyrenees	AI	14	0.9986	0.0316	0.0411		**0.0482**				0.88	36.17
PNASM (Central Pyrenees)	NE	42	1.0000	0.0350	0.0509	-0.0160	**0.0594**				0.94	49.77
	AM	24	1.0003	0.0294	**0.0608**	-0.0183	0.0549	0.0173			0.95	55.17
	MO	25	0.9965	**0.0495**	0.0462	-0.0209	0.0288				0.86	45.76
	CO	19	1.0001	**0.0381**	0.0312	-0.0211	0.0341				0.94	44.01
	GE	39	0.9957	0.0334	0.0463	-0.0195	**0.0515**				0.88	40.31
	LL	45	0.9959	**0.0350**	0.0323	-0.0186	0.0305				0.96	47.62
	TS	10	0.9919	**0.0431**	0.0301		0.0361				0.88	34.44

	MI	31	0.9941	0.0402	0.0479	-0.0208	**0.0538**	0.0164			0.94	53.89
	LA	21	1.0055								0.44	——
	MA	8	0.9888	**0.0586**	0.0501		0.0544	0.0402			0.80	37.12
	SM	20	0.9828	0.0467	0.0307		**0.0694**	0.0232			0.96	38.23
Central Pyrenees	CG	15	0.9992	**0.0339**	0.0263	-0.0274	0.0210				0.57	32.29
	VM	12	0.9932	**0.0493**			0.0334				0.38	25.96
	BI	9	0.9754	**0.0683**				0.0459			0.44	22.44
PNOMP (Central Pyrenees)	SB	26	0.9931	**0.0369**	0.0211						0.93	19.28
	SC	38	0.9750	**0.0677**			0.0160				0.51	25.77
	ON	11	0.9804	**0.0562**							0.84	14.04
	CU	8	0.9739	**0.0769**							0.56	29.34
	MR	17	0.9846	**0.0479**	0.0241						0.81	17.83
Western-central Pyrenees	RE	16	0.9865	**0.0531**	0.0291						0.49	29.19
	PA	7	0.9773	**0.0586**							0.88	14.18
Western Pyrenees	AT	15	0.9928	**0.0408**					-0.0150	0.0395	0.95	9.60
	CN	20	0.9782	**0.0497**	-0.0453	0.0203					0.74	21.88
Pre-Pyrenees	GU	22	0.7413	**0.0677**	0.0346		0.0294	0.0220			0.82	30.67
Iberian System	TE	26	0.9855	**0.0544**	0.0501			0.0385	0.0016	-0.0232	0.98	30.04
	VI	22	1.0007	**0.0513**	0.0496	0.0115					0.98	33.17

Table S4. Significant relationships (Spearman correlation coefficients) obtained by relating environmental and tree variables and the tree growth-index responses to monthly climatic variables (columns of the table, i.e. coefficients calculated between growth indices and climatic variables). For instance, the growth-index responses to mean maximum temperature of the previous November were negatively related to altitude and tree age. Significant coefficients (P_B) were calculated after a Bonferroni correction ($P \leq 0.005$). Main climatic variables affecting growth-index: mean maximum temperatures of the previous November (pTMx11); mean minimum temperatures of current March (TMi3) and May (TMi5); precipitation of the previous December (pP12) and the current June (P6).

Variable	Climatic variable affecting growth index				
	pTMx11	TMi3	TMi5	pP12	P6
Altitude	-0.203	-0.299	0.312	0.304	-0.197
Sapwood area		-0.193	0.183		
Basal area		-0.250			-0.144
Tree age	-0.137	-0.217		0.194	-0.127

... A tree says: a kernel is hidden in me, a spark, a thought; I am life from eternal life. The attempt and the risk that the eternal Mother took with me is unique, unique the form and veins of my skin, unique the smallest play of leaves in my branches and the smallest scar on my bark. I was made to form and reveal the eternal in my own smallest special detail.

... Un árbol dice: en mí se oculta una semilla, una chispa, un pensamiento, soy vida de la vida eterna. El esfuerzo y el riesgo que la Madre eterna asumió conmigo son únicos, única es mi forma y únicas las venas de mi piel, único el juego más insignificante de las hojas en mis ramas y la más pequeña cicatriz de mi corteza. Fui creado para dar forma y mostrar lo eterno en mi más pequeño detalle.

Chapter 3

Drought-induced weakening of growth-temperature associations in a high-elevation pine network across the Pyrenees

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Summary

The growth/climate relationship of theoretically temperature controlled high-elevation forests has weakened over the last decades. This is likely due to new limiting factors, such as an increasing drought risk for ecosystem functioning and productivity across the Mediterranean Basin. In addition, declining tree growth sensitivity to spring temperature may emerge in response to increasing drought stress. Here, we evaluate these ideas by assessing the growth/climate sensitivity of 1500 tree-ring width (TRW) and 102 maximum density (MXD) measurement series from 711 and 74 trees, respectively, sampled at 30 high-elevation Iberian *Pinus uncinata* forest sites. Different dendroclimatological standardization and split period approaches were used to assess the high- to low-frequency behaviour of 20th century tree growth in response to temperature means, precipitation totals and drought indices. Variations in TRW track summer temperatures until about 1970 but diverge afterwards, whereas MXD captures the recent temperature increasing fairly well. In contrast to the observed low-frequency trend offset between TRW and summer temperature was the high-frequency signal stable until present. Summer drought has increasingly driven TRW along the 20th century, although it has shown a diverging trend from MXD after the 1970s. Our results imply fading temperature sensitivity of high-elevation *P. uncinata* forest growth in the Spanish Pyrenees, and reveal the importance of summer drought that is recently becoming the emergent limiting factor of ring width formation in many parts of the Mediterranean Basin.

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Introduction

Trees growing in cold-limited environments such as high-latitude and mountain forests including the arctic and alpine ecotones can record temperature variations in their annual ring width (TRW) and maximum latewood density (MXD) (Fritts 2001). In fact, temperature might be the main climatic driver of tree growth and thus constrains wood formation during overall short growing seasons (Körner 2012). Old growing treeline species, together with modern dendroclimatological methods are therefore regarded as reliable proxy archives that enable annually resolved temperature reconstructions to be continuously developed for several centuries to millennia (Büntgen et al. 2011). At the European-scale, several examples from the high-northern latitudes in Fennoscandia (Briffa et al. 1990, Grudd 2008), and higher elevations along the Carpathian arc (Büntgen et al. 2007, 2013; Popa and Kern 2008) and the Alps (Rolland et al. 1998; Büntgen et al. 2005, 2006; Corona et al. 2010) demonstrated the palaeoclimatic potential of tree rings.

The vast majority of the mid-latitudes are, however, characterized by more periodic moisture deficits, because climate may alternate between arid and humid conditions southwards or northwards respectively. Complex growth/climate relationships are therefore known for the Mediterranean Basin and the Sierra Nevada in California (Tardif et al. 2003, Bunn et al. 2005, Carrer et al. 2010, Büntgen et al. 2012). In these ecosystems, daily to seasonal precipitation changes can mediate intra and inter-annual patterns of forest growth, and summer drought can be strong enough to even interrupt cell formation (Nicault et al. 2001, De Luis et al. 2007). If such drought-induced growth responses also occur in high-elevation forests of the mid-latitudes and may even affect water-saturated upper treeline sites remains unknown. If however true, such hydroclimatic stressors would question the reliability of temperature reconstructions.

Spatiotemporal instability in growth/climate relationships, the so-called divergence phenomena (D'Arrigo et al. 2008), may indeed be magnified by predicted future drought across the Mediterranean Basin (Lebourgeois et al. 2012), which would subsequently dampen the temperature control of tree growth. Testing this hypothesis of a recently more complex growth/climate relationships in Mediterranean mountain forest ecosystems is, however, complicated by the scarcity of high-elevation sites that were temperature-controlled (Körner 2012). The Pyrenees constitutes the only mountain system where undisturbed temperature-driven upper treelines can be found south of the Alpine arc.

Here we seek to assess if the growth/climate relationship in a high-elevation network of *Pinus uncinata* forest sites across the Pyrenees changed over the last century and, if so, to pinpoint the relevant drivers. We therefore compile 30 TRW chronologies together with MXD measurements from six of these sites between 1750 and 2451 m asl. Various tree-ring detrending and chronology development techniques, together with split-period approaches and multiple intra-annual intervals are considered and evaluated to assure that the observed associations between tree growth and climate are by no means artificially induced or spatiotemporally biased.

Materials and methods

Study species and sites

Pinus uncinata Ram. is a long-lived, slow-growing and shade-intolerant conifer with a large ecological amplitude concerning topography and soil type (Ceballos and Ruiz de la Torre 1979). In this species ca. 80% of the annual width is formed between June and July and latewood formation lasts from July up to October (Camarero et al. 1998). Warm autumn and spring temperatures before and during ring formation enhance *P. uncinata* radial growth in Pyrenean forests, respectively (Tardif et al. 2003). We sampled 30 *P. uncinata* sites of which 27 sites are located in the Pyrenees, one site is in the Pre-Pyrenean Sierra de Guara and two southern relict populations were located in the Iberian System. Data cover the whole geographical range of the species in the Iberian Peninsula and thus capture most of the ecological variability experienced by this species (Fig. 1, Table 1). Most of the Pyrenean sites (19 sites) were located within or near protected areas, ensuring that these populations are not likely to have been logged for much of the 20th century. Specifically seven sites were sampled within or near the Ordesa y Monte Perdido National Park (PNOMP; 42º40'N, 00º03'E; established in 1918), and twelve sites were sampled in the Aigüestortes i Estany de Sant Maurici National Park area (PNAESM; 42º35'N, 00º57'E; established in 1955). Pyrenean *P. uncinata* forests are usually low-density open-canopy stands located in steep and elevated sites forming isolated patches near the alpine treeline. The macroclimate of the Pyrenees is strongly influenced by east–west and north–south gradients with increasing Mediterranean conditions (e.g. warm and dry summers) eastwards and southwards, whereas continental conditions prevail in the Central Pyrenees, which explains the high climatic heterogeneity of this area (López-Moreno et al. 2008). Mean annual temperature and total precipitation in the studied sites ranged from 2.0 to 4.9 °C and from 1200 to 2000 mm, respectively, with January and July as the coldest (mean -2.0 °C) and warmest (mean 12.5 °C) months respectively (Camarero 1999). The relict populations of Teruel and Soria and the Prepyrenean site Guara are subjected to typically Mediterranean conditions such as warm and dry summers. For its part, the Pyrenees are included in the Mediterranean Basin but still influenced by both oceanic (wet and cool winters) and continental (cold winters) conditions. Mediterranean summer drought is more prevalent at PNOMP than at PNAESM sites (Balcells and Gil-Pelegrín 1992).

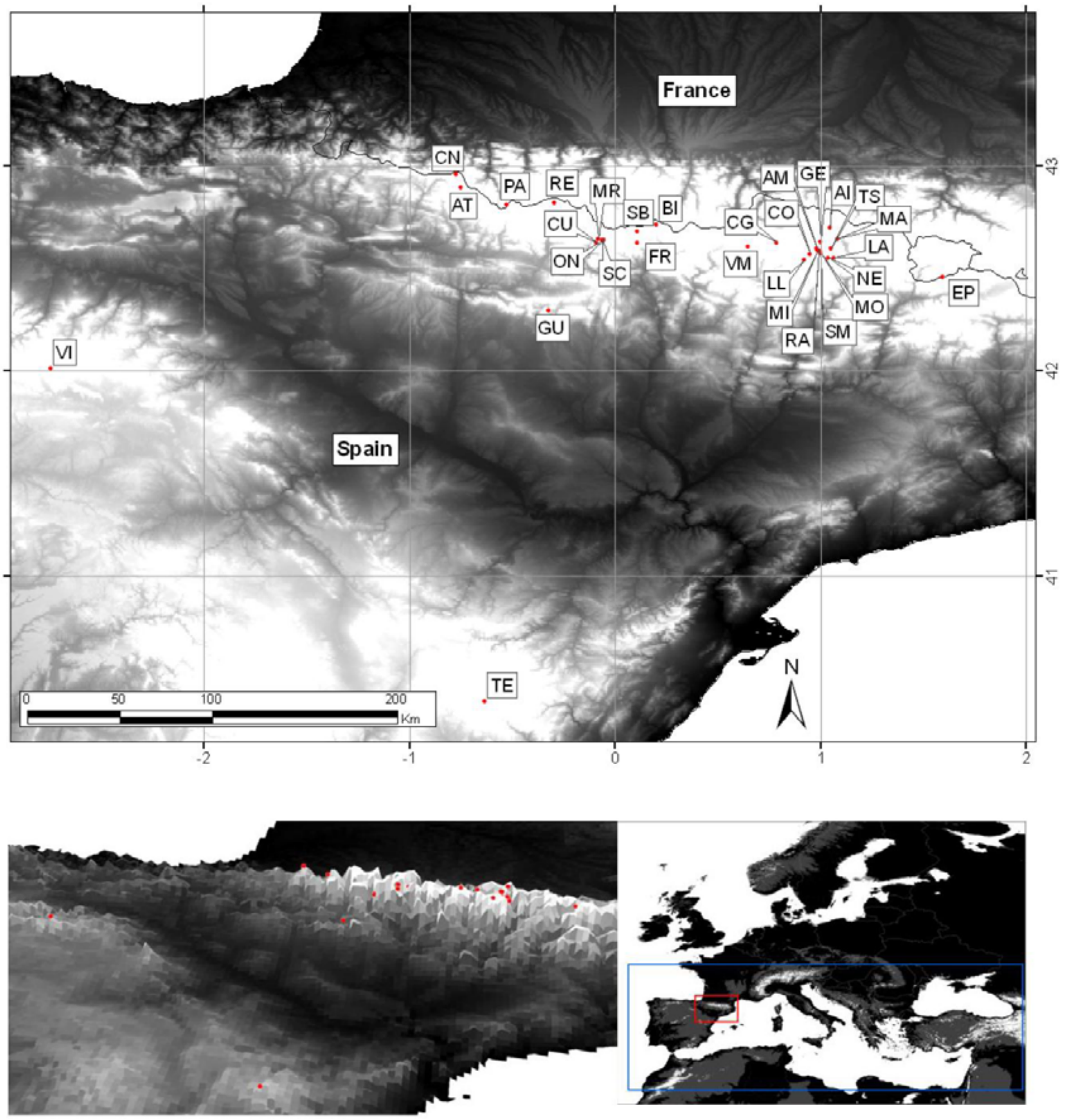

Figure 1. Network of the 30 Iberian *Pinus uncinata* sampled sites (white areas indicate high-elevation sites). The left lower 3D graph emphasizes the sampled sites located at high altitudes, mostly in the Spanish Pyrenees. The right lower map shows the location of the study area (red box, NE Spain) within the Mediterranean Basin (blue box).

Table 1. Geographical, topographical and ecological characteristics of the sampled *P. uncinata* sites. Stands are arranged from East to West. Sites' codes are as in Figure 1. Values are means ± SD. In bold, sites where samples for maximum density (MXD) were obtained.

Site (code)	Latitude (N)	Longitude (E / W)	Altitude (m a.s.l)	Aspect	Slope (°)	Dbh (cm)	Height (m)	Age at 1.3 m (years)
Estanys de la Pera (EP)	42° 27'	1° 35' E	2360	SW	30 ± 0	65.2 ± 11.0	7.8 ± 2.0	339 ± 117
Mata de València (MA)	42° 38'	1° 04' E	2019	N-NW	19 ± 10	43.2 ± 3.6	12.0 ± 3.1	237 ± 72
Estany de Lladres (LA)	42° 33'	1° 03' E	2120	NW	35 ± 12	52.1 ± 9.8	8.3 ± 1.6	313 ± 123
Airoto (AI)	42° 42'	1° 02' E	2300	W	37 ± 29	58.5 ± 13.5	7.4 ± 1.6	288 ± 100
Tessó de Son (TS)	42° 35'	1° 02' E	2239	N-NE	42 ± 14	74.5 ± 18.8	9.3 ± 3.8	346 ± 202
Estany Negre (NE)	42° 33'	1° 02' E	2451	SE	35 ± 18	71.0 ± 26.0	6.6 ± 1.9	411 ± 182
Estany Gerber (GE)	42° 37'	0° 59' E	2268	W	15 ± 15	53.5 ± 14.6	6.9 ± 1.4	426 ± 147
Estany d'Amitges (AM)	42° 35'	0° 59' E	2390	S-E	40 ± 21	69.0 ± 26.0	9.3 ± 3.8	355 ± 106
Mirador (MI)	42° 35'	0° 59' E	2180	SE	33 ± 18	55.1 ± 25.8	7.6 ± 2.3	401 ± 132
Ratera (RA)	42° 35'	0° 59' E	2170	N	40 ± 5	28.3 ± 8.1	10.4 ± 2.0	380 ± 146
Sant Maurici (SM)	42° 35'	0° 59' E	1933	S-SE	16 ± 15	38.2 ± 5.7	11.5 ± 1.7	204 ± 23
Monestero (MO)	42° 34'	0° 59' E	2280	SE	28 ± 13	64.4 ± 16.1	9.3 ± 2.1	346 ± 110
Corticelles (CO)	42° 34'	0° 56' E	2269	W-NW	24 ± 17	83.1 ± 28.8	10.7 ± 3.8	509 ± 177
Barranc de Llacs (LL)	42° 32'	0° 55' E	2250	N-NW	44 ± 38	71.7 ± 20.0	10.5 ± 2.5	616 ± 175
Atxerito (AT)	42'53'	0°45' E	1875	N	57 ± 22	64.7 ± 27.2	7.7 ± 2.4	422 ± 159
Conangles (CG)	42° 37'	0° 44' E	2106	S-SW	43 ± 15	56.0 ± 14.5	6.4 ± 2.7	318 ± 117
Vall de Mulleres (VM)	42° 37'	0° 43' E	1800	N-NE	34 ± 13	69.0 ± 26.0	9.8 ± 1.8	437 ± 184
Bielsa (BI)	42° 42'	0° 11' E	2100	E	60 ± 4	45.1 ± 9.4	7.7 ± 3.0	270 ± 67
Sobrestivo (SB)	42° 40'	0° 06' E	2296	S	38 ± 2	61.7 ± 17.5	7.6 ± 1.7	341 ± 97
Foratarruego (FR)	42° 37'	0° 06' E	2031	W	37 ± 11	49.5 ± 18.3	8.3 ± 2.9	433 ± 50
Senda Cazadores (SC)	42° 38'	0° 03' W	2247	N	39 ± 12	60.9 ± 16.5	9.4 ± 1.6	357 ± 145
Ordesa-Cara Norte (ON)	42° 38'	0° 03' W	2270	N	40 ± 12	50.2 ± 12.5	9.8 ± 1.7	311 ± 45
Mirador del Rey (MR)	42° 38'	0° 04' W	1980	SW	25 ± 10	53.3 ± 15.3	10.9 ± 4.6	117 ± 18
Las Cutas (CU)	42° 37'	0° 05' W	2150	S-SW	20 ± 5	33.3 ± 8.3	9.9 ± 2.5	129 ± 16
Guara (GU)	42° 17'	0° 15' W	1790	N-NW	35 ± 5	44.5 ± 8.1	9.0 ± 1.7	149 ± 36
Respomuso (RE)	42° 49'	0° 17' W	2350	S	30 ± 19	49.5 ± 15.1	7.6 ± 1.5	280 ± 83
Pic d'Arnousse (PA)	42° 48'	0° 31' W	1940	NW	32 ± 4	65.4 ± 5.1	9.4 ± 0.7	248 ± 83
Valdelinares-Teruel (TE)	40° 23'	0° 38' W	1800	SW-W	10 ± 5	63.8 ± 12.4	10.2 ± 1.8	214 ± 107
Larra-La Contienda (CN)	42° 57'	0° 46' W	1750	SW	38 ± 24	46.4 ± 14.0	7.8 ± 2.2	350 ± 108
Castillo de Vinuesa (VI)	42° 00'	2° 44' W	2050	W	21 ± 1	85.6 ± 23.0	9.4 ± 2.9	368 ± 148

Field sampling and dendrochronological methods

We sampled 711 living trees between 1994 and 2011, following standard dendrochronological methods: at each site, five to 65 dominant trees (mean ± SD = 24 ± 14 sampled trees per site) were randomly selected, with the number of sampled trees per site depending on the estimated density of available trees within each site. Except for a few cases, distance between trees was sufficient to avoid capturing local effects on tree growth due to spatial autocorrelation. All individuals were cored with a Pressler increment borer taking two or three cores per tree (n =

1500 cores, mean ± SD = 47 ± 27 sampled cores per site). Each core was mounted and sanded with progressively finer grain until tree rings were clearly visible (Stokes and Smiley 1968). Samples were then visually cross-dated and measured to a precision of 0.01 mm using a LINTAB measuring device (Rinntech, Germany). Cross-dating was evaluated using the program COFECHA (Holmes 1983), which calculates cross correlations between individual series of each core and a master chronology. For the MXD measurements, we cored a subsample (n = 74 trees) by taking cores perpendicular to the stem from 6 sites (4 sites located in PNAESM plus 2 sites from PNOMP) with a thicker Pressler increment borer (1 cm diameter); MXD cores were glued onto wooden supports and thin wooden laths (~1 mm) were cut with a twin-bladed saw. Density was measured with an Itrax WoodScanner from Cox Analytical Systems (http://www.coxsys.se), where laths are scanned using a focused high-energy x-ray beam. The radiographic image is analyzed with the software WinDendro (Regent Instruments, Canada), which performs a light calibration of the grey values using a calibration wedge (Grudd 2008).

Tree-ring data and detrending

Since MXD data was collected only from the Pyrenees (Tables 1 and 2), we combined all the MXD series in one single chronology set called *Pyrenees*. TRW was assigned three chronology subsets depending on the geographical location of the sites: (i) the whole network of 30 sampled sites, (ii) the 27 Pyrenean sites, and (iii) the 15 PNAESM sites; hereafter called *AllSites*, *Pyrenees* and *Aigüestortes* subsets respectively. As explained before, PNOMP is more influenced by Mediterranean and drier conditions than PNAESM; therefore, and in order to assess possible Mediterranean drought influences, we used an additional TRW subset called *Ordesa,* which compiles the series coming from the 6 PNOMP sites. The *Aigüestortes* subset was taken considering also the relative robust convergence of the principal components (PCs) scores of the PNAESM sites in the two dimensional space of a principal component analysis based on the covariance matrix of the standard chronologies of the 30 sampled sites, considering their common period 1901-1994 (see yellow symbols in Fig. S1). The first and second PCs explained 47.2% and 8.1% of the whole site growth variability, respectively. Sites near the distribution limits of the species (e.g. GU, TE, CN, PA) are arranged at relatively lower altitudes (i.e. PC1 scores). In spite of chronologies showing different loadings with the PC1, all of them had positive correlations within it, showing that they shared a common variance.

Table 2. Statistical characteristics for each site TRW chronology. Variables of raw tree-ring series for the time span analysed: SD, standard deviation; AC, first-order autocorrelation. Variables of residual chronologies: ms_x, mean sensitivity, a measure of year-to-year growth variability; r_{bt}, mean correlation between trees which evaluates the similarity in growth among trees; E1, variance explained by the first principal component. The reliable time span was defined as the period with EPS > 0.85, where the EPS (Expressed Population Signal) is a measure of the statistical quality of the mean site chronology as compared with a perfect infinitely replicated chronology (Wigley et al. 1984). *N trees* is the number of trees needed to reach the EPS threshold for each site. The mean length was calculated for the time span, while tree-ring width, AC, ms_x, r_{bt} and E1 are calculated from 1901 to 1994. In bold, sites with MXD data.

Raw data								Residual chronology		
Site	No. trees / radii	Time span	Mean length (years)	Tree-ring width ± SD (mm)	AC	Reliable time span (EPS > 0.85)	N trees	ms_x	r_{bt}	E1 (%)
EP	20 / 39	1586-1997	198	0.95 ± 0.36	0.77	1775-1997	10	0.15	0.35	37.84
MA	10 / 20	1668-1997	175	0.92 ± 0.51	0.85	1785-1997	9	0.18	0.40	47.19
LA	36 / 74	1390-2009	243	0.80 ± 0.40	0.85	1390-2009	13	0.13	0.27	32.34
AI	16 / 31	1651-1996	194	1.02 ± 0.35	0.77	1748-1996	7	0.14	0.45	49.00
TS	10 / 17	1537-1995	252	0.88 ± 0.38	0.84	1773-1995	13	0.12	0.32	38.43
NE	46 / 86	1393-2009	242	0.74 ± 0.33	0.79	1652-2009	11	0.14	0.36	38.34
GE	41 / 79	1270-2010	278	0.59 ± 0.26	0.81	1423-2010	11	0.12	0.43	50.06
AM	25 / 56	1592-2009	229	0.83 ± 0.33	0.77	1665-2009	7	0.15	0.48	51.79
MI	33 / 85	1390-2009	252	0.59 ± 0.32	0.83	1596-2009	12	0.16	0.34	37.25
RA	5 / 13	1818-2009	192	1.07 ± 0.70	0.88	1856-2009	5	0.17	0.40	50.36
SM	20 / 40	1811-1996	164	0.94 ± 0.68	0.89	1819-1996	9	0.18	0.48	50.57
MO	30 / 76	1481-2009	246	0.92 ± 0.50	0.87	1691-2009	13	0.12	0.31	34.24
CO	25 / 43	1509-1995	274	0.64 ± 0.25	0.78	1594-1995	15	0.14	0.34	37.51
LL	17 / 17	1338-1997	435	0.59 ± 0.29	0.88	1548-1997	17	0.11	0.33	38.51
AT	17 / 43	1317-2010	339	0.59 ± 0.21	0.75	1474-2010	16	0.13	0.28	31.52
CG	25 / 54	1510-1994	215	0.82 ± 0.36	0.82	1700-1994	14	0.15	0.26	30.37
VM	12 / 23	1476-1994	234	0.77 ± 0.37	0.83	1816-1994	12	0.14	0.29	34.34
BI	11 / 20	1707-1996	196	0.80 ± 0.53	0.82	1766-1996	10	0.21	0.40	46.27
SB	53 / 95	1512-2009	285	0.84 ± 0.51	0.85	1617-2009	16	0.15	0.30	32.1
FR	12 / 25	1438-1947	305	0.50 ± 0.29	0.82	1582-1947	5	0.16	0.30	47.41
SC	65 / 119	1421-2010	256	0.72 ± 0.41	0.85	1571-2010	27	0.12	0.28	29.51
ON	14 / 27	1531-1998	234	0.76 ± 0.36	0.81	1716-1998	6	0.21	0.28	33.43
MR	17 / 34	1795-1998	156	0.77 ± 0.44	0.86	1836-1998	12	0.15	0.31	34.39
CU	10 / 20	1871-1997	98	1.71 ± 0.65	0.74	1892-1997	10	0.22	0.39	47.56
GU	27 42	1800-2011	122	1.85 ± 1.00	0.81	1873-2011	11	0.23	0.39	42.26
RE	20 / 47	1572-2010	202	0.84 ± 0.42	0.81	1742-2010	18	0.15	0.26	31.40
PA	8 / 16	1755-1994	170	1.14 ± 0.62	0.84	1778-1994	5	0.18	0.32	40.58
TE	35 / 68	1730-2008	157	1.33 ± 0.74	0.83	1741-2008	13	0.14	0.41	46.57
CN	25 / 57	1364-2010	252	0.68 ± 0.42	0.82	1670-2010	13	0.16	0.33	36.93
VI	24 / 42	1561-2010	238	0.99 ± 0.49	0.81	1731-2010	14	0.18	0.31	42.10

For building the *Allsites*, *Pyrenees*, *Aigüestortes* and *Ordesa* combined chronologies, we joint all the individual series from the sites covered by each area. For example, for building the *Allsites* chronology we combined all the 1500 TRW series, and in the case of the *Ordesa* chronology we joint all the series from the PNOMP sites, i.e. ON, CU, SC, MR, SB and FR. To remove tree-age related, non-climatic growth trends from the raw TRW and MXD measurement series (Cook and Kairiukstis 1990), and to assess the effects of the chosen standardization techniques on the final chronology shape, we applied ten different detrending methods to the TRW subsets and the MXD set using the ARSTAN program (Cook and Holmes 1986). Specifically, we preserved variability at inter-annual to multi-decadal scales detrending each TRW and MXD individual series by means of cubic smoothing splines with 50% frequency-response cutoffs equal to 150 and 300 years (Cook and Peters 1981). Using shorter and, hence, more flexible splines, would allow registering non-desired trends, e.g. the characteristic down slope age trend of the TRW raw series which also characterizes our data (not shown). A negative exponential function detrending was also applied together with an alternative linear regression of slope of any sign (detrending called hereafter 'negative exponential *1*') or with an alternative linear regression of negative slope ('negative exponential *2*'). We also applied the age-aligned regional curve standardization (RCS; Esper et al. 2003) for preserving inter-annual to centennial-scale variability.

For these different detrendings, dimensionless indices were calculated as residuals from the estimated growth curves after power transformation (*pt*) of the raw measurements (Cook and Peters 1997), and as ratios after using the raw measurements without any transformation (*nt*). We performed a variance stabilization technique to every chronology for minimizing the putative effects of changing sample size throughout time (Frank et al. 2007). Mean chronologies were then calculated using a bi-weight robust mean (Cook 1985). We exclusively used the standard chronologies (via ARSTAN routine), and applied the Expressed Population Signal (EPS) calculated over 30-year windows lagged by 15 years to estimate signal strength of these records (Wigley et al. 1984). Throughout the paper, we refer to TRW chronologies derived from the whole sampled network (i.e. *Allsites* TRW subset), and to MXD chronologies derived from the 6 Pyrenean sampled sites from where we obtained MXD data (i.e. *Pyrenees* MXD subset).

Instrumental target data and growth-climate response analyses

Monthly temperature (mean, maximum and minimum) and precipitation data (CRUTS3.10; Harris et al. 2013) were used for growth/climate response analysis. We considered 0.5° resolution grid-box data covering the different sampled sites of each subset. We also used the standardized precipitation evapotranspiration drought index (SPEI; Vicente-Serrano et al. 2010), calculated from the CRUTS3.20 dataset. SPEI quantifies water deficit in a more accurate and objective way than using the precipitation information itself since it considers the diverse time scales of droughts (Vicente-Serrano et al. 2010). Negative (positive) SPEI values correspond to dry (wet) conditions.

The detrended 30 TRW chronologies (derived from the three TRW subsets) and the 10 MXD chronologies (derived from the MXD *Pyrenees* set, i.e. including the whole MXD dataset) were correlated against monthly and seasonal means of maximum, mean, and minimum temperatures and totals of precipitation. We restrict the analyses to the period 1901-2009, which covers the available CRU data period, acknowledging that some potential uncertainty in the meteorological data during the first half of the twentieth century can be present (Büntgen et al. 2008a). We used monthly data from October of the previous year to December of the current year and seasonal means performed from March to September, including therefore the growing season. We also correlated the chronologies to the SPEI index for the 12 months of the year at different time scales from 1 to 24 accumulated months, covering the same period. In order to assess the temporal stability in the growth/climate relationships along the second half of the 20th century, we performed the correlations with maximum temperatures and SPEI in two independent 40-year sub-periods: 1930-1969 and 1970-2009. We quantified spatial correlation fields between the tree-ring series and monthly and seasonal climatic variables for different periods using the web Climate Explorer (http://climexp.knmi.nl). We further evaluated instability in the growth/climate relationship by calculating 31-year moving correlations between growth (TRW, MXD) and climate variables (temperature, SPEI).

Results

Chronology characteristics

TRW (MXD) chronologies span from 1270 to 2010 AD (1407 to 2009 AD), with a mean length of 240 (192) years. TRW (MXD) series have a mean ± SD annual value of 0.66 ± 0.11 mm (0.77 ± 0.39 g cm^{-3}) and a series inter-correlation of 0.44 (0.40). In both TRW and MXD, the eight different spline and exponential detrendings showed a very similar shape (Fig. S2); hence we averaged them in a single chronology, hereafter abbreviated as *TRWmean* and *MXDmean*. Raw and RCS TRW chronologies show the typical negative exponential trend until ~1450; from then on, RCS chronologies grow with a long and steady positive trend (Fig. 2a). From the 1950s onwards, all the TRW chronologies decline until the present. Raw and RCS MXD chronologies show a negative trend until ~1800, and then they rise up to the 1950s for decreasing again. Since the 1970s all the MXD chronologies start trending upwards up to the present (Fig. 2b). These results are essential the same as the ones observed in the *Pyrenees* and *Aigüestortes* subsets (not shown). The RCS chronologies highlight the decrease in TRW in the transition between the warm Medieval Climatic Anomaly and the cold Little Ice Age (LIA) starting in 1300 AD and lasting until 1850 AD, where temperatures started to increase again (Moreno et al. 2012). Both TRW and MXD chronologies display a valley shape in 1816 following the eruption of Mount Tambora in 1815, which caused the "year without summer" (Trigo et al. 2009). There is another sharp decrease in TRW and MXD around 1700 AD. The decrease in growth in the last 50 years is not unprecedented and lower growth rates occurred in some periods over the LIA, for instance during the fifteenth century (Fig. 2a). Expressed population signal (EPS) and signal-to-noise ratio (SNR) are very consistent among the 10 different detrendings (Table 3). TRW (MXD) chronology stays above the 0.85 EPS threshold since 1500 (1777) AD (Figs. S3 and S4). Mean segment lengths of the TRW site chronologies show how aging trees display a decreasing growth rate (Fig. S5).

Figure 2 (next page). Comparison between the RCS standard chronology from non-transformed (continuous dark lines) and power-transformed (dotted dark lines) raw data with the mean standard chronology derived from the 8 different spline and negative exponential detrendings (continuous light lines), for (a) TRW and (b) MXD. Upper insets show the chronologies comparison for the period 1850-2009 for MXD and 1850-2010 for TRW (areas delimited by the black rectangles). Similar results are displayed in the *Pyrenees* and *Aigüestortes* subsets.

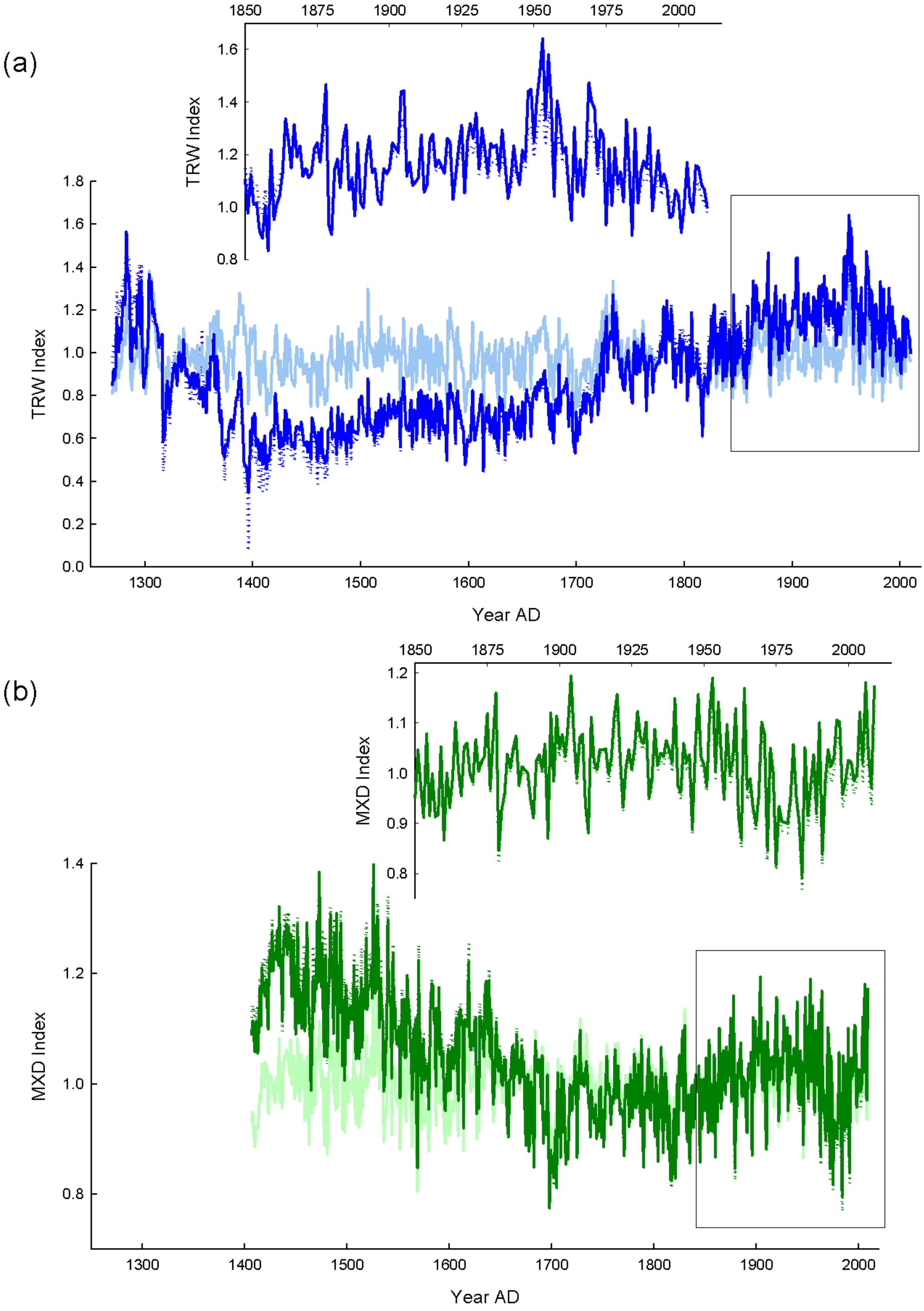

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Table 3. Statistical characteristics of TRW and MXD chronologies (from the whole dataset) resulting from the 10 different detrending methods applied. Variables of standard tree-ring series for the period 1901-2009: *corr*, correlation coefficient with the maximum temperature of the period MJJAS; EPS, Expressed Population Signal, a measure of the statistical quality of the mean site chronology as compared with a perfect infinitely replicated chronology (Wigley et al. 1984); SNR, signal-to-noise ratio, the statistical size of the common variance between the trees; PC1, variance explained by the first principal component; ms_x, mean sensitivity, a measure of year-to-year growth variability.

	Data transformation method	Detrending method	*corr*	EPS	SNR	PC1 (%)
TRW	non-transformed	neg exp1	0.013	0.995	23.666	28.35
		neg exp2	0.087	0.994	23.365	30.56
		150-yr spline	0.213	0.994	23.365	27.42
		300-yr spline	0.219	0.995	23.366	28.07
		RCS	-0.066	0.995	23.366	22.58
	power-transformed	neg exp1	-0.012	0.995	23.366	27.42
		neg exp2	0.064	0.994	23.365	32.14
		150-yr spline	0.180	0.995	23.366	28.03
		300-yr spline	0.119	0.995	23.366	26.52
		RCS	-0.149	0.996	23.367	25.86
MXD	non-transformed	neg exp1	0.244	0.919	11.381	37.07
		neg exp2	0.277	0.919	11.381	36.16
		150-yr spline	0.336	0.920	11.490	55.31
		300-yr spline	0.301	0.919	11.381	42.59
		RCS	0.247	0.918	11.274	46.27
	power-transformed	neg exp1	0.246	0.921	11.599	33.32
		neg exp2	0.274	0.921	11.599	31.76
		150-yr spline	0.339	0.923	11.820	37.87
		300-yr spline	0.306	0.921	11.599	45.07
		RCS	0.198	0.920	11.490	47.96

Growth-climate responses patterns

TRW and MXD correlations with previous-year October to current-year December monthly temperature data show that they are mainly influenced by previous-year November, May and March temperatures (Fig. 3). Seasonal correlations, i.e. combining several months, did not increase significantly the strength of the main relationships observed at monthly scales (Fig. 3). TRW correlations with May and previous November maximum temperatures are stronger in the first sub-period (1930-1969) than in the second one (1970-2009) (except in the case of the spline-detrended chronology, see Fig. 3a), indicating temporal instability of the growth/climate relationships. All the different detrendings applied display high synchrony between their correlations with temperature in the first sub-period.

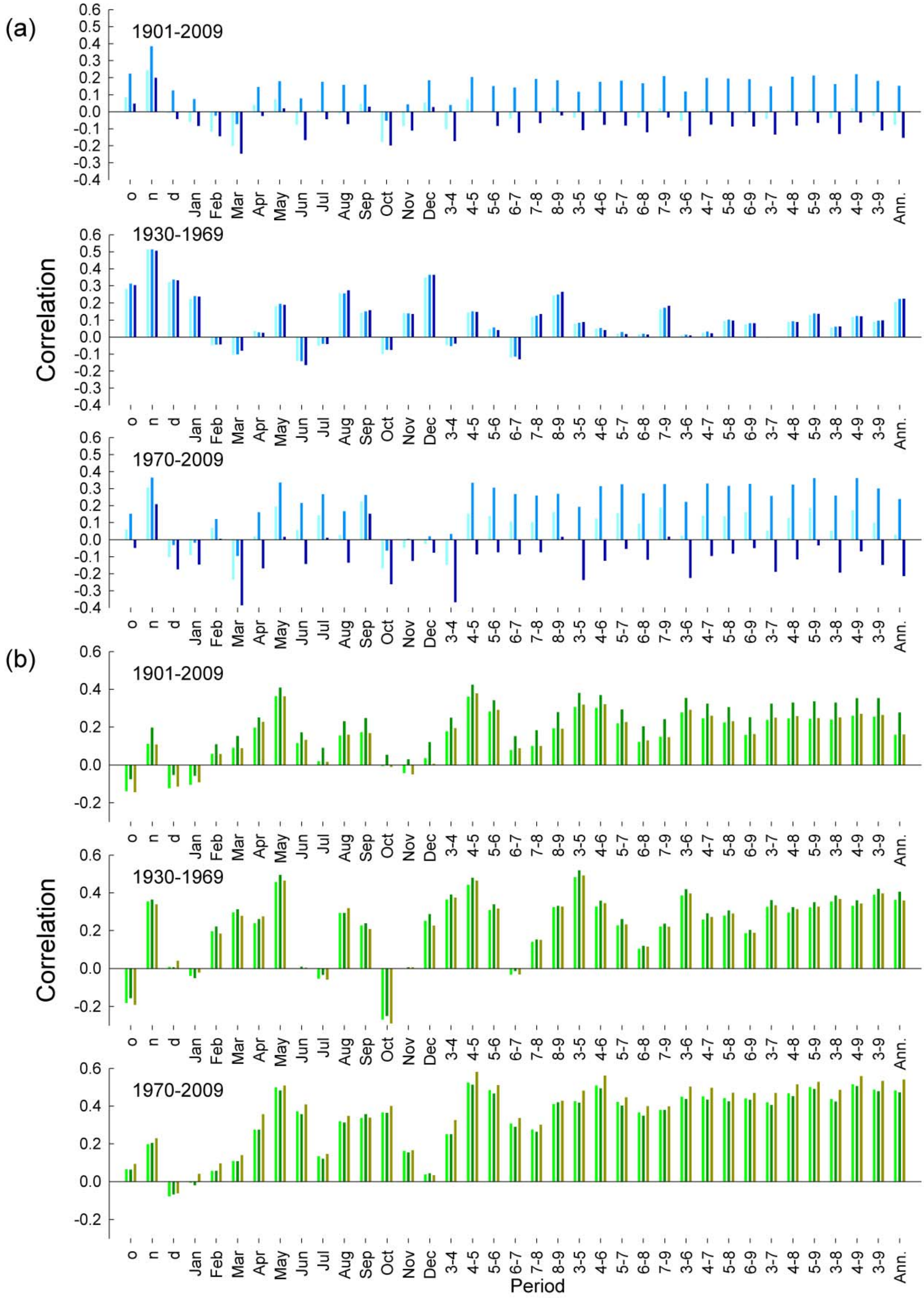


Figure 3 (legend in the next page).

Figure 3 (previous page). Growth/climate responses between maximum temperatures and (a) TRW or (b) MXD standard chronologies. Monthly correlations are computed from previous-year October (o) to current-year December (Dec), and seasonal correlations are computed from current-year March to September, over the common period 1901-2009 and two sub-periods: 1930-1969 and 1970-2009. Period numbers in the x-axis denote months: 3 for March, 4 for April and successively. We show the influence of three detrendings with different colours, from left to right: negative exponential *1*, 150-year spline, and RCS. Negative exponential *1* and 2 happened to behave almost the same, and so do 150-year and 300-year splines, therefore we only display three detrendings for the sake of clarity. We only show the growth/climate responses derived from non-transformed raw data.

In contrast, in the period 1901-2009 and in the second sub-period, RCS chronologies show a smaller or even negative correlation with temperature compared with the rest of the detrendings (Fig. 3a, Table 3). This indicates that an out-of-phase behaviour in the recent decades between TRW and temperature is more evident when using RCS chronologies than with the other detrendings. For the period 1901-2009, TRW RCS chronologies display more negative correlations with minimum and mean temperatures compared with the other detrendings (not shown). The same analyses only for the period 1901-2009 were performed for the *Pyrenees*, *Aigüestortes* and *Ordesa* subsets with no raise in monthly or seasonal correlation coefficients (results not shown).

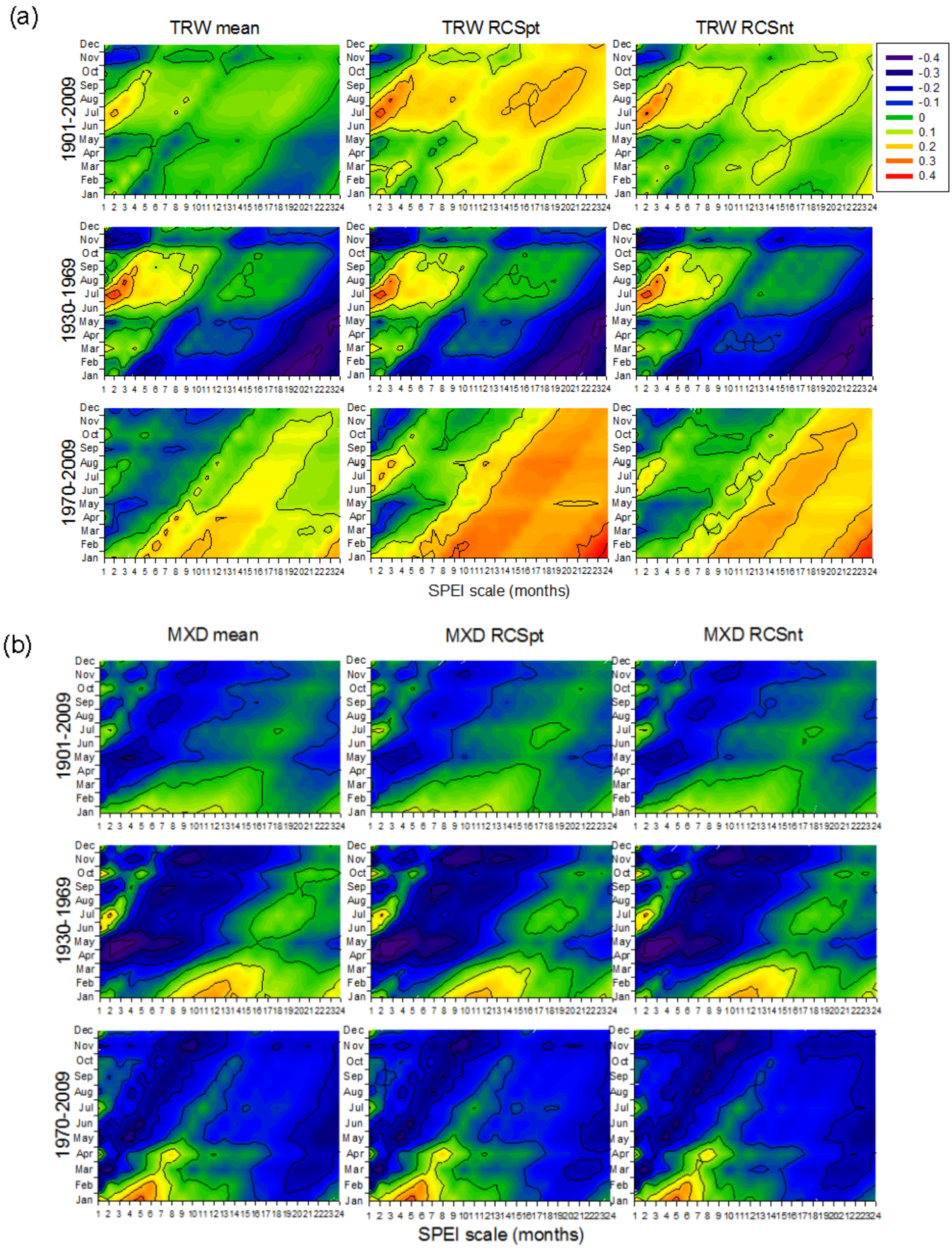
MXD displays higher correlations with temperature than those for the TRW. Monthly correlation analysis shows the main influences of previous-year November and current-year April to September temperatures on MXD, being May the most prominent month (Fig.3b). Seasonal correlations comprising the growth period (e.g. AMJJAS) show higher correlation in the second sub-period (Fig. 3b). These differences between sub-periods indicate again a temporal instability of the growth/climate relationships. Contrary to the TRW, the different MXD detrendings display the same sign and behaviour in their climate response functions (Figs. 3b and Table 3).

Lastly, for both TRW and MXD the 150-year spline detrending shows higher positive correlations along all monthly and seasonal correlation pairings for the period 1901-2009. RCS detrending brings the highest correlations with temperature for MXD in the second sub-period. There are no remarkable differences between power-transformed and non-transformed detrending methods in both sub-periods.

Growth/precipitation correlations are found to be minor and smaller than those found for temperature in both TRW and MXD data sets (not shown). Contrastingly, SPEI gives highest correlations, (Fig. 4). The main drought driver of TRW of Iberian *P. uncinata* forests is the SPEI for June and July accumulated at scales from one to two months, especially for the period 1901-2009 and the sub-period 1930-1969 (Fig. 4a). As we pointed out before, PNOMP area has stronger Mediterranean influences than PNAESM area. Correspondingly, TRW RCS chronologies from the *Ordesa* subset shows this Mediterranean background in the TRW-SPEI relationship (using SPEI data from the CRU 0.5°-grid boxes covering the PNOMP area), where the influence of drought on growth extends until August and, in general, correlation coefficients with summer SPEI are stronger than in the case of *Aigüestortes* and *Pyrenees* subsets, consecutively (Fig. S6).

In the case of MXD for the first sub-period, the highest negative (~ -0.4) and positive (~ 0.2-0.3) correlations occur with the May SPEI for 4 to 5 months, and with July SPEI at 1-month scale, respectively. This greatly changes for the second sub-period, when the highest positive MXD/SPEI correlations (~0.4) are found in the period from previous September to current January (Fig. 4b). Both TRW and MXD showed higher correlations with SPEI in the second than in the first sub-period, which indicates an increase in drought influence on growth in recent decades. Finally, spatial correlations displayed between MXD values and temperatures were stronger and more spatially coherent across SW Europe than those observed with TRW (Fig. S7).

Figure 4 (next page). Contour plots summarizing the Pearson correlation coefficients (*r*) calculated between (a) TRW and (b) MXD standard chronologies and the SPEI index for the 12 months of the year (y axis) at different time scales (1-24 months, x axis), considering the period 1901-2009 and two sub-periods: 1930-1969 and 1970-2009. For SPEI index we used averaged data from 0.5° grids covering (a) the 30 TRW sampled sites and (b) the 6 MXD sampled sites. *TRW/MXD mean* refers to the mean chronology coming from averaging the 8 different standard chronologies derived from spline and exponential detrendings (from both power transformed and non-transformed raw data); *RCSpt* and *RCSnt* refer to the standard RCS chronologies derived from power transformed and non-transformed raw data, respectively. Legends in the right side show the correlation coefficients from negative values in blue to positive values in red. Significant values ($p < 0.05$) are those with $r > 0.19$ or $r < -0.19$ for the period 1901-2009, and $r > 0.35$ or $r < -0.35$ for both sub-periods (1930-1969 and 1970-2009).



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Proxy-temperature divergence

Our results show a temporal instability of the growth/climate relationships of *P. uncinata* forests along the 20th century. Divergent trends for TRW and maximum temperature are found since the 1950s. This is most apparent in the low-frequency trends (Fig. 5b) but the opposite effect is shown in the high-frequency series, which parallel the temperature anomalies in the second half of the 20th century (Fig. 5c). On the contrary, TRW displays a convergent trend with SPEI in the low-frequency range (Fig. 5e). Similar results are observed for the *Pyrenees* and *Aigüestortes* subsets (not shown). For its part, MXD low-frequency trend parallels with the low-frequency temperature warming, which started in the 1970s (Fig. 6b), but it diverges from SPEI from the 1980s onwards (Fig. 6e).

Moving correlation analyses for the MJJAS period indicate variable relationships. For the relationship of TRW with both maximum temperature and SPEI, a generally unstable trend is present in the moving correlation records (Figs. 5a,d), but a more steady negative (positive) trend is displayed with temperature (SPEI) in the low-frequency range (Figs. 5b,d). In the high-frequency domain, stronger correlations with temperature are obtained after the 1950's (Fig. 5c), and a negative trend in the moving correlations with SPEI is found (Fig. 5f). MXD moving correlations display an increase with temperature and a decrease with SPEI in low-frequency domains (Fig. 6b,e). Low-frequency moving correlations in TRW seem more stable than in MXD, where we can observe cyclic increases and decreases in the moving correlations along the 20th century (Fig. 6b,e).

Focusing on the growing season, May temperature shows a direct correlation with TRW and MXD while summer months usually show a smaller or negative one (Fig. 3). To find out if the divergence phenomenon is due to a loss of temperature sensitivity or to an increasing effect of summer drought, we repeated the moving correlation analyses with summer (June-July) and May temperatures. Results are very similar to the ones obtained with the maximum temperature of May-September period (Fig. S8 and S9), again highlighting a TRW-temperature divergence and also a recent increase in the correlation between MXD and temperature.

To obtain a hint about potential differences in the divergence occurrence along the altitudinal we compared high- (>2150 m, 15 sites, 940 series) and low-elevation (< 2150 m, 15 sites, 572 series) TRW RCS chronologies with climatic variables (SPEI and MJJAS maximum temperature series). In both high- and low-elevation chronologies the divergence phenomenon with temperature in the low-frequency range is clear and the convergent trend with MXD in the low-frequency range too (Figs. S10 and S11). In the high-elevation chronology the low-frequency divergence with temperature seems to appear shortly delayed compared with the low-elevation chronology.

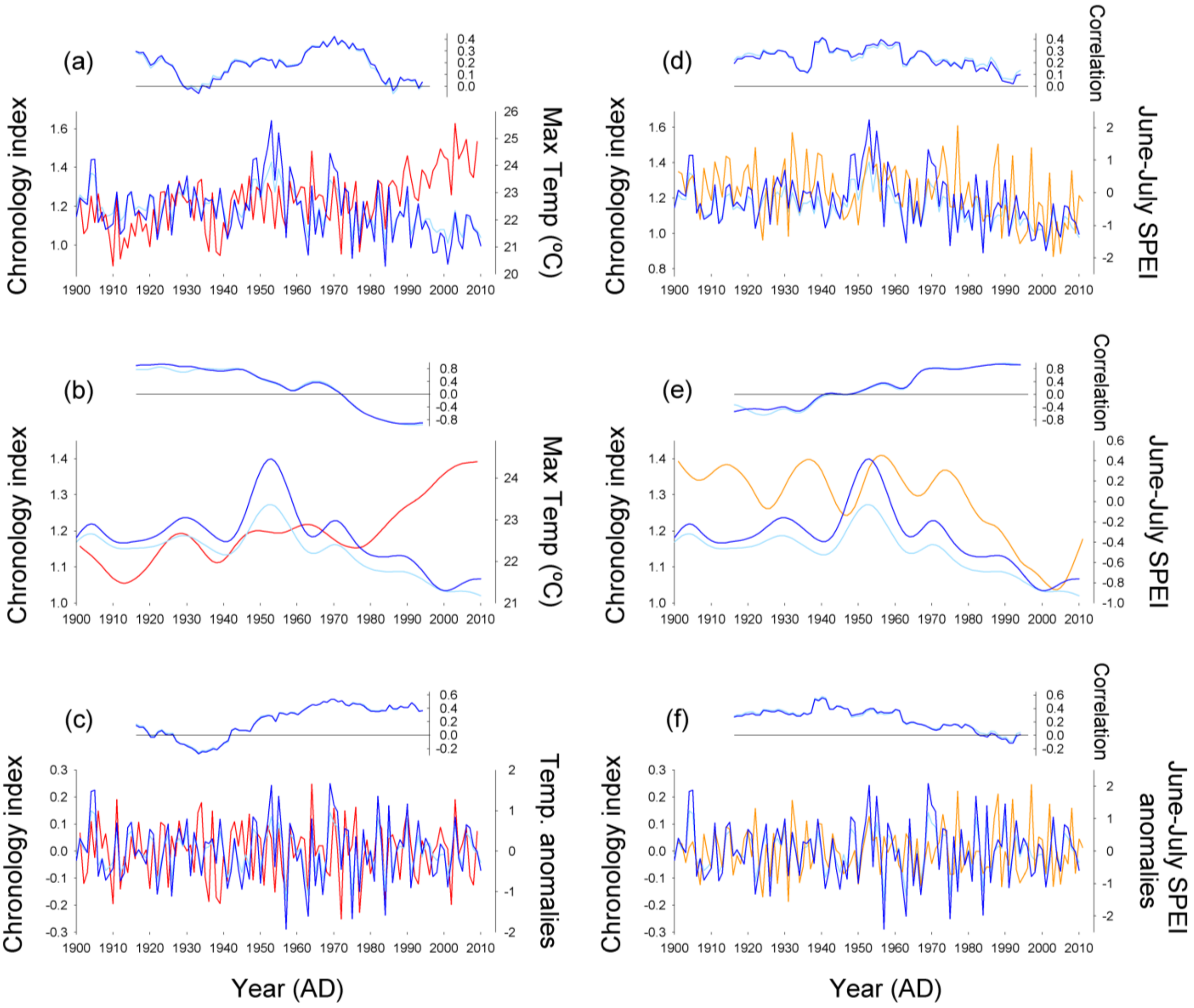

Figure 5. (a) May-September maximum temperature (red lines) and (d) June-July SPEI series (orange lines) compared with TRW RCSnt (dark blue lines) and RCSpt chronologies (light blue lines) for TRW. Upper graph indicates 31-year moving correlations between the climatic series and the RCSnt and RCSpt chronologies, coloured in dark and light blue lines respectively. Each moving correlation point refers to the central value of a 31-year window. For May-September maximum temperature, the same analyses for (b) 20-year low- and (c) high-pass (anomalies) series are displayed. For June-July SPEI, the same analyses are also displayed for (e) 20-year low- and (f) high-pass series.

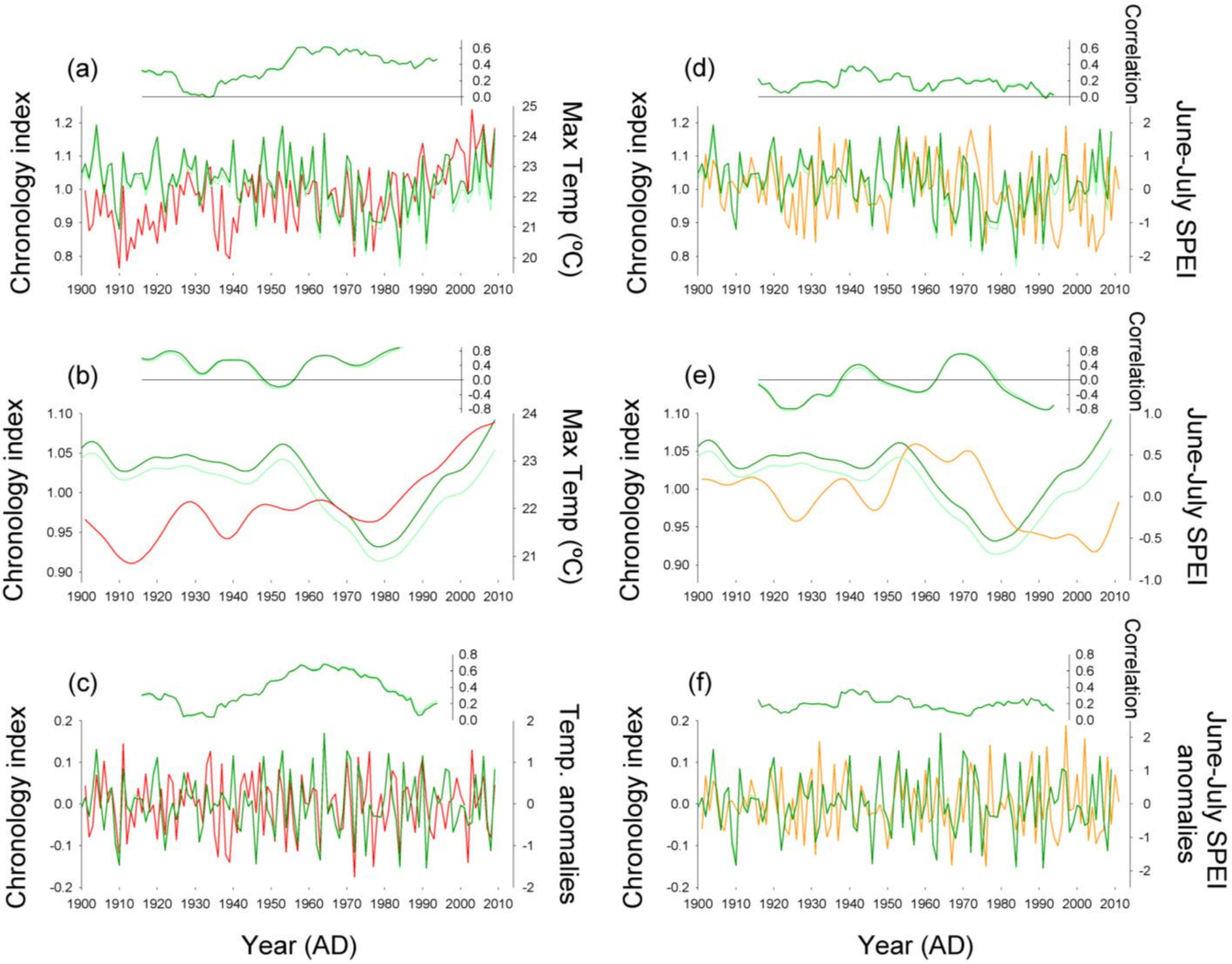

Figure 6. (a) May-September maximum temperature (red lines) and (d) June-July SPEI series (orange lines) compared with MXD RCSnt (dark green lines) and RCSpt chronologies (light green lines) for MXD. The rest of explanations are as in Figure 5.

Discussion

Our results show low frequency trend offsets since the second half of the 20th century between the TRW series and temperature records. This evidences the weakness of theoretically temperature-sensitive proxies (TRW) to capture recent warming trends such as those observed since the 1950s. Such 'divergence' phenomena have also been displayed in other subalpine and boreal forests (Büntgen et al. 2006; Wilmking et al. 2004, 2005; D'Arrigo et al. 2004; Briffa et al. 1998). Nevertheless, this low-frequency trend fork between growth and temperature is not found in the high-frequency climate sensitivity of our TRW series, which increasingly parallels temperature anomalies along the 20th century (Fig. 5c). Spring cambial resumption in *P. uncinata* starts in May, and typically the tree growth is faster or slower depending mainly on the temperatures prevailing on this month. The moving correlations between May temperatures and TRW highlight that this spring temperature sensitivity is fading during the last decades (Fig. S8b). Contrary to TRW, MXD low-frequency positive trends follow the warming trend started in the 1970s. This is in agreement with data from the European Alps which suggest that the divergent behaviour is expected to occur in TRW more often than in MXD (Büntgen et al. 2006). MXD shows higher correlations with temperature over the growing season compared to TRW (Büntgen et al. 2010). This can be explained because TRW is more strongly autocorrelated, incorporating previous-year climatic and ecological conditions, and ecological carryover effects (e.g., the formation of earlywood with carbohydrates synthesized the previous season) and temperature forcing over a wider (seasonal or annual) time window (Fritts 2001).

The divergence phenomenon has been attributed to various causes including temperature-induced drought stress (D'Arrigo et al. 2004), nonlinear growth-climate thresholds (Loehle 2009), methodological issues techniques including "end effects" of chronology development (Esper and Frank 2009, Briffa and Melvin 2011), biases in instrumental data or additional anthropogenic influences (see D'Arrigo et al. 2007, and references therein). Our sampled sites are located within the drought-prone Mediterranean region, make us focusing about a possible temperature-induced drought explanation of the TRW-temperature divergence observed.

In this sense, drought is becoming a more limiting factor for our high-elevation *P. uncinata* growth in the last decades, when both TRW and MXD show higher seasonal correlations with June-July SPEI. The aforementioned TRW-temperature divergence of the second half of the 20th century is opposite to the relationship between TRW and SPEI trends, with low-frequency moving correlations steadily rising and reaching a maximum level after the 1970s (Fig. 5e). These results indicate that summer drought is increasingly influencing TRW along the 20th century, which agrees with observations from Iberian mountain forests (Andreu et al. 2007, Macias et al. 2006). This can be due to a potential loss in the positive thermal response of trees when some absolute temperature threshold is exceeded, leading to an increase in the influence of other potential factors like soil moisture or drought (D'Arrigo et al. 2004). This TRW-drought parallelism present in our high-elevation study disagrees with results from low-elevation drought sensitive tree-ring central European sites, where growth/drought or growth/precipitation relationships weaken after the 1970s (Wilson and Elling 2004). Consequently, emerging elevation-specific factors influencing tree growth can be acting differently between high and low elevation sites or between central and southern European forests, producing these contrasting responses in the last decades. Contrastingly, our simplified comparison between high- and low-elevation chronologies does not show important differences (Figs. S10 and S11).

Summer drought is becoming less influential on MXD instead, specifically since the 1970s, when low-frequency moving correlations between SPEI and MXD begin to fall and both trends diverge (Fig. 6e). In any case, the moving correlations of MXD-drought and MXD-temperature relationships show in general more instability than in the case of TRW along time (Fig. 6b,e). When it is too hot or dry for an optimal growth to occur, the rate of tracheid production decreases and a higher MXD is caused because of the formation of denser latewood cells with thicker cell walls than their earlywood counterparts (Jyske et al. 2009). This thickening and lignification of latewood cell walls improves the mechanical strength of stems but also allows tracheids withstanding higher xylem tension due to the lowered water potential (Hacke et al. 2001). Specifically, MXD development is directly linked to climate conditions during spring and also during late summer to early autumn, when the latewood is formed (Briffa et al. 1998). During the first part of the growing season, climatic variations affect radial tracheid enlargement, whereas during the later part of the growing season climate mainly affects the cell wall thickening process (Camarero et al. 1998) (Fig. S12). In this sense, for the sub-period 1930-1969, the lowest correlations (~ -0.4) of MXD with SPEI were found for May SPEI (Fig. 4b). This means that wet and cool spring conditions could enhance earlywood formation potentially leading to more and wider earlywood tracheids with thinner cell walls and a subsequent delayed summer lignification producing a less dense latewood, i.e. lower MXD values. The highest positive correlation (~ 0.2-0.3) for the same period corresponds to July SPEI which suggests that wet late summers will entail denser latewood production through enhanced lignification and carbohydrates synthesis at the end of the growing season. In the sub-period 1970-2009 the highest positive MXD-SPEI correlations (~0.4) are found in January considering the cumulative drought since the previous September (5-month SPEI scale), which means that wet conditions in the previous autumn and winter of a specific year would imply the production of a dense latewood during the late summer of the next year. This is an unexpected observation since we unveil not only influences of late summer/early autumn conditions of the current year on MXD but also of climatic conditions of the previous year as it is usually the case in TRW (Tardif et al. 2003, Fritts 2001). The interpretation may be the same as in TRW since previous wet conditions might enhance carbon uptake later used for lignifying latewood cells the following growing season. Note that these indirect influences of previous winter conditions on latewood production were also observed in xeric *Pinus halepensis* stands, which constitute typical lowland Mediterranean forests (Pasho et al. 2011). Overall, the SPEI drought index provided a superior signal of tree growth than precipitation data in the study forests. Differences in responses between sub-periods could be due to different drought stress intensities from one sub-period to the other, different temperature conditions or climatic variability (e.g. the first half of the 20th century was climatically less variable than the second half) or indirect effects of other drivers like CO_2 and N rising levels.

Current data supports the occurrence of climate warming and its effects on various forest ecosystem services in the Pyrenees during the last decades. From 1880 to 1980 AD at least 94 glaciers disappeared in the whole Pyrenees, 17 of them did it on the Spanish side since 1980 (Morellón et al. 2012). Camarero and Gutiérrez (2004) observed an increase in tree establishment and density within the treeline ecotone along the 20th century. In a European context there is a positive trend in temperatures (+0.90°C) from the beginning of the 20th century and, although lower than in central and northern Europe, the warming trend in the Mediterranean region has intensified since the 1970s (IPCC 2007). Among Mediterranean mountains, the Pyrenees mountains have two ecological drawbacks to face global-change effects. First, they constitute a mountain area east-west arranged, i.e. perpendicularly to the expected northern (or upward) migratory routes. Second, they are tightly influenced by Mediterranean climatic conditions characterized by a severe summer drought. Hence, the Pyrenees are more likely to be vulnerable against climate warming and drying trends than other Mediterranean and European ranges (Schröter et al. 2005). Under the forecasted scenarios of warmer temperatures and intensified aridification along the following decades, the negative effects on forest growth could be even worse than expected if drought stress effect plays a complementary role together with the rising temperatures.

Several dendrochronological studies have focused on Pyrenean growth-climate relationships at Pyrenean high-elevation forests (e.g. Gutiérrez 1991, Rathgeber and Roche 2003, Tardif et al. 2003, Andreu et al. 2007, Büntgen et al. 2008a, Esper et al. 2010). Our study constitutes a step forward in the sense that (i) we use a larger dataset covering a broad biogeographical gradient including the southern and western distribution limits of this species and, mainly, that (ii) we find a weakening in the TRW-temperature relationships possibly connected to an increasingly important role of drought as growth driver during the last decades. The divergence phenomenon here exposed should be considered in the assessment and performance of Pyrenean climate reconstructions from tree rings, which are based on short calibration periods. Trees are showing increasing drought and decreasing temperature sensitivities in the last decades even in these high-elevation ecosystems where we would expect a strong temperature response. This would imply that a Pyrenean climate reconstruction based on present-day growth-climate relationships is questionable and should be considered carefully. According to our results, temperature reconstructions performed in the Pyrenean range using MXD (Büntgen et al. 2008a, Dorado-Liñán et al. 2012) are reliable since they are based on MXD/temperature relationships where no divergence was found.

This divergence phenomenon has been mainly explained here in terms of temperature-induced drought stress, but we should not ignore additional factors potentially influencing the degree and intensity of the growth/climate offset. For instance, nitrogen fertilization or increasing atmospheric CO_2 concentrations may enhance radial growth thus leading to the formation of a less dense earlywood (Lundgren 2004). Our research next step would be a site-level study of the low- and high-frequency signals in the growth/climate correlations, which would allow us drawing conclusions for larger scales in a more accurate way (Büntgen et al. 2008b). A more exhaustive MXD sampling of several tree species should be also necessary to make a more accurate comparison between TRW and MXD responses.

To conclude, rising temperatures led to an increase in drought stress of Pyrenean high-elevation forests as has been observed in other Mediterranean mountain forests (Jump et al. 2006; Piovesan et al. 2008). Therefore, high-elevation forests growing in typically temperature-limited conditions might have become more limited by water availability. This effect could be particularly strong in steep sites on rocky substrates where soils show a poor capacity to hold water. We may be attending how a physiological threshold in terms of optimal temperature for growth is surpassed, reinforcing the role of drought as a plausible growth-limiting factor of high-elevation forests during the last decades.

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Supporting Information

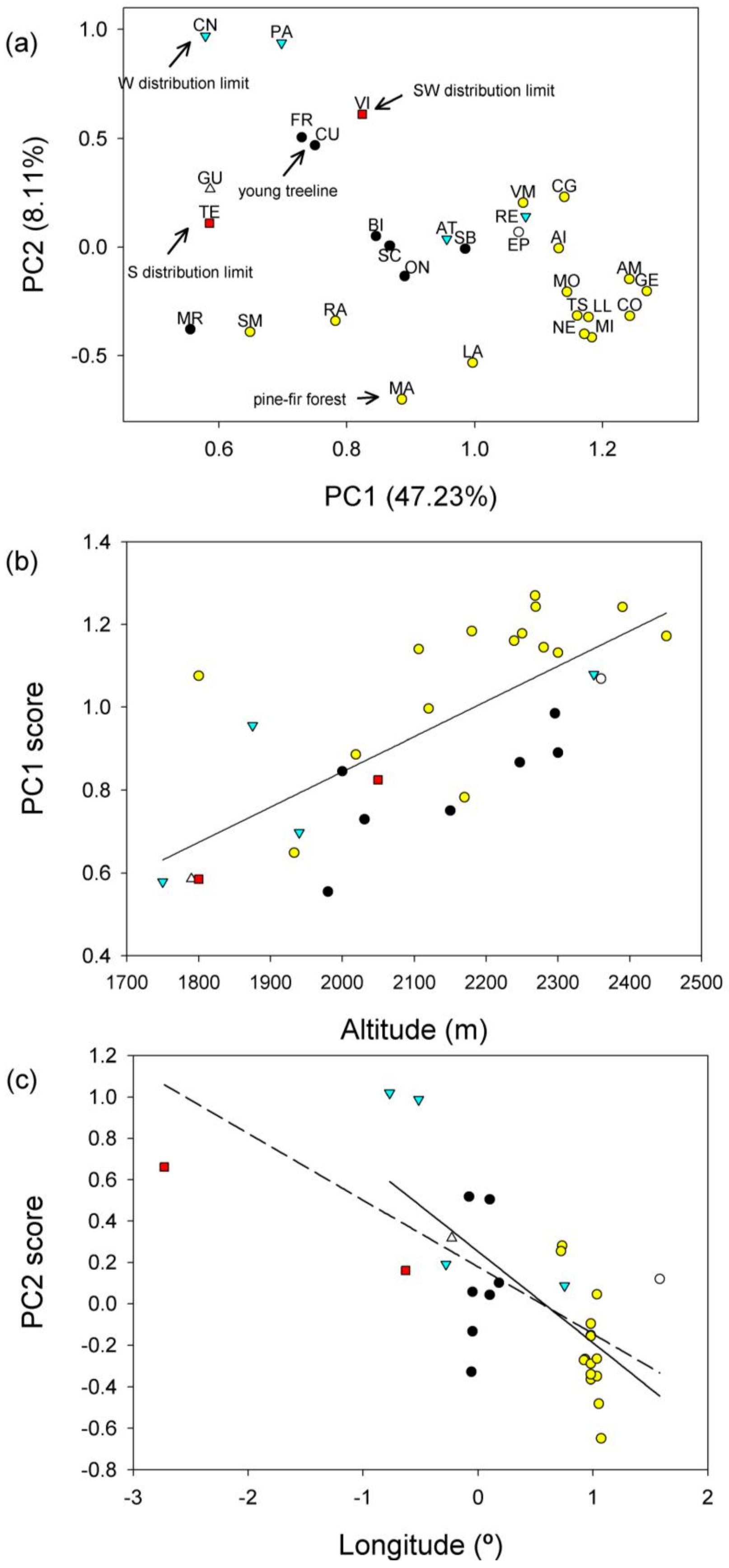

Figure S1 (previous page). (a) Principal Components Analysis based on 30 TRW chronologies showing the scores of the first two principal components PC1 and PC2 (sites codes are as in Table 1; analysed period is 1901-1994, covered by chronologies from all sites). PC1 and PC2 scores change as a function of altitude (a) and longitude (b), respectively. Stands with special characteristics or located near the distribution limit of the species are indicated. Different symbols correspond to sites from different geographical areas (PNOMP, black circles; PNASM, yellow circles; western and central Pyrenees, downward blue triangle; Iberian System, red square; eastern Pyrenees, white circle; Pre-Pyrenees, upward white triangle). The continuous line in (c) indicates the regression line without considering the red outlier on the left.

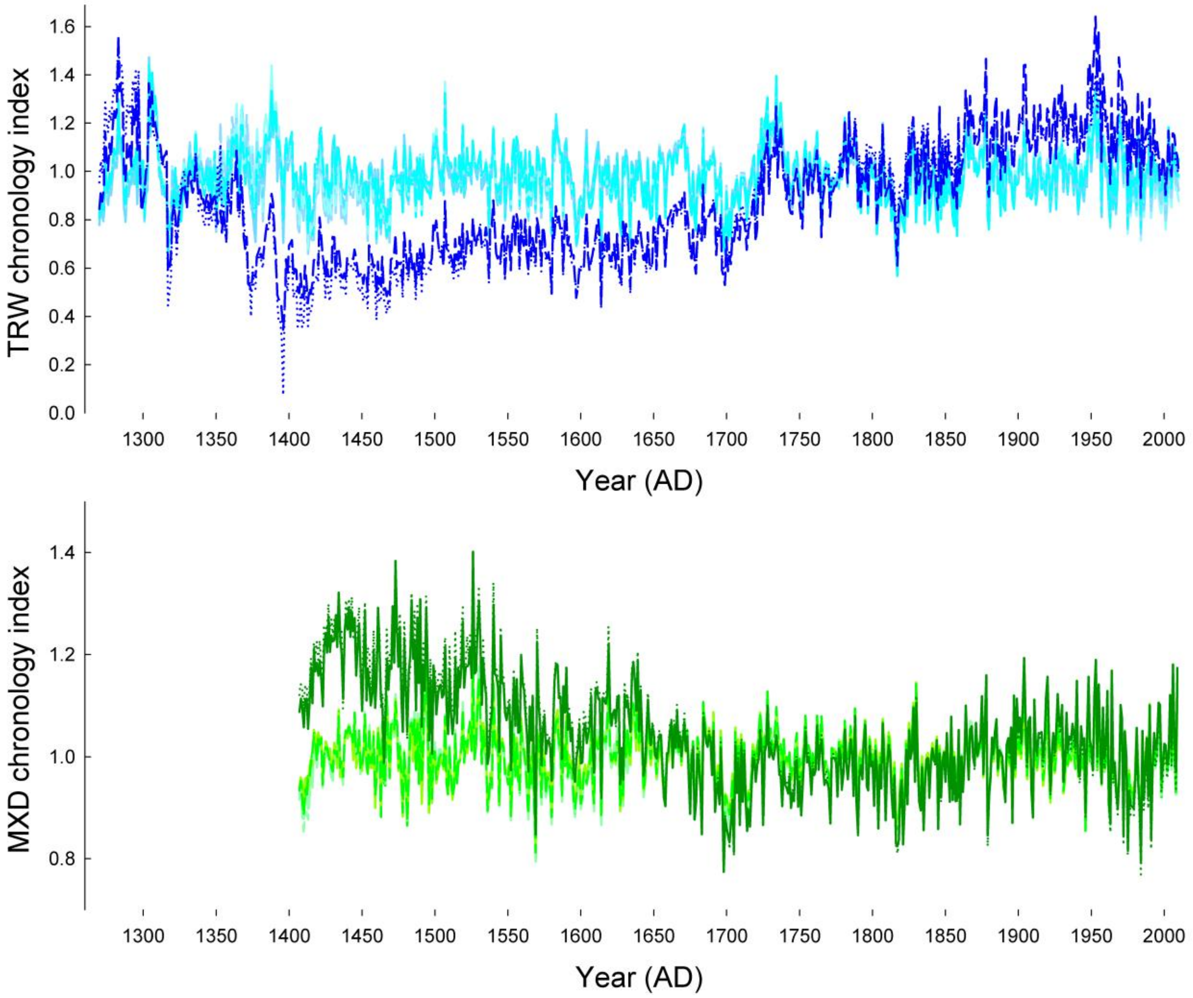

Figure S2. Upper and lower graphs show the different TRW (blue) and MXD (green) chronologies, respectively, coming from 10 different detrendings applied. Dark blue and dark green indicate the TRW and MXD RCS chronologies, in that order. Light blue and light green indicate the eight different chronologies coming from exponential and spline detrendings. Continued and dotted lines refer to chronologies derived from non-transformed and power-transformed data, correspondingly.

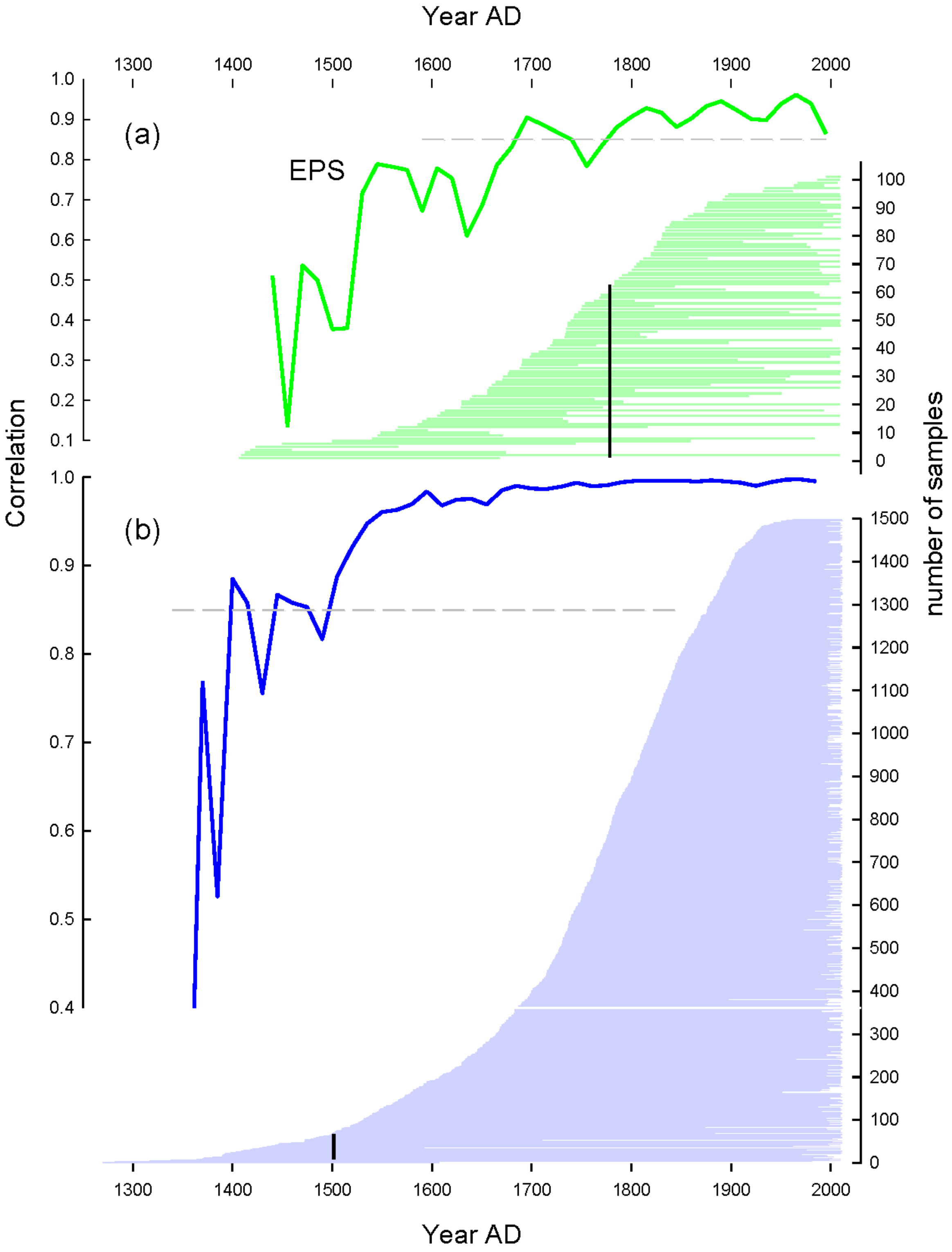

Figure S3. Temporal distribution of (a) 101 MXD and (b) 1500 TRW core samples of *Pinus uncinata*, ordered by calendar age of their innermost ring, and EPS statistic (calculated over 30 years lagged by 15 years) of the whole set (i.e. 6 MXD sites and 30 TRW sites) of raw chronologies. The vertical black lines show the temporal limit of the signal strength acceptance (EPS > 0.85): 1777 AD for MXD and 1500 AD for TRW. The grey horizontal dashed lines denote the 0.85 EPS criterion for signal strength acceptance (Wigley et al. 1984).

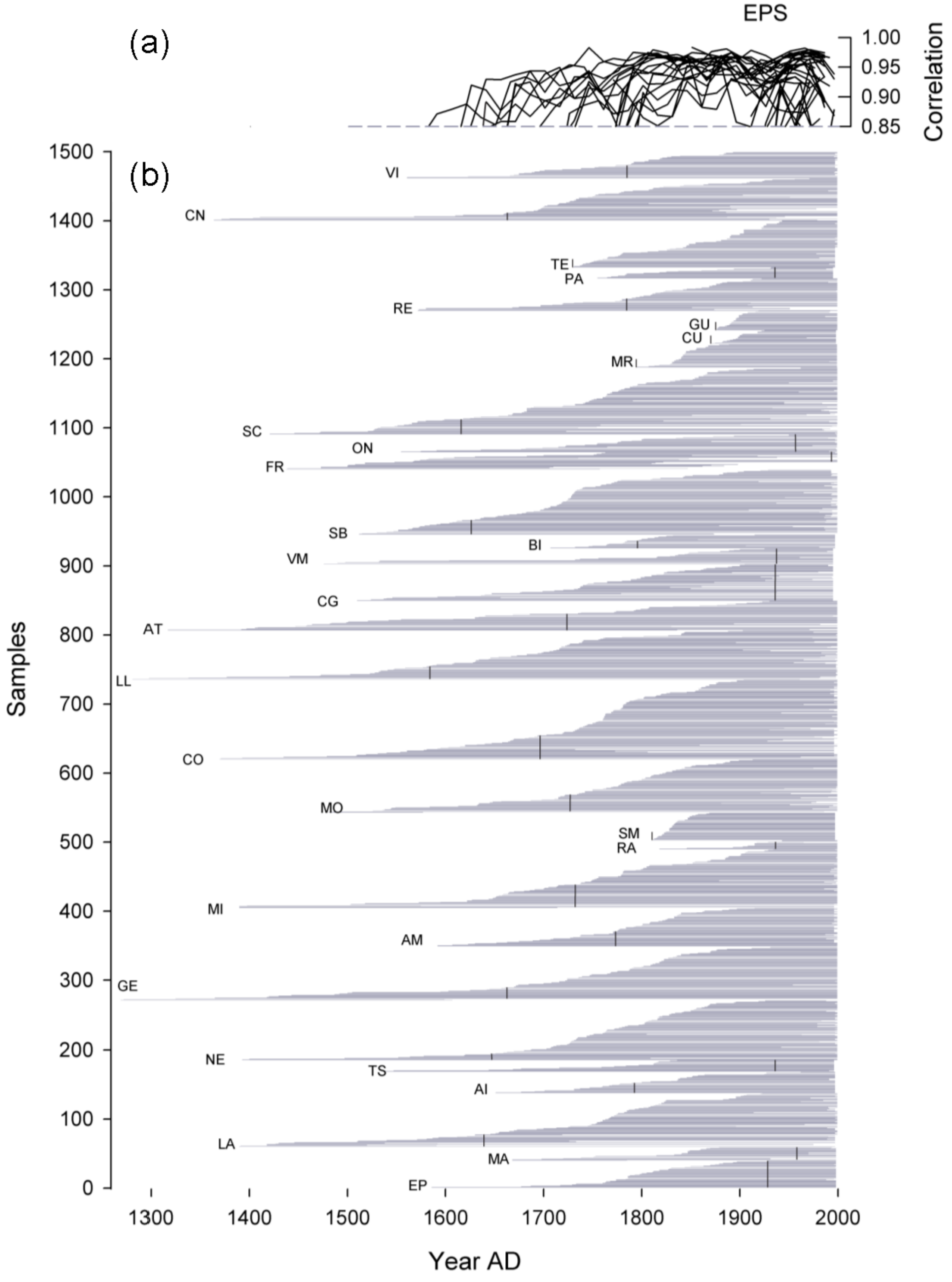

Figure S4. (a) EPS statistic (calculated over 30 years lagged by 15 years) of each site raw chronology without variance adjustment. (b) Temporal distribution of the 1500 *Pinus uncinata* TRW cores, grouped by site (from bottom West to top East) and ordered by calendar age of their innermost ring. Vertical lines show the limit of the signal strength acceptance (EPS > 0.85; see Wigley et al. 1984).

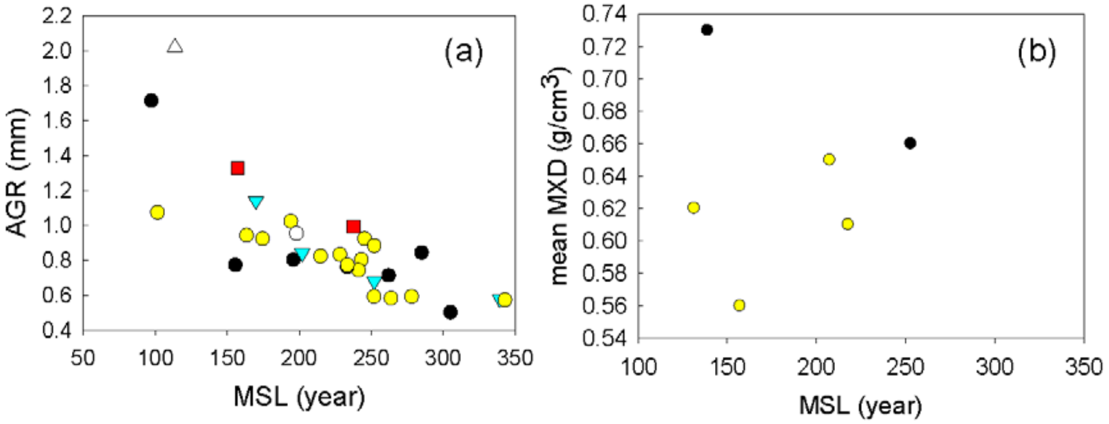

Figure S5. Relationships between mean segment length (MSL) vs. mean TRW growth rate (AGR) (a) and MXD (b). Different symbols correspond to sites as in Fig. S1.

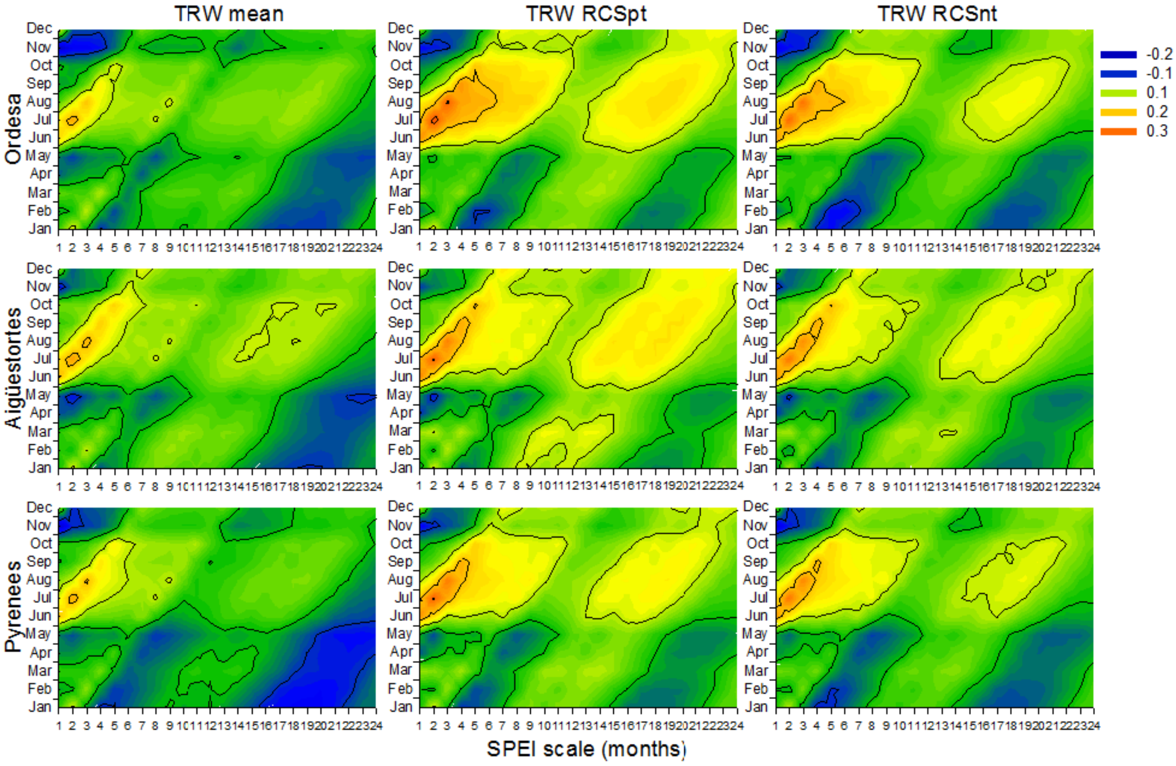

Figure S6. Contour plots summarizing the Pearson correlation coefficients (*r*) calculated between TRW chronologies and June-July SPEI index for the 12 months of the year (y axis) at different time scales from one to 24 accumulated months (x axis), covering the period 1901-2009. For the SPEI index we used averaged data from 0.5°-gridded data covering the sampled sites from *Ordesa, Aigüestortes* and *Pyrenees* subsets. *TRW mean* refers to the mean chronology averaging the eight different standard chronologies derived from spline and negative exponential detrendings (from power transformed and non-transformed raw data); *TRW RCSpt* and *TRW RCSnt* refer to the TRW standard RCS chronologies from power transformed and non-transformed raw data, respectively. Legends in the right side show the correlation coefficients from negative values in blue to positive values in orange and red. Significant values ($p < 0.05$) correspond to $r > 0.19$ or $r < -0.19$.

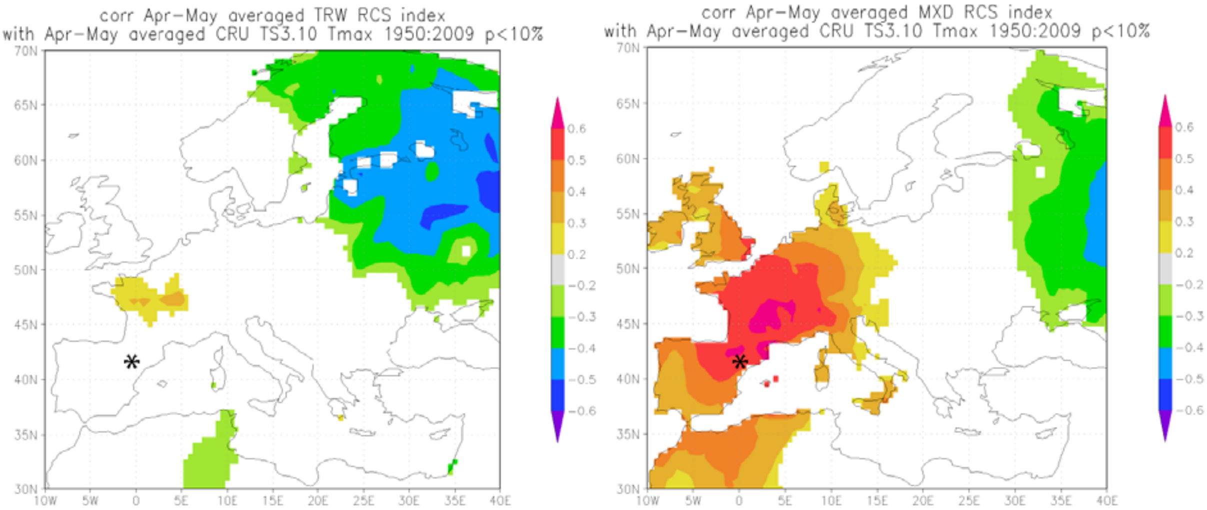

Figure S7. Comparison between the highest spatial field correlations of *AllSites* TRW RCS and *Pyrenees* MXD RCS chronologies against April-May maximum temperatures for the period 1950-2009 (climate data were derived from the CRUTS3.10 dataset). The asterisk indicates the approximate location of the centroid of the study area in NE Spain.

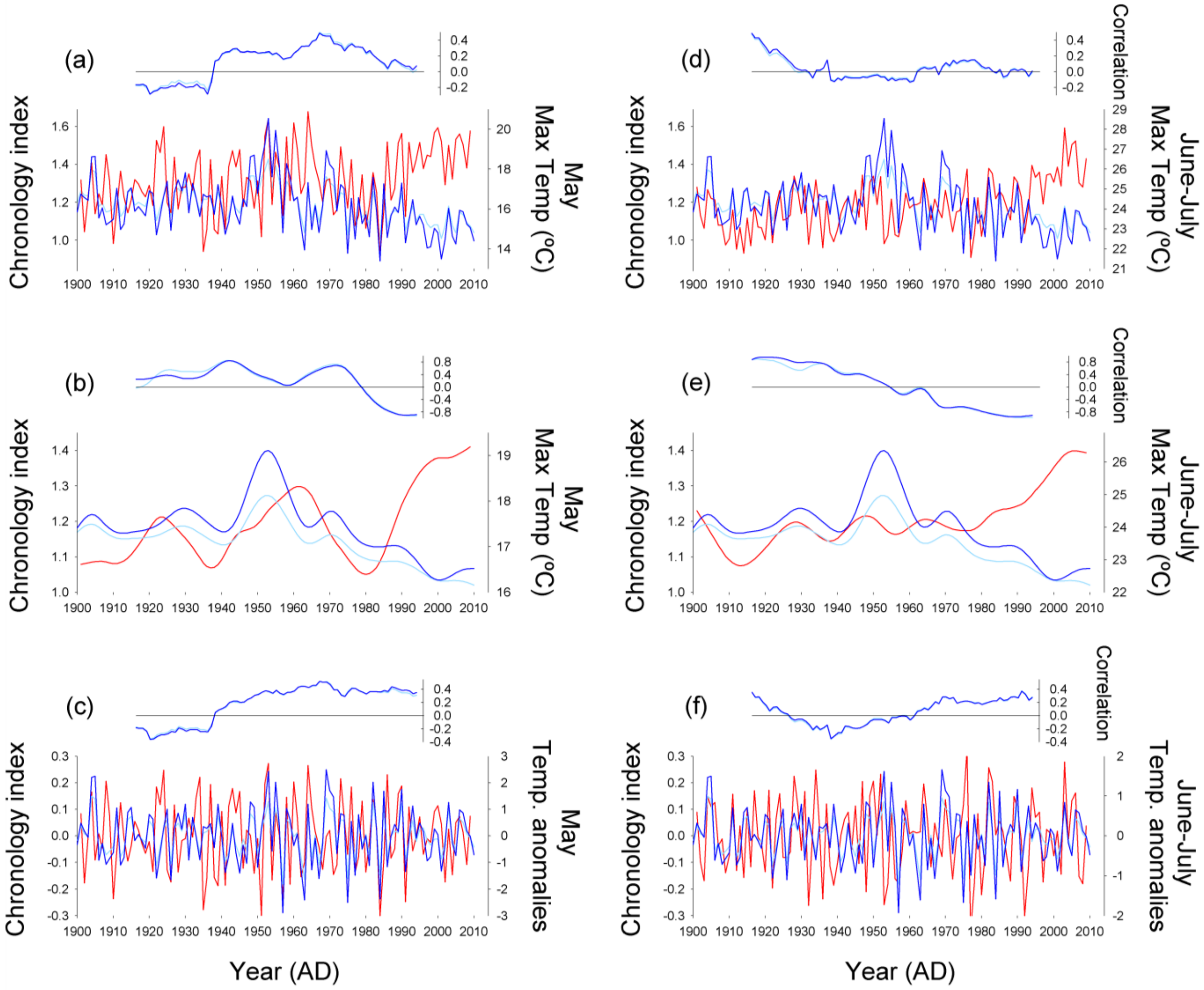

Figure S8. Comparison between May (left column; subfigure a) and June-July (right column; subfigure d) CRUTS3.1 maximum temperature record (red) for the period 1901-2009, and TRW RCSnt (dark blue) and TRW RCSpt chronologies (light blue) for the *Allsites* TRW subset. Upper graphs indicate 31-year moving correlations between the temperature records and the chronologies. Each moving correlation point refers to the central year of a 31-year window. Subfigures (a), (b) and (c) show the standard, 20-year low- and high-pass (anomalies) filtered datasets, respectively, for May temperature. Subfigures (d), (e) and (f) show the same for June-July maximum temperature.

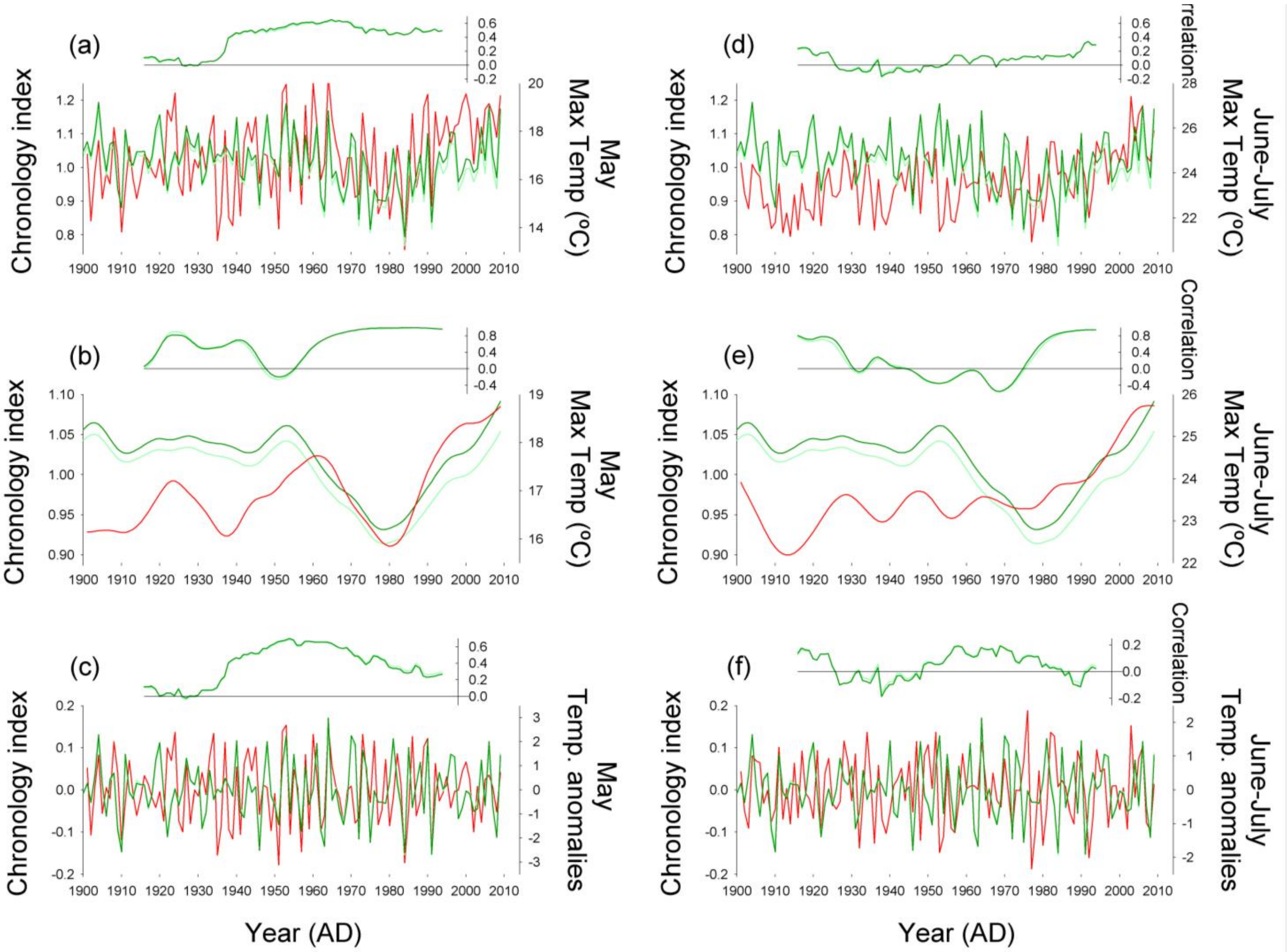

Figure S9. Comparison between May (left column; subfigure a) and June-July (right column; subfigure d) CRUTS3.1 maximum temperature records (red) for the period 1901-2009, and MXD RCSnt (dark green) and TRW RCSpt chronologies (light green) for the *Allsites* TRW subset. Upper graphs indicate 31-year moving correlations between the temperature records and the chronologies. Each moving correlation point refers to the central year of a 31-year window. Subfigures (a), (b) and (c) show the standard, 20-year low- and high-pass (anomalies) filtered datasets, respectively, for May temperature. Subfigures (d), (e) and (f) show the same for June-July maximum temperature.

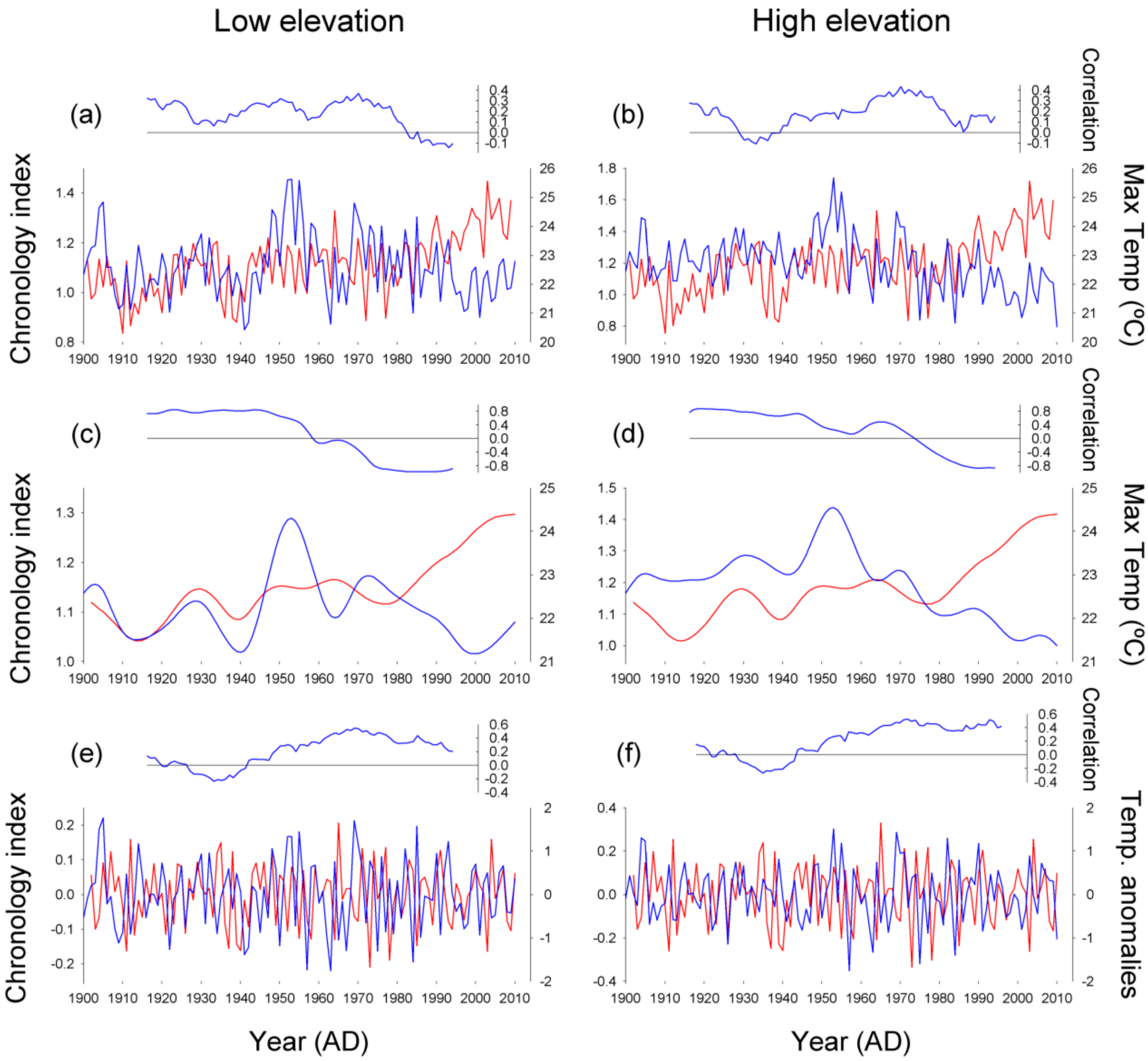

Figure S10. Comparison between low- (left column) and high-elevation (right column) chronologies. In (a) and (b) May-September maximum temperature (red) is compared with the TRW RCSnt chronology (dark blue) for the *Allsites* TRW subset. Upper graph indicates 31-year moving correlations between the 1901-2009 May-September maximum temperature and the RCSnt chronology. Each moving correlation point refers to the central value of a 31-year window. Subfigures (c, d) and (e, f) show the same for 20-year low-, and high-pass (anomalies) series, respectively.

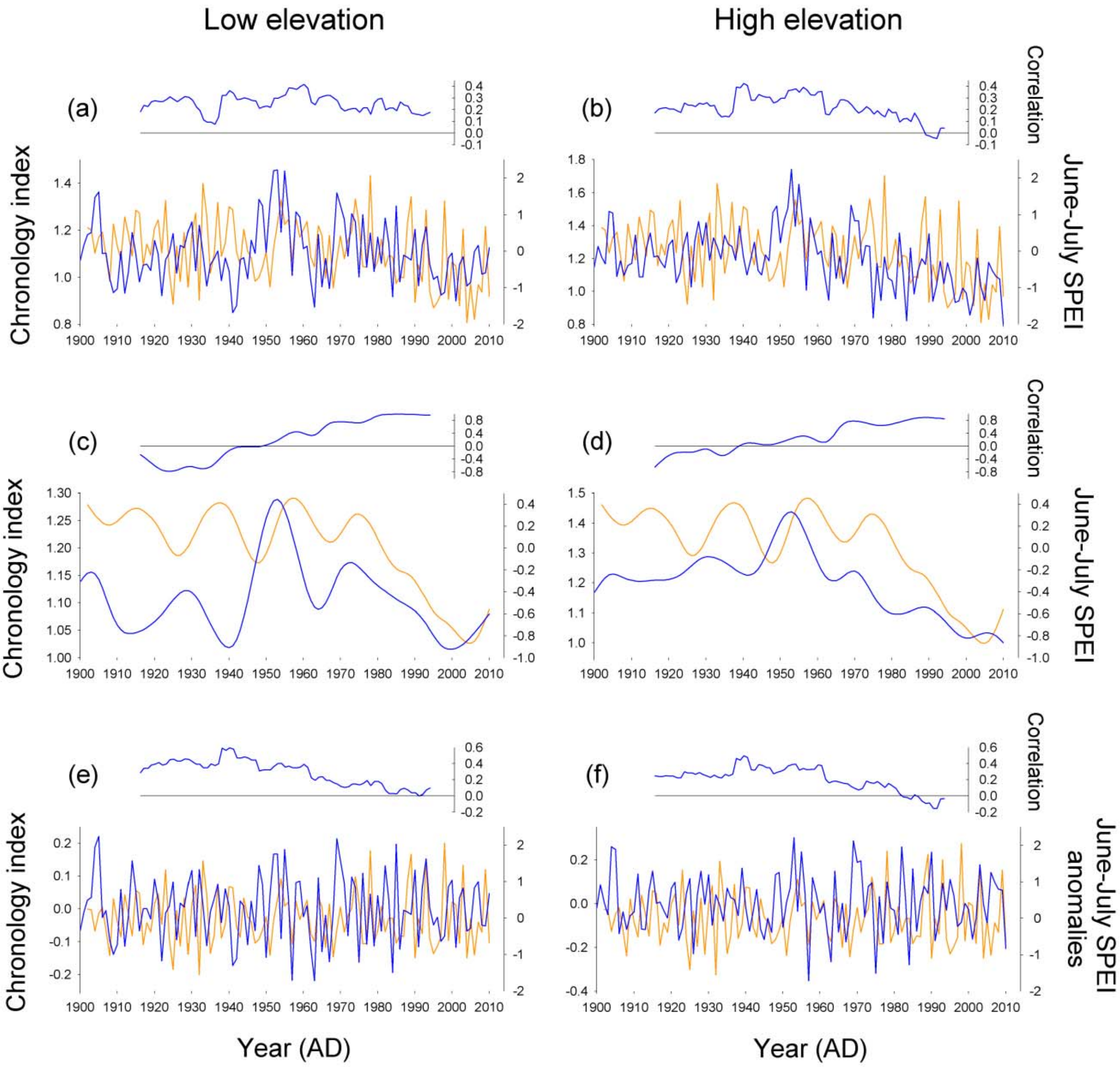

Figure S11. Comparison between low- (left column) and high-elevation (right column) chronologies. In (a) and (b) June-July SPEI (orange) is compared with TRW RCSnt chronology (dark blue) for the *Allsites* TRW subset. Upper graph indicates 31-year moving correlations between the 1901-2009 May-September maximum temperature and the RCSnt chronology. Each moving correlation point refers to the central value of a 31-year window. Subfigures (c, d) and (e, f) show the same for 20-year low-, and high-pass (anomalies) series, respectively.

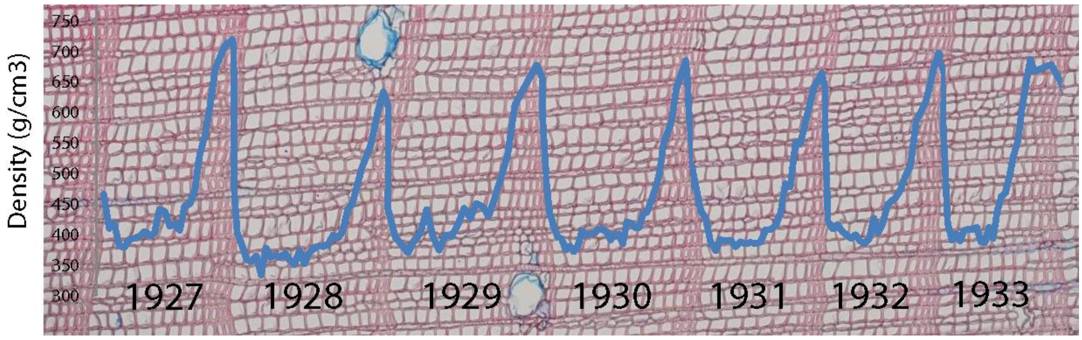

Figure S12. Example of a densitometric profile covering seven annual rings (period 1927-1933) showing intra-annual MXD and wood-anatomical variability for a *Pinus uncinata* tree from Gerber site (PNAESM). MXD reaches the maximum values during the late growing season, usually from August up to September, when cell-walls are thickening.

... A tree says: Trust is my strength. I know nothing about my parents; I know nothing about the thousand children that every year spring out of me. I live out the secret of my seed to the very end, and care for nothing else. I trust that God is in me. I trust that my labour is holy. Out of this trust I live.

... Un árbol dice: mi fuerza es la confianza. No sé nada de mis padres, no sé nada de los miles de retoños que cada año surgen de mí. Vivo hasta el fin del secreto de mi semilla, y no tengo otra preocupación. Confío en que Dios está en mí. Confío en que mi tarea es sagrada. De esta confianza vivo.

Chapter 4

Spatial diversity in recent Mediterranean tree growth patterns

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Summary

Increasing temperatures and shifting precipitation regimes define the Mediterranean Basin as one of the world's most sensitive climate change hot-spots. Among a variety of ecological effects have disruptions in the growth-climate response of Mediterranean forest species been observed during the last decades. Complex topography and climatology, however, cause contrasting patterns of recent tree growth, for which biotic and abiotic drivers often remain debatable. Here, we compile dendrochronological evidence of recent growth trends after 1970 from 1076 cases at 724 sites that were reported in 75 peer-reviewed publications for the Mediterranean Basin (30° to 46° N and 10° W to 40° E). It is highlighted a synoptic pattern where positive trends are generally found in cooler and wetter environments across the north-western part of the Basin, whereas negative trends often coincide with xeric sites in the south-western and eastern regions. This response pattern reveals both, beneficial as well as detrimental effects of climate change on pan-Mediterranean forest ecosystem functioning and productivity. Likely biased by selective sampling efforts towards higher elevations and older trees within a few countries in the north-west, our review emphasizes the need of a more evenly distribution of study sites and age classes that better reflect ecological rather than political and methodological criteria. Data coming from different sources and treatments result in heterogeneous uncertainty levels when assigning a sign to each trend, and stresses the importance of free data access to allow novel tree-ring networks to be compiled and additional data analyses to be performed.

Manuscript in preparation.

Introduction

The Mediterranean Basin (MB) has been defined as a major climate change hot-spot (Giorgi 2006), where increasing temperatures and modifications in precipitation patterns may have diverse impact on terrestrial ecosystems (Luterbacher et al. 2006). In fact, shifts in plant and animal species distribution (Parmesan et al. 1999, Meshinev et al. 2000, Peñuelas and Boada 2003, Petriccione 2003, Sanz-Elorza et al. 2003, Lenoir et al. 2008), species disappearance (Otero et al. 2011, Stefanescu et al. 2011), altered insect phenophases (Peñuelas et al. 2002), fungi productivity decrease (Büntgen et al. 2012) or reduced river floods (Frihy et al. 1996) have been recorded. Moreover, forest ecosystems have experienced losses in productivity (Kotar et al. 1996, Tomé et al. 1996, Jump et al. 2006a), drought-induced dieback (Martínez-Vilalta and Piñol 2002, Camarero et al. 2011), phenological changes like time shifts in the starting point of the growing season (Menzel and Fabian 1999) or advances in the timing of leaf expansion and flowering (Peñuelas and Filella 2001), and rapid genetic changes (Jump et al. 2006b). Biome alterations related to climate change have not only been recorded in terrestrial but also in Mediterranean sea-ecosystems (Chisholm et al. 1995, Nieder et al. 2000).

Long-term changes in forest often-complex growth-climate relationships across the MB have also been documented by dendrochronological approaches (Lebourgeois 2012 and Appendix S1 of Supporting Information including 75 peer-reviewed publications). The vast majority of these studies have assessed the most traditionally used dendrochronological variables, namely: tree-ring width (TRW), basal area increment (BAI), tree-ring maximum latewood density (MXD) and C and O isotope composition of tree-ring wood or cellulose ($\delta^{13}C$, $\delta^{18}O$). TRW and BAI reflect radial growth due to cambial activity, while MXD best captures variations in summer temperature (Büntgen et al. 2007). Some advantages of MXD over TRW records include a stronger common signal between trees (Esper et al. 2010), reduced age trend and reduced biological persistence (i.e. autocorrelation) (Büntgen et al. 2008). In contrast, $\delta^{13}C$ and $\delta^{18}O$ in wood are mainly related to drought stress in seasonally dry climates like the MB (Warren et al. 2001, Andreu-Hayles et al. 2011). Together with the aforementioned, other usually considered variables are the net primary productivity (NPP) usually estimated from TRW series (in Rathgeber et al. 2000), height increment (HI; in Levanič et al. 2008), intrinsic water use efficiency (carbon gain per unit of water lost) derived from $\delta^{13}C$ (WUE; in

Linares et al. 2009a) and mean and maximum vessel area (MVA, MAX; in Campelo et al. 2010). Trends in interannual mean sensitivity (ms_x, relative TRW changes among consecutive years) were also registered (Tardif et al. 2003, Andreu et al. 2007), as well as shifts in growth-climate associations (Carrer 2011).

Species-specific growth-climate relationships vary across different environments of the MB due to the climatic, topographic and environmental diversity defining this area. At a local scale, the complex topography (Giorgi and Lionello 2008) derives from luv-lee (e.g. Xoplaki et al. 2000, Fox and Deil 2004) and slope aspects (e.g. Karschon et al. 1979, Kutiel 1992) or effects of concave-convex micro-topography (e.g. Ruiz-Flaño et al. 1992, Ozkan 2009). An intricate elevation gradient ranging from the depressions around the Israeli Sea of Galilee (-209 m asl) to the highest peaks of the Pyrenees (> 3000 m asl), or the Atlas and Alps (> 4000 m), also explains the MB characteristic diversity in tree growth-climate relationships. At a synoptic scale, differences in the depth of the atmospheric boundary layer between neighbouring areas can establish precipitation gradients across a particular region (Amit et al. 2006). Subtropical atmospheric high pressures from the North African arid zone and westerly circulations from central-northern Europe, together with other influences (South Asian Monsoon in summer, western Russian/Siberian High Pressure System in winter) shape the complex climate of the MB (Lionello et al. 2006). In this way, several studies have revealed distinct synoptic-scale climate areas ranging from north to south (Carrer et al. 2010) and from east to west (Roberts et al. 2011) of the MB, along a distance over ~4000 km. This Mediterranean climatic diversity and environmental complexity at multiple scales may result in spatially contrasting growth-climate response patterns (Tardif et al. 2003, Carrer et al. 2010). That is, populations growing in different areas of the MB are expected to react differently to climate change. In fact, studies concerning tree growth patterns across the MB have been showing contrasting behaviour in the tree-ring variables during the last decades of the 20th century (Appendix S1 and references therein).

In seeking to assess spatial patterns in recent tree growth across the MB, 75 dendrochronological peer-reviewed works published along the period 1996-2013 were revisited. 1076 positive, neutral or negative growth trends after the 1970s were extracted from the publications. We discuss the observed geographical patterns of trends in light of possible drivers ranging from local effects to synoptic scales. The importance of denser tree-ring networks that follow ecological criteria is also stressed, and the general issue of free data access is highlighted.

Materials and methods

Following a meta-knowledge approach (i.e. harvesting knowledge about knowledge; see Evans and Foster 2011) we compiled dendrochronological evidence of recent growth or productivity trends after 1970 from 75 peer-reviewed publications (Appendix S1). The bibliographic search was performed through website search tools like Web of Science, Scopus and Google Scholar. Making use of key terms like "Mediterranean" and "tree-ring" or key prefixes like "dendro-" the search was limited to MB dendrochronological studies. In most of the papers (60) the title makes direct reference to the Mediterranean location of the sampling site(s). To avoid double counting, meta-analyses of previously published data were generally dismissed or, if not, we excluded the corresponding previous study instead. The publications were obtained from 36 journals (Appendix S2). Two of the papers were not published yet but submitted to a journal instead. These publications deal mainly with dendrochronological variables related to tree growth or productivity in the last decades across the MB (Table S1). The Mediterranean region is here defined as the area between 30° and 46° N and 10° W and 40° E, which comprises a wide variety of climatic types from dry north-African regions to humid forests of the northern MB shore and areas bordering with the Atlantic Ocean in the west to the Black Sea in the east, with an altitudinal gradient ranging from -3 to 2,600 m asl.

The 75 reviewed publications included 724 locations from where 1076 individual trends were reported. The number of trends is bigger than the number of locations due to some locations with more than one studied variable. Specifically for TRW, 48 peer-reviewed publications with 528 locations and 688 trends were registered, and for MXD they were 6 publications with more than 36 locations and 36 trends (one from each location). When a publication referenced multiple sites, each site was treated as independent. In publications comparing managed/natural (Martín-Benito et al. 2010), experimental/control (e.g. Tognetti et al. 2006) or infested/non-infested tree populations (Camarero et al. 2003, Solla et al. 2006, Linares et al. 2010b), only the natural, control and non-infested cases were considered.

Geographic coordinates and the linear trend sign – positive, negative or neutral – estimated from 1970 onwards for each of the 1076 cases were registered, among other information (Table S1). The trend sign was estimated by means of three different approaches depending on the sort of available data. In 36% of the cases we used affirmations about the trend sign provided in the “results” and/or “discussion” sections, or else visually estimating it from the graphic representation of the raw time series. In 38% of the cases, a visual estimation of the trend sign from the graphic representation of the detrended series was used, since neither raw data nor written information about the trend sign were provided. In these cases no “authentic” trend could be assessed since the detrended series do not contain any trend *per se*; instead the trend sign was considered to be negative (positive) when most of the detrended values appeared to be generally lower (higher) than the steady mean value. In 26% of the cases a third approach for the trend estimation was applied inferring the tree-ring variable trend from the trend of the climatic series reconstructed. These three approaches possess increasing uncertainty degree in terms of inferring post-1970 trends: raw data logically provides more accurate trend estimation than detrended series and reconstructed climate data.

Potential geographic patterns were assessed by means of the geographic coordinates registered for the 724 study sites. Using GIS each location was positioned in a MB map with its corresponding dendrochronological trend sign coloured in blue, green and red for negative, neutral and positive trends, respectively. 62 sites were considered as having a neutral trend due to overlapping positive and negative trends coming from different variables. Specifically three MB maps were performed (Fig. 1), each of them displaying a different environmental or climatic factor in the background: elevation, mean temperature and total precipitation for the period from April to September (AMJJAS) – taken here as a general time window comprising the growing season in the MB – from CRUTS3.10 climatic data (Harris et al. 2013). The aim in using these three factors is to get potential topographic and/or climatic patterns influencing dendrochronological trends in a large scale. Lastly, cases with negative or positive trends were plotted in relationship to AMJJAS mean temperature and total precipitation, in order to detect potential climatic gradients determining the spatial arrangement of both positive and negative trends occurrence over the MB (Fig. 2).

Results

The variables considered in the 1076 cases are mainly TRW (63.9% of the cases), BAI (21.7%) and MXD (3.1%). The remaining 11.1% deal with the other minority variables registered (see Introduction). Speaking about number of papers, most of them also consider TRW (69.3% of the publications), BAI (21.3%) and MXD (9.3%), as well as $\delta^{13}C$ (10.6%) – the percentage values add up more than 100% since some studies deal with more than one variable –.

Overall 41 species from ten genera appear in the review: *Pinus* (61.6% of the cases), *Abies* (13.4%), *Larix* (8.1%), *Quercus* (5%), *Cedrus* (3.2%), *Juniperus* (3%), *Picea* (2.6%), *Fagus* (2.9%), *Arbutus* (0.1%) and *Fraxinus* (0.1%). The eight most studied species were *Pinus sylvestris* (212 cases), *Pinus uncinata* (139), *Abies alba* (126), *Pinus cembra* (116), *Pinus nigra* (97), *Larix decidua* (87), *Pinus halepensis* (66) and *Quercus* sp. (54). In all of them except *P. sylvestris* most of the cases dealt with TRW (Table 1). When analysing TRW cases exclusively, 36 species from ten genera are displayed: *Pinus* (55.2% of the cases), *Larix* (12.2%), *Abies* (10.3%), *Quercus* (7.6%), *Cedrus* (4.9%), *Juniperus* (4.2%), *Fagus* (2%), *Picea* (3.2%), *Arbutus* (0.15%) and *Fraxinus* (0.15%). Five species from three genera appear in the MXD cases: *Pinus* (71% of the cases), *Abies* (23%) and *Picea* (6%).

Table 1. Eight most abundant species and their percentage of cases dealing with the different tree-ring related variables. Variables' abbreviations are: TRW, tree-ring width; BAI, basal area increment; MXD tree-ring maximum latewood density; δ, C or O isotope composition of tree-ring wood or cellulose; NPP, net primary productivity; ms_x, interannual mean sensitivity.

Species	Percentage of cases dealing with these variables						
	TRW	BAI	MXD	δ	NPP	ms_x	others
Abies alba	**50.79**	38.1	6.35	1.59		3.17	
Larix decidua	**96.34**	2.44					1.22
Pinus cembra	**96.36**	1.82					1.82
Pinus halepensis	**62.90**	3.23			33.87		
Pinus nigra	**64.95**	11.34	1.03	11.34		9.28	2.06
Pinus sylvestris	24.53	**68.40**		0.94		6.13	
Pinus uncinata	**53.73**		18.66	4.48		21.64	1.5
Quercus sp.	**96.30**						3.7

Species growing at higher altitudes (*P. uncinata*, *P. sylvestris*, *L. decidua*) have a higher percentage of positive trends than trees of lower altitude ranges (*A. alba*, *P. halepensis*, *P. nigra*, *Quercus* sp.) (Table 2). Each dendrochronological variable shows different proportions in its trend signs; speaking about the four most common variables, TRW shows higher percentage of negative trends meantime BAI, MXD and $\delta^{13}C$ show higher proportion of positive trends (Table 3).

Table 2. Eight most abundant species and their percentage of cases showing the different three trend signs.

Species	Trend sign (%)		
	negative	neutral	positive
Abies alba	**53.97**	29.36	16.67
Larix decidua	32.93	1.22	**65.85**
Pinus cembra	30.91	34.55	34.55
Pinus halepensis	27.42	**72.58**	0.00
Pinus nigra	**52.58**	21.65	25.77
Pinus sylvestris	11.32	9.43	**79.24**
Pinus uncinata	32.84	8.21	**58.96**
Quercus sp.	25.96	**64.81**	9.26

Table 3. Main tree-ring variables (TRW, BAI, MXD and $\delta^{13}C$) and their percentage of cases showing the different three trend signs. See variables' abbreviations in Table 1.

Variable	Trend sign (%)		
	negative	neutral	positive
TRW	**42.66**	35.17	22.17
BAI	22.87	7.62	**69.51**
MXD		10.81	**89.20**
$\delta^{13}C$	10.00	40.00	**50.00**

From a geographical perspective, higher proportion of positive trends are located towards the wetter Northwest MB, whereas negative trends are more arranged towards the south-western and eastern MB regions where drier conditions prevail (Fig. 1b). Likewise, warmer areas like the Atlas region in northern Africa show negative trends meanwhile cooler regions at the northern shore of the MB (e.g. northern Iberian Peninsula, southern Alps) display more positive trends (Fig. 1c).

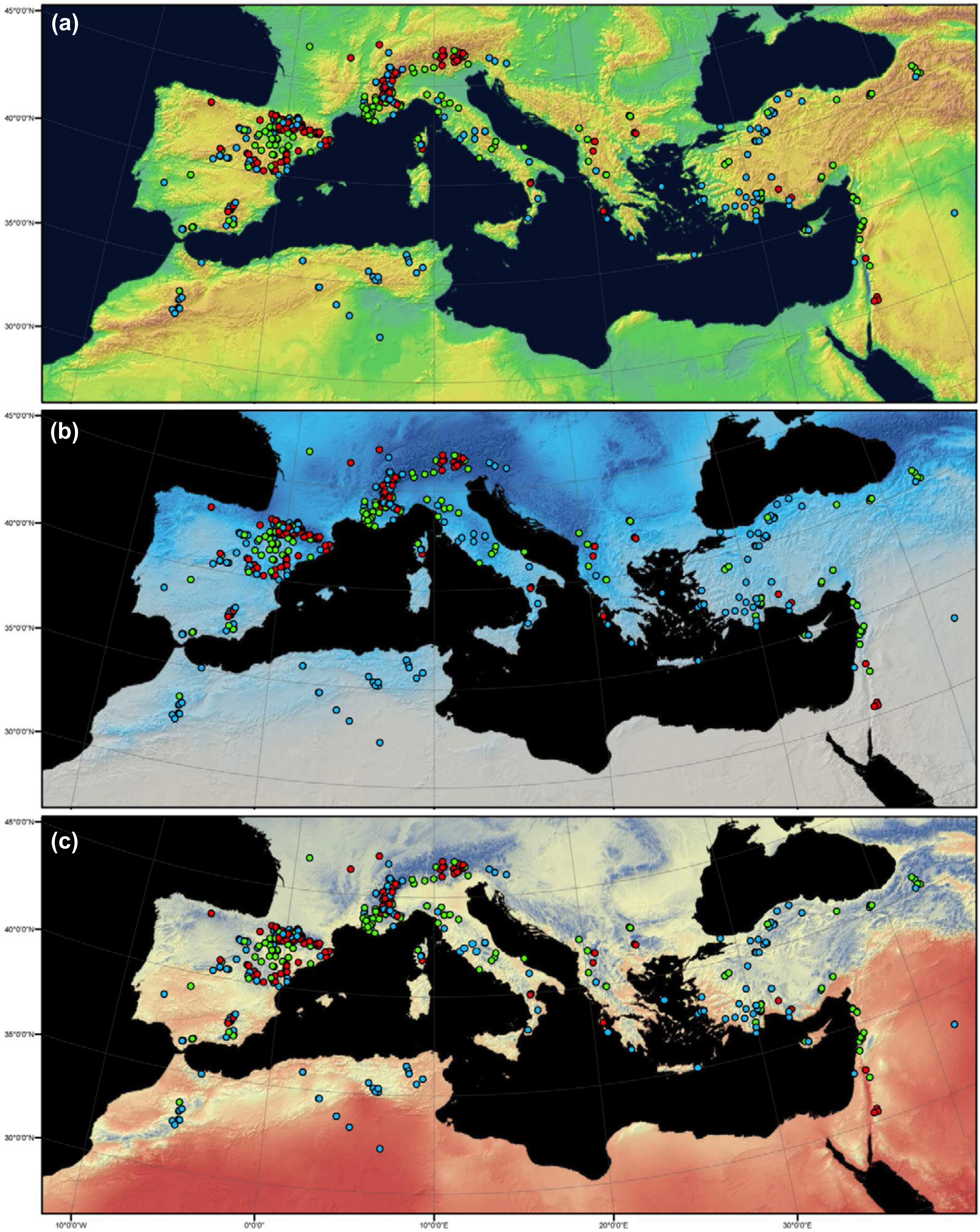

Figure 1 (legend in next page).

Figure 1 (previous page). Map of the Mediterranean Basin showing the reviewed chronologies and the detected post-1970 trends for tree-ring variables (mostly TRW, BAI and MXD). The map shows the geographical points with negative (blue) or positive (red) trends. Green dots correspond to neutral trends. The background of *a*, *b* and *c* figures displays elevation, AMJJAS total precipitation and mean temperature, respectively. In (a) greenish and brownish colours indicate lower and higher altitudes respectively, in (b) sharpest blue indicates rainier areas, and in (c) colours from red to blue indicate warm to cold areas, respectively.

These observations agree with the climatic perspective where post-1970 positive trends tend to be located in cooler and wetter areas of the Mediterranean Basin compared with more xeric and warmer sites displaying more often negative growth trends (Fig. 2). These observations occur also in the case of TRW (Fig. S1). MXD trends are mostly positive, corroborating our observations from the Pyrenees (see chapter 3), although more studies concerning MXD trends are needed (Fig. S2).

The mean (± SD) altitude of all the reviewed cases is 1530 (± 589) m asl. Specifically, the mean (± SD) altitude of the TRW cases was 1687 ± 547 m and 1904 ± 479 m for MXD. These results highlight that most of the reviewed sites are geographically biased towards high-elevation areas such as the Alps, Pyrenees, Apennines, Balkans, Anatolian and Iberian plateaus, Atlas, etc. (represented by brownish colours in Fig. 1a), and that the revisited publications deal with trees growing in more mountainous and hence colder and rainier environments than the average MB lowland conditions. In fact, according to mean temperature and precipitation for the period AMJJAS from CRUTS3.10 data averaged for the whole Mediterranean Basin, most of the reviewed cases are located outside the "average Mediterranean climatic envelope" (grey area in Fig. 2), reflecting the prevailing mountainous character of the studied sites. This is likely the result of the dendrochronologists fingerprint, traditionally looking for the most climate-sensitive trees usually located in harsh environments such as alpine tree-lines.

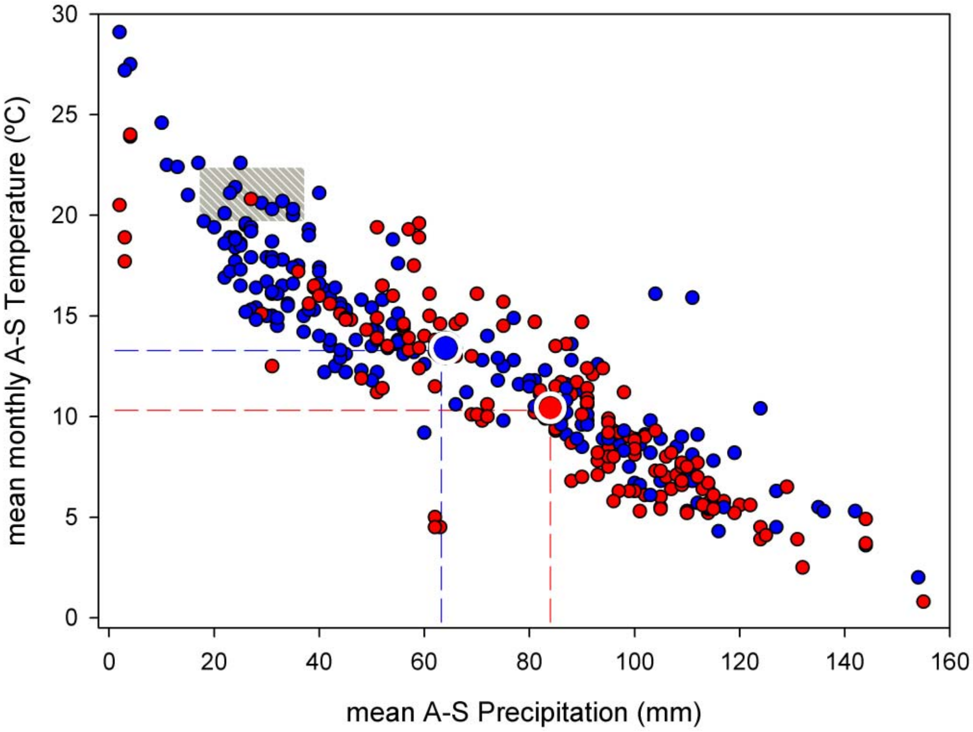

Figure 2. Relationship between April to September (A-S) total precipitation vs. A-S mean temperature of the reviewed tree-ring width cases. The shaded grey area highlights the mean A-S temperature and precipitation averaged for the area 10° W-40° E and 46°-30° N, which includes the whole Mediterranean Basin. Discontinuous red and blue lines indicate the A-S mean temperature and precipitation averaged for the whole set of sites with positive and negative trends, respectively.

Furthermore, sampling sites are not evenly distributed across the MB, but rather concentrated on the northern shore. A possible geographical bias in our bibliographic search was first considered as a possible reason for this pattern. A cross-check of this potential bias was performed using the web tool JournalMap (http://www.journalmap.org) aimed at general ecological studies with geographic literature searching. Researches performed in the MB dealing with the biome type "Mediterranean forests, woodlands and scrub" (obtained from the "Biome" tab of the web) were selected to overview the geographical distribution of ecology studies. The biased site distribution observed in a dendrochronology-scale was confirmed in a wider ecological scale, finding again an overrepresentation of the MB northern shore in terms of number of publications. Specifically JournalMap returned 30 and 102 publications in the southern and northern shores, respectively.

Discussion

This review highlights that the intricate topography and diverse climate, both characteristics of the MB, produce varied and often opposite trend signs even between neighbouring sites. In spite of this complexity, our findings emphasize a pattern acting at synoptic scales, where the distribution of recent positive trends in tree-ring variables related to growth or productivity are biased towards wetter and cooler areas of the MB located in the northwest. Negative trends are generally displayed at more xeric and warmer areas, at the south and east of the MB. These observations could indicate that, in spite of the characteristic climatic and topographic local complexity, on a global scale tree growth across the MB is limited by drought or low water availability during the growing season (e.g. Martínez-Vilalta and Piñol 2002, Camarero et al. 2004, Jump et al. 2006, Sarris et al. 2007, Piovesan et al. 2008, Linares et al. 2011b, Linares et al. 2012, Sánchez-Salguero et al. 2012). Water-use efficiency improvements (WUEi) seem to be insufficient to compensate the negative effects of the reduced water availability on growth (Andreu et al. 2011). A reduction in forest productivity due to water limitations could have serious implications regarding the degree of carbon sequestration by the Iberian forests, affecting the terrestrial biosphere carbon cycle.

A sampling bias towards high-elevation sites at the MB scale is also shown, and it is very likely the result of the dendrochronologists' signature, which traditionally have sought the most climate-sensitive trees usually growing at harsh high-elevation environments (Fritts 2001). On the other hand, older trees tend to grow at higher altitudes due to their traditionally smaller anthropic pressure (i.e. logging) over the last decades, as well as to the low growth rate and extended life span happening in these harsh environments (Bigler and Veblen 2009). Finally, most well-preserved European forests are located in mountains. Hence it is assumed that many of the dendrochronological studies and their findings here compiled are also biased towards an overrepresentation of old slow-growing trees living in high-elevation areas.

Only a few reviewed papers differentiate growth trends between different age classes (e.g. Rozas et al. 2009, Dorado-Liñán et al. 2012a, Linares et al. 2012, Dorado-Liñán et al. 2012a, Linares et al. 2012), competition intensities (e.g. Martín-Benito et al. 2009, Linares et al. 2009a, 2010a) or health stages (e.g. Camarero et al. 2003, Solla et al. 2006, Linares et al. 2010b). Considering these factors when reviewing publications would allow reaching less vague, more explicit conclusions about growth trends of forests with specific vitality, age or social status levels. Furthermore, apart from a few cases (e.g. Linares et al. 2010a, Carrer et al. 2011, Rozas and Olano 2012), papers included in this review have mainly a population-based approach and refer to the mean trend of specific populations. But dendrochronologists cannot overlook the fact that, when analysed in an individual-level, different growth trends in response to climate can be observed among different trees (Ettl and Peterson 1995; see chapter 2). In spite of this, the predominantly population-based approach of this review is suitable since our aim was not disentangling the individual responses or the microsite mechanisms, but finding regional patterns in tree growth across the MB.

A lack of evenly distributed sampled sites across the MB is underscore, with northern countries showing higher amount of publications. This can be explained by three factors. First of all, the lack of homogeneity in the forest cover degree is an evident limitation in tracking the tree growth behaviour over the whole MB. An absence of cases in the southern shore of the Mediterranean Sea (Libya, Egypt) is apparent (Fig. 1) and in coherence with the scarcity in forested areas in these regions (Sebukeera et al. 2006). Apart from that, ecologists' study site selections are geographically biased towards protected areas, the temperate zone and countries with high gross national income (GNI) and therefore more scientific outputs (Martin et al. 2012); southern European countries have higher GNI than northern African countries (World Bank 2012) and more land surface covered by protected areas (IUCN and UNEP 2013). Consequently our review is likely biased towards an overrepresentation of the northern Mediterranean shore, which is also wetter and cooler along the year in general terms. More abundance of sampled trends in the southern MB shore would provide a more precise distinction between negative and positive trends arrangement regarding temperature and precipitation (Fig. 2). Our results can be taken as an advice for dendrochronologists, policy makers or funding companies about improving dendrochronological research going in quest of currently understudied areas.

Concerning this geographic bias, an emergent weakness when looking for publications performed in a particular area of the world arises from the lack of consideration of the geographic location in which the research has been performed; this happens in search tools like Web of Science, Scopus or Google Scholar. Geographic information about the coordinates and characteristics of the study sites is not always provided neither – in our case five papers could not be used for the review because of this reason. Searching for science literature not only thematically but also geographically and making site coordinates available would allow the achievement of better meta-analyses and explanations of environmental patterns (Karl et al. 2013).

In this review different data sources were used: raw and detrended series, and indirect inference of the trends sign from climatic reconstructions. Obtaining all raw data would have allowed us to perform further statistical trend analyses. Hence, not only making geographical information available is important, but also providing raw tree-ring series in order to allow secondary analyses with minor uncertainty level. In this sense, the International Tree-ring Data Bank (Grissino-Mayer and Fritts 1997) is a very useful tool but the dendro-scientific world must aspire to an even more globally spread database. The imbalance between the number of TRW and MXD studies is also emphasized; further prospecting in MXD series across the MB would improve the knowledge about synoptic patterns in trends of this proxy.

This review is an important step towards obtaining a first exhaustive geographical overview of the main body of dendrochronological literature concerning MB post-1970 growth and productivity trends, and it should be completed in a continuous and iterative way as new peer-reviewed studies concerning MB tree growth or productivity, analysed by means of dendrochronological methods, are published.

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Appendix S2. Journals used for this review. Numbers in brackets indicate the number of papers used in this review that comes from each journal.

Agricultural and Forest Meteorology (1)
Annals of Forest Science (1)
Boreas (1)
Canadian Journal of Forest Research (1)
Climate Dynamics (3)
Climate of the Past (3)
Climate Research (1)
Climatic Change (5)
Comptes Rendus Biologie (1)
Dendrochronologia (2)
Ecological Monographs (1)
European Journal of Forest Research (2)
Forest Ecology and Management (2)
Forests (1)
Geophysical Research Letters (2)
Global and Planetary Change (1)
Global Change Biology (8)
Global Ecology and Biogeography (1)
International Journal of Biometeorology (2)
International Journal of Climatology (4)
Journal of Arid Environments (2)
Journal of Ecology (2)
Journal of the American Water Resources Association (1)
Journal of Vegetation Science (1)
New Phytologist (2)
Oecologia (3)
PLoS ONE (1)
Quaternary Research (2)
Radiocarbon (1)
Regional Environmental Change (1)
The Holocene (2)
TRACE Proceedings (1)
Tree Physiology (2)
Tree-Ring Bulletin (1)
Trees (7)
Zubía (1).

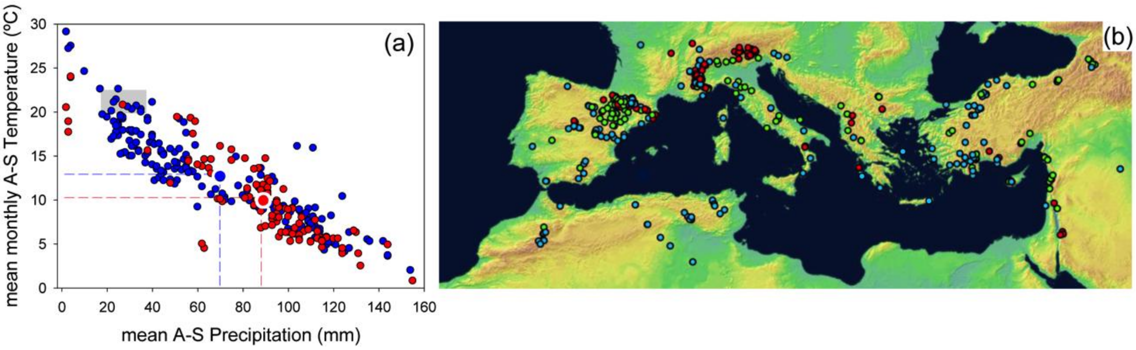

Figure S1. (a) Relationship between April to September (A-S) total precipitation vs. A-S mean temperature of the reviewed TRW cases. The shaded grey area highlights the CRUTS3.10 mean A-S temperature and precipitation averaged for the area 10° W-40° E and 46°-30° N, which includes the whole Mediterranean Basin. Discontinuous red and blue lines indicate the A-S mean temperature and precipitation values averaged for the whole set of sites with positive and negative trends, respectively. (b) Map of the Mediterranean Basin showing the reviewed tree-ring width series and the detected trends after 1970. The map shows the geographical points with negative (blue) or positive (red) trends. Green dots indicate neutral trends.

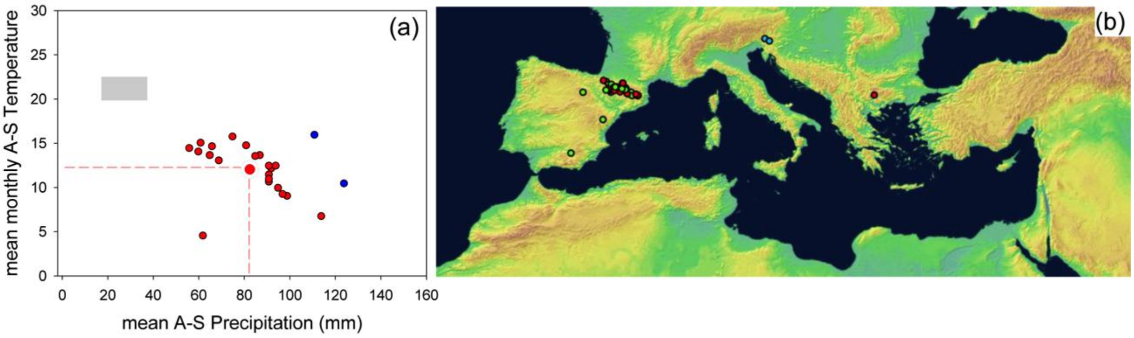

Figure S2. (a) Relationship between April to September (A-S) total precipitation vs. A-S mean temperature of the reviewed MXD cases. The rest of explanations are as in Figure S1.

Table S1. A summary of papers studying tree-ring parameters trends after 1970. Parameters: *Δ* Isotopic discrimination between the C of atmospheric CO_2 and plant C, *cJJ* correlation between TRW detrended chronologies and June-July Temperature, *cSD* correlation between TRW detrended chronologies and September-December Temperature, *HI* height increment, *MAX* maximum vessel area, *MVA* mean vessel area, *TRW* tree-ring width, *BAI* basal area increment, *MXD* tree-ring maximum density, $\delta^{13}C$ ^{13}C signature, $\delta^{18}O$ ^{18}O signature, *NPP* net primary productivity, ms_x interannual mean sensitivity, *WUEi* water use efficiency. Post-1970 parameter trend sign: + positive, *0* neutral, – negative. Time-span: longer time span covered by the parameters used in each study. Inferred variable in the reconstruction: *Temp* temperature, *Prec* precipitation, *Cloud* cloud coverage, *AI* De Martonne Aridity Index, *Aridity* aridity anomalies, *PDSI* Palmer Drought Severity Index.

Source	**Sites**	**Countries**	**Elevation (m asl; mean ± SD)**	**Parameter**	**Post-1970 parameter trend**		**Time-span**	**Species**	**Material origin**	**Reconstruction**		
					Sign	**Estimation approach**				**Inferred variable**	**Period**	**Post1970 trend**
Akkemik 2000	1	Turkey	70	TRW	–	detrended	1887-1995	*Pinus pinea*	living trees			
Akkemik & Aras 2005	2	Turkey	1475 ± 318	TRW	+	detrended	1568-1994	*Pinus nigra*	living trees	Prec	AMJJA	+
Akkemik et al. 2005	1	Turkey	2050	TRW	–	residual	1611-2001	*Quercus* spp.	living trees, historical data	Prec	MAMJ	0
Akkemik et al. 2008	6	Turkey	1436 ± 284	TRW	–	detrended	1800-2000	*Pinus sylvestris*	living trees, historical buildings	Prec	MJ	–
					0		1872-2000	*Abies bornmuelleriana*		Streamflow	MJJA	–
					0		1749-2000	*Pinus sylvestris*		Streamflow	MJJA	–
					–		1611-2001	*Quercus* spp.		Prec	MJ	–
					0		1624-2004	*Quercus* spp.		Streamflow	MJJA	–
					0		1606-2000	*Quercus* spp.		Prec	MJ	–
					–			*Pinus* spp.		Prec	MJ	–
					–			*Pinus* spp.		Streamflow	MJJA	–
Andreu et al. 2007	3	Spain	1833 ± 25	$\delta^{13}C$	+	raw	1600-2002	*Pinus nigra, P. sylvestris, P. uncinata*	living trees	Prec	JJ	–
Andreu-Hayles et al. 2007	38	Spain	1758 ± 393	ms_x	+	detrended	1331–2002	*Pinus nigra, P. sylvestris, P. uncinata*	living trees			
Andreu-Hayles et al. 2011	2	Spain	1850 ± 141	$\delta^{13}C$	+	raw	1800-1999	*Pinus sylvestris, P. uncinata*	living trees			
Biondi & Visani 1996	22	Italy	1106 ± 581	TRW	0	detrended	1036-1989	*Abies alba, Fagus sylvatica, Quercus robur, Larix decidua, Picea excelsa, Pinus leucodermis, P. nigra, P. sylvestris, P. pinea*	old living trees			
Büntgen et al. 2008	2	Spain	2313 ± 53	MXD	+	raw	924-2005	*Pinus uncinata*	living and dry-dead trees	Temp	MJJAS	+
Büntgen et al. 2010	28	Andorra, France, Spain	1826 ± 397	TRW	+	detrended	924-2005	*Abies alba, Pinus sylvestris, P. uncinata*	living trees			
Büntgen et al. 2012	4	Italy	2154 ± 70	TRW	+	detrended	933-2007	*Larix decidua*	living and dead trees			
Camarero et al. 2003	2	Spain	~1424	TRW	–	raw	1900-2000	*Abies alba*	living trees			

			± 147									
Camarero & Gutiérrez 2004	7	Spain	2199 ± 111	TRW	0 †	detrended	1700-1995	*Pinus uncinata*	living trees			
Camarero et al. 2011	32	Spain	1361 ± 185	BAI	– 0	raw	1900-2000	*Abies alba*	living trees			
Campelo et al. 2009	1	Portugal	~200	TRW	–	residual	1876-2001	*Quercus ilex*	living trees			
Campelo et al. 2010	1	Spain	300	TRW MVA MAX	– + +	raw	1984-2004	*Quercus ilex*	living trees			
Carrer 2011	2	Italy	2100	cJJ cJJ cSD	0 + –	correlation	1815-1980	*Larix decidua, Pinus cembra*	living trees			
Carrer et al. 2007	33	France, Italy	~2100	TRW	0 +	detrended	961-2003	*Pinus cembra*	living trees			
Corcuera et al. 2006	1	Spain	900	TRW	–	raw	1970-2000	*Quercus pyrenaica (overaged)*	living trees			
Corona et al. 2010	17	France, Italy	2161 ± 93	TRW	+ – ††	detrended	751-2000	*Larix decidua, Pinus cembra*				
Corona et al. 2011	34	France	2054 ± 185	TRW	+	detrended	751-2000	*Larix decidua*	living and dry-dead trees, historical timbers	Temp	JJA	+
Čufar et al. 2008		Slovenia	450	TRW	–	detrended	1442-2003	*Quercus* spp.	living trees, historical buildings	AI	June	–
DiFilippo et al. 2012	8	Italy	1194 ± 463	BAI	–	raw	1500-2008	*Fagus sylvatica*	living trees			
Dorado-Liñán et al. 2012a	2	Spain	1950 ± 212	TRW MXD EW LW $\delta^{13}C$ $\delta^{18}O$	+ 0 + + 0 0	detrended	1900-2006	*Pinus nigra, P. uncinata*	living trees			
Dorado-Liñán et al. 2012b	21	Andorra, France, Spain	1857 ± 412	MXD	+	detrended	924-2005	*Abies alba, Pinus uncinata*	living and dry-dead trees	Temp	MJJAS	+
Esper et al. 2007		Morocco	2170 ± 48	TRW	–	detrended	977-2001	*Cedrus atlantica*	living trees	PDSI	FMAMJ	–
Galván et al. (chapter3)	30	Spain	2148 ± 195	TRW MXD	– +	raw	1270-2010	*Pinus uncinata*	living trees			
Gea-Izquierdo et al. 2012	5	Morocco, Spain	~690 ± 255	TRW	–	raw	1828-2008	*Quercus canariensis*	living trees			
Gimeno et al. 2012	3	Spain	1137 ± 153	BAI	+	raw	1941-2008	*Juniperus thurifera*	living trees			
Griggs et al. 2007	24	Greece, Turkey		TRW	0	detrended	1081-1989	*Quercus* spp.	living trees, historical buildings	Prec	MJ	0
Guiot et al. 2005	12	France, Italy, Spain	1667 ± 698	TRW	+	reconstruction	~1000-2001	*Quercus robur, Larix decidua, Pinus cembra, P. nigra, P. leucodermis, P. sylvestris*	living and dead trees, historical buildings	Temp	AS	+

Körner et al. 2005	3	Greece	183 ± 126	TRW	–	raw	1900-2000	*Pinus halepensis, P. brutia*	living trees			
Köse et al. 2011	17	Turkey	1538 ± 206	TRW	–	reconstruction	1163-2005	*Pinus nigra*	living trees	Prec	MJ	–
Koutavas 2013	1	Greece	~1450	TRW	+	detrended	1820-2001	*Abies cephalonica*	living trees			
Levanič et al. 2008	2	Slovenia	800 ± 636	$\delta^{13}C$ TRW MXD HI	0 – 0 –	raw	1950-2002	*Picea abies*	living trees			
Linares et al. 2009a	2	Spain	1488 ± 370	BAI Δ WUE_i	+ 0 – +	raw	~1950-2005	*Abies pinsapo*	living trees			
Linares et al. 2009b	3	Spain	1511 ± 265	BAI	+ 0	raw	~1950-2005	*Abies pinsapo*	living trees			
Linares et al. 2010a	1	Spain	1200	BAI	0	raw	1940-2004	*Abies pinsapo*	living trees			
Linares et al. 2010b	1	Spain	1200	BAI	–	raw	1970-2009	*Abies pinsapo*	living and dead trees			
Linares & Tíscar 2011a	8	Spain	1443 ± 293	BAI	+	raw	1800-2000	*Pinus nigra*	living trees			
Linares et al. 2011b	1	Morocco	1860	BAI	–	raw	1900-2009	*Cedrus atlantica*	living trees			
Linares et al. 2013	1	Morocco	1860	TRW	0*	detrended	1900-2000	*Cedrus atlantica*	living trees			
Linares & Camarero 2012a	4	Spain	1162 ± 148	BAI	+ 0	raw	1900-2000	*Abies alba*	living and declining trees			
Linares & Camarero 2012b	8	Spain	1269 ± 166	$\delta^{13}C$ BAI	–	raw	1900-2000	*Abies alba*	declining and non-declining trees			
Martín-Benito et al. 2010	1	Spain	1050	BAI	–	raw	1970-2006	*Pinus nigra*[1]	living trees			
Martínez-Vilalta et al. 2008	135	Spain	884 ± 324	BAI	+	raw	1901-1997	*Pinus sylvestris*	living trees			
Motta & Nola 2001	1	Italy	~2200	BAI	– +	raw	1790-1990	*Larix deciduas, Pinus cembra*	living trees			
Nicault et al. 2008	160	Algeria, Cyprus, France, Greece, Italy, Morocco, Spain, Turkey	1842 ± 326	TRW MXD(7 sites)	– –	reconstruction	1500-2000	*Abies alba, A. cephalonica, A. nordmanniana, Cedrus atlantica, C. brevifolia, C. libani, Juniperus excelsa, Larix decidua, Picea abies, Pinus cembra, P. halepensis, P. mugo, P. nigra, P. sylvestris, P. uncinata*		PDSI	AMJJAS	–

Panayotov et al. 2010	2	Bulgaria	2088 ± 53	TRW	+	detrended	1250-2008	*Pinus heldreichii, Pinus peuce*	living trees			
Panayotov et al. 2013	4	Bulgaria	1238 ± 421	TRW	0	raw	1900-2005	*Pinus nigra, P. peuce, P. sylvestris*	living trees			
Pasho et al. 2011	56	Spain	1006 ± 472	TRW	0	detrended	1950-2005	*Abies alba, Juniperus thurifera, Quercus faginea, Q. ilex, Pinus halepensis, P. nigra, P. pinea, P. sylvestris*	living trees			
Peñuelas et al. 2008	3	Spain	1253 ± 342	$\delta^{13}C$ WUEi BAI	– + 0	raw	1920-2003	*Fagus sylvatica*	living trees			
Planells et al. 2006	1	Spain	2120	$\delta^{13}C$ TRW $\delta^{18}O$	+ – +	raw detrended raw	1600-2003	*Pinus uncinata*	living trees	Aridity	JJ	+
Rathgeber et al. 2000	21	France	409 ± 183	NPP	0	detrended	1815–1994	*Pinus halepensis*	living trees			
Rathgeber & Roche 2003	1	France	2200	TRW	0	raw	~1830-1997	*Pinus uncinata*	living trees			
Rolland et al. 1998	14	France	2063 ± 122	TRW	+	raw	1750-1990	*Picea* sp., *Pinus Cembra, P, uncinata, Larix* sp.	living trees			
Rozas et al. 2009	1	Spain	1200	TRW	+ 0	raw	1945-2004	*Juniperus thurifera*[2]	living trees			
Sánchez-Salguero et al. 2012	2	Spain	1475 ± 116	BAI	0	raw	1973-2006	*Pinus halepensis, P. nigra, P. pinaster, P. sylvestris*	living trees			
Sarris et al. 2007	3	Turkey	225	TRW	–	raw	1964-2001	*Pinus brutia*	living trees			
Sarris et al. 2011	4	Greece	321 ± 135	TRW	–	detrended	1930-2000	*Pinus halepensis*	living trees			
Saz & Creus 2008	8	Spain	1824 ± 60	TRW	+	reconstruction	1385-2006	*Pinus sylvestris, P. uncinata*	living trees	Temp	Annual	+
Seim et al. 2012	3	Albania	1900 ± 100	TRW	0	detrended	617-2008	*Pinus heldreichii*	living trees, buildings logs			
Solla et al. 2006	1	Spain	1015	TRW	0	raw	1930-2002	*Abies alba*[3]	living trees			
Szymczak et al. 2012	4	France	1550 ± 158	$\delta^{13}C$	0 +	raw	1448-2008	*Pinus nigra*	living trees	Temp Cloud	AS MJJA	+ –
Tardif et al. 2003	17	Spain	2057 ± 203	ms_x	+	raw	1850-1994	*Abies alba, Pinus sylvestris, P. uncinata*	living trees			
Tegel et al. (in review)	3	Albania, Macedonia	1450	TRW	+	raw		*Fagus sylvatica*	living trees and historical timbers			
Tognetti et al. 2000	1	Italy	210	TRW	–	raw	~1925-1997	*Arbutus unedo, Fraxinus ornu, Quercus cerni, Q. Ilex, Q. pubescens*	living trees			

Touchan & Hugues 1999	4	Jordan	~731 ± 412	TRW	+ – 0 +	detrended	1600-1995	*Juniperus phoenicia* *Quercus aegilops* *Pinus halepensis* *Pinus halepensis*	living trees	Prec	ONDJFMAM	+
Touchan et al. 1999	2	Jordan	~1250	TRW	+	reconstruction	1600-1995	*Juniperus phoenicia*	living trees	Prec	ONDJFMAM	+
Touchan et al. 2005a	43	Cyprus, Greece, Lebanon, Syria, Turkey	~1598 ± 466	TRW	0	reconstruction	1400-2000	*Abies cilicica, Cedrus brevifolia, C. libani, Juniperus excelsa, Pinus brutia, P. leucodermis, P. nigra, P. sylvestris*	living trees	Prec	MJJA	0
Touchan et al. 2005b	6	Turkey	~1696 ± 325	TRW	0	reconstruction	1251-1998	*Juniperus excelsa*	living trees	SPI	MJJ	0
Touchan et al. 2007	4	Turkey	~1816 ± 89	TRW	0	reconstruction	1097-2000	*Juniperus excelsa*	living trees	Prec	MJ	0
Touchan et al. 2008a	13	Algeria, Tunisia	1244 ± 392	TRW	–	reconstruction	1456-2002	*Cedrus atlantica, Pinus halepensis*	living trees and remnant wood	PDSI	MJJA	–
Touchan et al. 2008b	4	Tunisia	806 ± 275	TRW	–	reconstruction	1771-2002	*Pinus halepensis*	living trees	Prec	ONDJFMAMJ	–
Trouet et al. 2012	1	Bulgaria	2050	MXD	+	reconstruction	1768-2008	*Pinus heldreichii*	living trees	Temp	Au	+

Trends' sign: † increase in interannual variability, which is the frequency of narrow and wide rings; †† only two sites; *more variability.

Species: [1] not thinned populations; [2] <101 year-old trees; [3] asymptomatic.

... So the tree rustles in the evening, when we stand uneasy before our childish thoughts. Trees have long thoughts, long-breathing and restful, just as they have longer lives than ours. They are wiser than we are, as long as we do not listen to them. But when we have learned how to listen to trees, then the brevity and the quickness and the childlike hastiness of our thoughts achieve an incomparable joy. Whoever has learned to listen to trees no longer wants to be a tree. He wants to be nothing except what he is. That is home. That is happiness.

... Susurra el árbol al atardecer, cuando afrontamos inquietos nuestros pensamientos infantiles. Los árboles tienen pensamientos amplios, prolijos y serenos, así como una vida más larga que la nuestra. Son más sabios que nosotros, mientras no les escuchamos. Pero cuando aprendemos a escuchar a los árboles, la brevedad y la rapidez y el apresuramiento infantil de nuestros pensamientos adquieren una alegría incomparable. Quien ha aprendido a escuchar a los árboles, ya no desea ser árbol. No desea ser más que lo que es. Eso es el hogar. Eso es la felicidad.

Wanderung: Aufzeichnungen
Hermann Hesse

General Discussion

Drivers of tree growth at individual level (Chapter 1)

In the network of tree and site characteristics, sapwood area is the main driver of the recent decelerating trends in basal area increment (BAI) observed in Iberian mountain *P. uncinata* forests. Trees which produce more sapwood area also show a higher BAI, and this association has increased in the last decades of the past century. BAI increased at higher rates in the first than in the second half of the 20th century. This may be due to trees reaching the senescent phase, characterized by a stabilization phase in BAI (Duchesne et al. 2003). A negative relationship between age and growth rate has been widely documented in several tree species (Johnson and Abrams 2009); in the same way, the negative effect of tree age on BAI agrees with numerous studies demonstrating how sapwood area decreases as trees age (Hazenberg and Yang 1991, Sellin 1994, Spicer and Gartner 2001). Nevertheless, the negative influence of age on BAI is becoming stronger based on our SEMs, and it can be mediated by changes in sapwood area, that is, older trees produced proportionately less sapwood area than younger ones in the late 20th century.

Why is BAI decreasing? We propose three explanations:

- First, the increasing length of the hydraulic pathway as trees age and accumulate biomass may be one of the answers. The ageing of conductive structures and the alteration of hydraulic networks of old trees and big stems (Martínez-Vilalta et al. 2007, McCulloh et al. 2010) may contribute to explain a sharp decrease in hydraulic conductivity and sapwood production as trees grow and age, thus leading to sapwood-mediated declining growth trends.

- Second, the harsh climatic conditions imposed by high altitudes may also explain this sapwood-mediated declining growth trends. The harsh environmental conditions in high-elevation forests (low air and soil temperatures, frequent freeze-thaw events, elevated radiation and high wind speed; see Barry 2008) are consistent with the finding that trees tend to be older at higher elevations plausibly because of a reduction in radial growth rates and increased longevity (Bigler and Veblen 2009). We also must acknowledge that dendrochronological protocols are usually biased towards collecting wood samples from older trees.

- Third, as altitude increases, air and stem temperatures decrease, producing an increment in water viscosity and hence in the sap flux resistance (Grace 1983). This, together with the windy conditions in high altitude forests leading to drying effects, may cause an enhanced sapwood area to compensate this hindered sap flux in high altitude forests (Gates 1980, Gutiérrez et al. 1991). Therefore, rising temperatures during the 20th century may have induced a decrease in water viscosity. This entails an enhanced sap flux and a reduction in sapwood production leading to slowing down growth rates.

Our findings suggest that:

- Any potential climate-induced effect on BAI will be mainly driven by sapwood production and preservation, which is mediated by tree age and altitude.

- Because slow-growing high-elevation trees get older than fast-growing low-elevation trees, we expect differential age-mediated BAI responses along the altitudinal gradient.

- A more realistic projection of future growth and productivity responses of mountain forests to climate warming can be strongly affected by individual tree features (e.g. sapwood area) and secondarily by local factors (e.g. altitude) modulating or buffering the regional effects of climate stress on growth (Case and Peterson 2005).

- Once trees reach a maximum age- or size related functional threshold linked to a stagnant sapwood production, they can become relatively insensitive to climate variability (Voelker 2011).

Individual tree growth responses to climate (Chapter 2)

Several xylogenesis studies and dendrochronological assessments of growth–climate relationships indicate that wood formation and growth responsiveness to climate can be age dependent (Carrer and Urbinati 2004, Rossi et al. 2008) and modulated by site conditions (Tardif et al. 2003). In chapter 2 we assess, following an individual-based approach, the TRW indices (TRWi) responses to climate and how tree and site characteristics can influence those responses.

We observe that the TRWi responses to climate at the species and site scales differ from those detected at the individual tree scale. At species and site levels the TRWi of *P. uncinata* is enhanced by warm conditions during the previous late fall and during late spring of the year of tree-ring formation, which indicates that the main climatic constrain of TRWi in these forests during the 20th century has been low temperature. High temperatures during the previous fall, when most aboveground growth is finished, probably contribute to enhanced photosynthesis and the production and storage of non-structural carbohydrates to be used for earlywood formation during the next growing period (year) (von Felten et al. 2007). Contrastingly, warmer spring conditions directly affect cambial activity and may trigger earlier growth resumption after winter dormancy and enhance wood production (Camarero et al. 2010).

At the individual scale, most trees form more wood in response to warmer maximum temperatures during the previous November, but some of them also react positively to wet conditions during early summer when radial-growth rates are usually the highest throughout the year (Camarero et al. 1998). The latter finding is to some degree unexpected since most sampled stands correspond to high-elevation subalpine forests where cold conditions constrain growth. However, the consideration of such ample network of sites allowed uncovering that summer water availability drives *P. uncinata* growth mainly in the most xeric sites of the species' distribution area subjected to Mediterranean climate influences, i.e. warmer and drier summer conditions. This implies that these trees are probably adapted to dry summers but if climate warming leads to even more arid conditions, *P. uncinata* forests located in marginal locations (Pre-Pyrenees, southern Iberian System) could show growth decline and die-back as has been observed in other xeric edges of distribution (Linares et al. 2009). Later on we will talk about an increase in the drought influence on growth indices also detected following a population-based approach (chapter 3).

The low variance amount (3-33%) accounted for by linear-mixed effects models using climatic predictors of *P. uncinata* TRWi at the individual scale evidences that climate plays a secondary role in controlling TRWi variability among coexisting trees even in harsh environments. Consequently, we must consider individual tree features such as sapwood cross-sectional area (chapter 1) or site conditions such as altitude as drivers of TRWi responses to climate. In addition, individual trees with significant TRWi responses to climate, which may represent a small proportion of the whole population, should be carefully monitored using ecophysiological methods to properly understand the mechanisms driving tree responses to climate warming.

Altitude plays a major role affecting *P. uncinata* TRWi responses to climate at the site and tree scales in agreement with previous works (Tardif et al. 2003) and with research in widely distributed conifers as Douglas fir (Chen et al. 2010). This suggests that the altitude-mediated decrease in air temperatures is the major driver of TRWi at both the site and tree levels determining the maximum elevation of the tree growth form (Ettinger et al. 2011). Trees living at higher altitudes possess also higher TRWi variance explained by climate.

We also observe an increase in climate-driven *P. uncinata* TRWi variability in the second half of the 20th century. These findings support other studies performed also in the Pyrenees for the same species showing the same trend towards the last decades (Tardif et al. 2003). A similar instability in the growth-climate relationships was found by Andreu et al. (2007) and related to changing climate conditions. We offer an alternative environmental explanation for this unstable behaviour. Warming has rapidly intensified over north-eastern Spain during the first half of the past century which could have partially ameliorated the coldness constrains on growth indices imposed by the altitudinal gradient. Our findings do support the "relaxation" of the altitudinal gradient due to rapid climate warming postulated by Tardif *et al*. (2003) particularly for the first half of the past century. Later on altitude was the main driver of temperature-mediated growth in mountain *P. uncinata* forests despite warming continued but at a rate lower than in the mid 20th century. Shifts in the growth-climate associations could also indicate non-linear relationships between growth and climatic drivers (see next sections). The loss of thermal responses in cold areas could be linked to alterations in carbon allocation and intra-annual growth patterns (Seo et al. 2011). Anyway, our findings emphasize the need to consider warming rates as major drivers of growth responses in forests.

Population tree growth responses to climate (Chapter 3)

In chapter 3 we detected low frequency trend offsets between the decreasing TRW (population means) series since the second half of the 20th century, and increasing temperatures. This evidences the weakness of theoretically temperature-sensitive proxies (TRW) to capture recent warming trends such as those observed since the 1950s. Such 'divergence' phenomena between climatic and dendrochronological variables have also been displayed in other temperature-constrained high-elevation and boreal forests (Briffa et al. 1998; D'Arrigo et al. 2004; Wilmking et al. 2004, 2005; Büntgen et al. 2006). Contrary to TRW, MXD low-frequency positive trends follow the warming trend started in the 1970s. This is in agreement with data from the European Alps which suggest that the divergent behaviour is expected to occur in TRW more often than in MXD (Büntgen et al. 2006).

The divergence phenomenon has been attributed to various causes including temperature-induced drought stress (D'Arrigo et al. 2004), nonlinear growth-climate thresholds (Loehle 2009), methodological issues techniques including "end effects" of chronology development (Esper and Frank 2009, Briffa and Melvin 2011), biases in instrumental data or additional anthropogenic influences (see D'Arrigo et al. 2007, and references therein). Our sampled sites are located within the drought-prone Mediterranean region, and we therefore focused on a possible temperature-induced drought explanation of the divergence phenomenon here observed.

In this sense, drought is becoming a more limiting factor for high-elevation *P. uncinata* growth in the last decades, when TRW series show higher seasonal correlations with June-July SPEI. These results indicate that summer drought is increasingly influencing TRW along the 20th century, which agrees with observations from Iberian mountain forests (Macias et al. 2006, Andreu et al. 2007). This can be due to a potential loss in the positive thermal response of trees when some temperature functional threshold is exceeded, leading to an increase in the influence of other potential factors like soil moisture or drought (D'Arrigo et al. 2004).

Summer drought is becoming less influential on MXD instead, specifically since the 1970s. When it is too hot or dry for tracheid enlargement to occur, the rate of tracheid production decreases and a denser wood (higher MXD) is formed because of the formation of tracheids with thicker cell walls and narrower lumens (Jyske et al. 2009). This thickening and lignification of the cell walls, illustrated by latewood tracheids, improves the mechanical strength of stems but also allows tracheids withstanding higher xylem tension due to lower water potential (Hacke et al. 2001). Specifically, MXD development is directly linked to climate conditions during spring and mainly during late summer to early autumn, when the latewood is formed (Briffa et al. 1998, Yasue et al. 2000). During the first part of the growing season, when the earlywood is formed, climatic variations affect radial tracheid enlargement, whereas during the later part of the growing season climate mainly affects the cell wall thickening process of latewood (Camarero et al. 1998). In this sense, for the sub-period 1930-1969, the lowest (negative) correlations of MXD with SPEI were found for May SPEI. This means that wet and cool spring conditions could enhance earlywood formation potentially leading to more and wider tracheids with thinner cell walls and a subsequent delayed summer lignification producing a less dense latewood, i.e. lower MXD values. The highest positive correlation for the same period corresponds to July SPEI which suggests that wet late summers will entail a production of denser latewood by means of enhancing the lignification and carbohydrates synthesis at the end of the growing season. Furthermore wet late summers may not necessarily lead to the production of wider lumens (JJ Camarero, personal communication, 2013). In the sub-period 1970-2009 the highest positive MXD-SPEI correlations are found in January considering the cumulative drought since the previous September (5-month SPEI scale), which means that wet conditions in the previous autumn and winter of a specific year would imply the production of a dense latewood during the late summer of the next year. This is an unexpected result since we unveil not only influences of late summer/early autumn conditions of the current year on MXD but also of lagged climatic conditions of the previous year as it is usually the case in TRW (Fritts 2001, Tardif et al. 2003). The interpretation may be the same as in TRW since previous wet conditions might enhance carbohydrates synthesis and storage later used for lignifying and thickening latewood cells the following growing season. Similar indirect influences of previous winter conditions on latewood production were also observed in xeric *Pinus halepensis* forests stands, which constitute typical lowland Mediterranean forests (Pasho et al. 2011). Differences in responses between sub-periods could be due to different drought stress intensities from one sub-period to the other, different temperature conditions or climatic variability (e.g. the first half of the 20th century was climatically less variable than the second half) or indirect effects of other global or local drivers like increasing atmospheric concentrations of CO_2 and rising N deposition.

To conclude, rising temperatures led to an increase in drought stress of Pyrenean and Iberian high-elevation forests as has been observed in other Mediterranean mountain forests (Jump et al. 2006, Piovesan et al. 2008). Therefore, high-elevation forests growing in typically temperature-limited conditions are becoming more limited by water availability. We may be attending how a physiological threshold in terms of optimal temperature for growth is surpassed, reinforcing the role of drought as a plausible growth-limiting factor of high-elevation forests during the last decades. But, how is tree growth responding to climate in other parts of the Mediterranean Basin? Are our findings and recent TRW negative trends comparable to other regions?

Biogeographical patterns in recent Mediterranean tree growth trends (Chapter 4)

The intricate topography and diverse climate, both characteristics of the Mediterranean Basin (MB), produce varied and often opposite trend signs even between neighbouring sites. In spite of this complexity, our findings emphasize a pattern acting at synoptic scales, where the distribution of recent positive trends in tree-ring variables related to growth or productivity are biased towards wetter and cooler areas of the MB located in the northwest. Negative trends are generally displayed at more xeric and warmer areas, at the southern and eastern parts of the MB. These observations could indicate that, in spite of the characteristic climatic and topographic local complexity, on a global scale tree growth across the MB is limited by drought or low water availability during the growing season (e.g. Martínez-Vilalta and Piñol 2002, Camarero et al. 2004, Jump et al. 2006, Sarris et al 2007, Piovesan et al. 2008, Linares et al 2011b, Linares et al. 2012, Sánchez-Salguero et al. 2012). Water-use efficiency improvements (WUEi) seem to be insufficient to compensate the negative effects of the reduced water availability on growth (Andreu et al. 2011). A reduction in forest productivity due to water limitations could have serious implications regarding the degree of carbon sequestration by the Iberian forests, affecting the terrestrial biosphere carbon cycle.

A sampling bias towards high-elevation sites at the MB scale is also shown, and it is very likely the result of the dendrochronologists' signature, which traditionally have sought the most climate-sensitive trees usually growing at harsh high-elevation environments (Fritts 2001). On the other hand, older trees tend to grow at higher altitudes due to their traditionally smaller anthropic pressure (i.e. logging) over the last decades, as well as to the low growth rate and extended life span happening in these harsh environments (Bigler and Veblen 2009). Finally, most well-preserved European forests are located in mountains. Hence it is assumed that many of the dendrochronological studies and their findings here compiled are also biased towards an overrepresentation of old slow-growing trees living in high-elevation areas.

Only a few reviewed papers in chapter 4 differentiate growth trends between different age classes (e.g. Rozas et al. 2009, Dorado-Liñán et al. 2012a, Linares et al. 2012, Dorado-Liñán et al. 2012a, Linares et al. 2012), competition intensities (e.g. Martín-Benito et al. 2009, Linares et al. 2009a, 2010a) or health stages (e.g. Camarero et al. 2003, Solla et al. 2006, Linares et al. 2010b). Considering these factors when reviewing publications would allow reaching less vague, more explicit conclusions about growth trends of forests with specific vitality, age or social status levels. Furthermore, apart from a few cases (e.g. Linares et al. 2010a, Carrer et al. 2011, Rozas and Olano 2012), papers included in this review have mainly a population-based approach and refer to the mean trend of specific populations. But dendrochronologists cannot overlook the fact that, when analyzed in an individual-level, different growth trends in response to climate can be observed among different trees (Ettl and Peterson 1995; chapter 2).

A Russian-doll story – Different insights from different observational scales

Using either an individual (chapters 1 and 2) or a population (chapters 3 and 4) approach gave us different but complementary information about the species reality, from the tree entity to the forest scale. We first assessed within-tree, structural relationships amongst individual characteristics (sapwood, size, age) and their influence on BAI, along a topographic and altitudinal gradient (chapter 1). Although altitude played an important factor, the individual conditions of the tree, specifically the sapwood area and the age, influenced BAI more. On the other hand, including the climate role (chapter 2) resulted in altitude becoming the factor influencing the most the individual TRWi responses to climate through the altitudinal thermal gradient (Körner 1998) (Table 1). The great variability in the TRWi responses to climate from site to site was also highlighted, which emphasizes the topographic and climatic complexity of high-elevation Iberian forests. Following a population-based approach (chapter 3), a broad-scale increase in the drought negative influence on TRWi was revealed, meantime the parallelism between temperature and TRWi variability progressively decreased. Positive, negative and neutral trends in TRW and other dendrochronological variables were recorded across the Mediterranean Basin (MB; chapter 4), emphasizing in a broader scale the high variability in growth responses depending on diverse factors like topography, microclimate conditions or species; still, a synoptic pattern with positive trends located towards wetter and cooler sites of the MB was detected.

Table 1. Using an individual approach, different information arose depending on whether climate was included in the analyses or excluded from them.

	Chapters	
	1. *Tree and site drivers of BAI*	*2.* *Tree and site drivers of TRWi responses to climate*
Major finding	Sapwood area and, to a minor extent, tree age were the main positive and negative drivers, respectively, controlling BAI during the 20th century, whereas altitude played a minor role.	Altitude was the main factor controlling TRWi responses to climate.
Implication	Sapwood and age became more influencing on BAI in the second half of the 20th century.	Climatic mixed models explained more TRWi variability in the second half of the 20th century.

Outlook for further research

- In the dendrochronological sampling, we aimed to obtain a wide representation of the population variability, although we mainly sampled adult, big-sized and likely old trees. Including a good representation of all age (including saplings, living and dead), size and social classes in future dendroecological studies would avoid the most common dendrochonological biases typically arising from sampling the oldest and biggest trees (Bowman et al. 2013). We also need better metadata (descriptions of trees) related to tree-ring data records and databases.

- This well sampled variability would also allow performing more accurate analyses of dendrochronological (e.g. TRW, MXD or sapwood area) or size variables and thus evaluating their variability along an altitudinal gradient (Premoli et al. 2007). It would also help in prospecting the age or size influences on tree growth. Further, this approach would help in assessing the allometric relationships between variables, as the ones observed between growth rate and leaf area/sapwood area ratio (Medhurst and Beadle 2002), or between length and basal area of branches (Osada 2006). Actually, although differences in tree age or size distribution can affect carbon storage in forests, they have not been explicitly represented in large scale models of forest productivity at global scale (Voelker 2011).

- In the sampled sites, older trees grow at higher altitudes (chapter 1). Furthermore, the older the trees are (i.e. trees living in higher altitudes), the higher the growth-index variance explained by climate (chapter 2), which is in agreement with other studies on conifers (Rozas and Olano 2013). This implies that elevation- and age-stratified sampling schemes would be useful to separate different growth-index responses to climate and would allow improving the robustness of paleoclimatic reconstructions.

• The TRWi-temperature divergence phenomenon exposed in chapter 3 should be considered in the assessment and performance of Pyrenean climate reconstructions based on tree-ring proxies, which are based on short calibration periods. Trees are showing increasing sensitivity to drought and decreasing sensitivity to temperature in the last decades even in these high-elevation ecosystems where we would expect a strong temperature response. This would imply that a Pyrenean climate reconstruction based on present-day TRW-climate relationships is questionable and should be considered carefully. Furthermore, after having assessed this divergence phenomenon in a species level, our next research step would be developing a site-level study of the low- and high-frequency signals in the growth/climate correlations, which would allow us drawing conclusions for larger scales in a more accurate way (Büntgen et al. 2008b).

• Structural equation models (chapter 1) and linear-mixed effects models (chapter 2) are linear methods. This linear approach is correct in order to attain a simplified acknowledge of natural mechanisms. But we cannot overlook that linear methods might not detect potential non-linear phenomena that are also present in nature, e.g. non-linear associations between altitude and radial growth rates (Paulsen et al. 2000, Coomes and Allen 2007, Voelker 2011) or between sapwood and basal area (Mehurst and Beadle 2002). Moreover, the relationship assessed between BAI and sapwood area in chapter 1, although significant, could be considered as following a logarithmic rather than a linear equation (see supplementary material of chapter 1). When representing sapwood area against altitude for *P. uncinata*, sapwood usually increases with altitude in order to override the augment in water viscosity, thus avoiding a decrease in sap flux (Gates 1980, Gutiérrez et al. 1991). But there is an altitudinal threshold coinciding with the overall elevation of Pyrenean forest limits (~2300 m asl) from which sapwood area begins to decay (Fig. 1). This decreasing rate from the forest limit range upwards seems faster than the increasing rate before reaching that threshold. When representing the same figure for north- and south-oriented trees separately, similar observations are found (not shown). At the same time, age and basal area behaves in a similar way (since older trees are also bigger; see chapter 1), and also similar to the sapwood area, i.e. decaying from the forest limit threshold upwards. Why does sapwood area and age seem to decay from the forest-limit threshold? First, in altitudes higher than the forest limit the compensatory increase of sapwood production may cease since the temperature becomes too limiting for growth. Hence, the hydraulic conductivity (Petit et al. 2010) and the production of new tissues decrease, and the accumulation of structural carbohydrates produces a decline in the photosynthetic rate by means of a negative feedback (Paul and Pellny 2003). Second, the higher the altitude, the shorter the growing season (Körner 1998); thus the radial growth rate becomes smaller, meantime inner tree rings leave the sapwood and become part of the heartwood (i.e. sapwood:heartwood ratio decreases). Third, an increasing size-mediated constraint of xylogenesis, photosynthesis and hydraulic conductivity in old trees, usually located at high altitudes (Bigler and Veblen 2009), would cause a more intense reduction of their growth and sapwood production than in low-elevation younger trees. Tradeoffs between these mechanisms might result in non-linear sapwood and age behaviours along the altitudinal gradient. Non-linear methods like generalized additive mixed models (GAMM) should be used to further analyse these relationships.

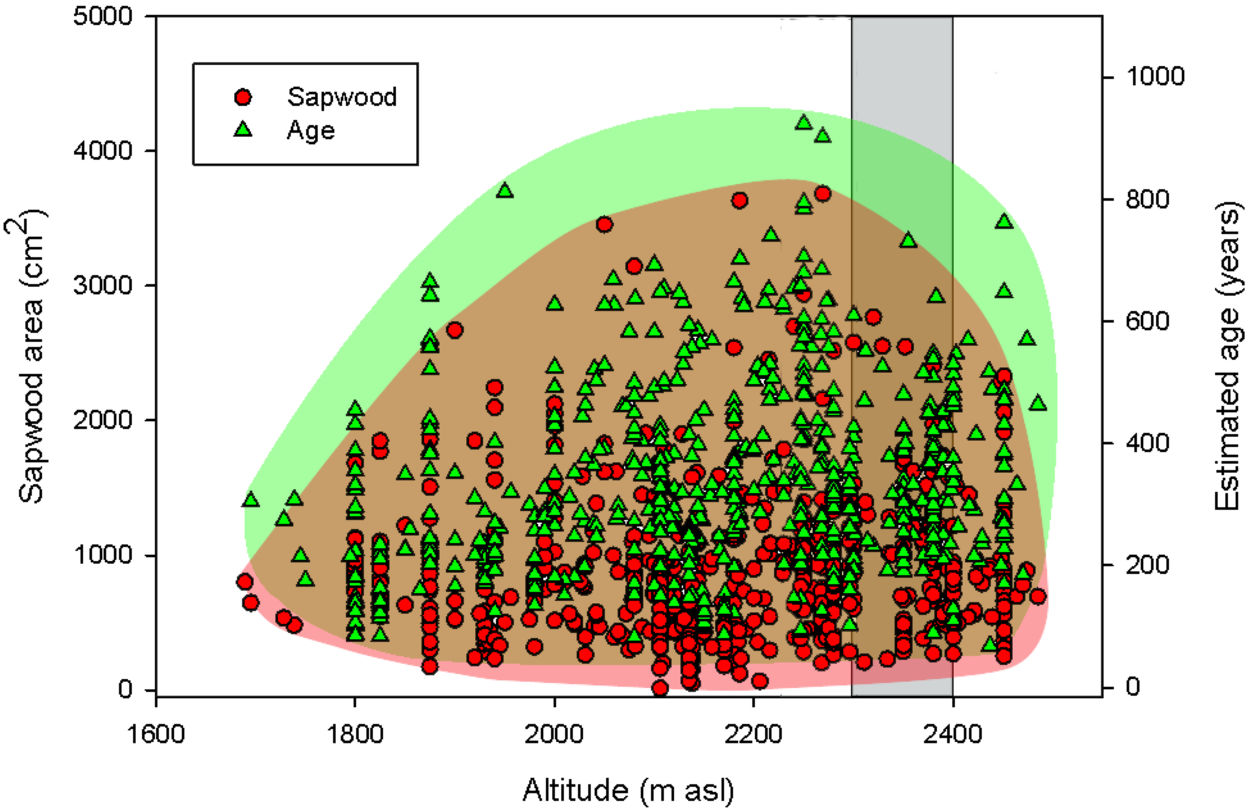

Figure 1. Relationship between sapwood area, tree age and altitude for the sampled *Pinus uncinata* trees of this thesis (n = 700 trees). The grey area denotes the potential altitudinal location of the forest limit in the Pyrenees (Ninot et al. 2008).

- Chapter 3 and chapter 4 evidence the need of a more exhaustive MXD sampling across the Mediterranean Basin. In high latitudes, MXD shows significant correlation with temperature for most of the summer but TRW appears to respond only to early summer temperature; further research on the reasons why this happens is needed. Furthermore, climate conditions acting at the early summer might be not relevant in controlling growth in late summer stage, and vice versa. We should try to separate the climatic signal which is contained in these both widely used tree-ring parameters in dendroclimatology. The method can be based on the removal of the relationship between TRW and MXD observed for narrow tree rings from high latitudes (Kirdyanov 2007), and a new MXD variable clean of TRW influences, called MXD', can be created. The association between the TRW and MXD master chronologies is high, although the relationship between them is not linear (Fig. 2). We can use the resulting fitted curves to obtain the modified MXD' chronology according to the equation: MXD' = MXD/MXD$_f$, with MXD being the maximum latewood density of a tree ring with a particular width (TRW) and MXD$_f$ being the value of the fitted curve for that particular tree-ring width. With this approach we can try to (i) separate the climatic signal located in the TRW and MXD variability and (ii) to analyse the response of these parameters to climate variability along the year. This approach would allow more stable reconstructions since temperature can have different effects on radial growth in different sub-periods of the growing season.

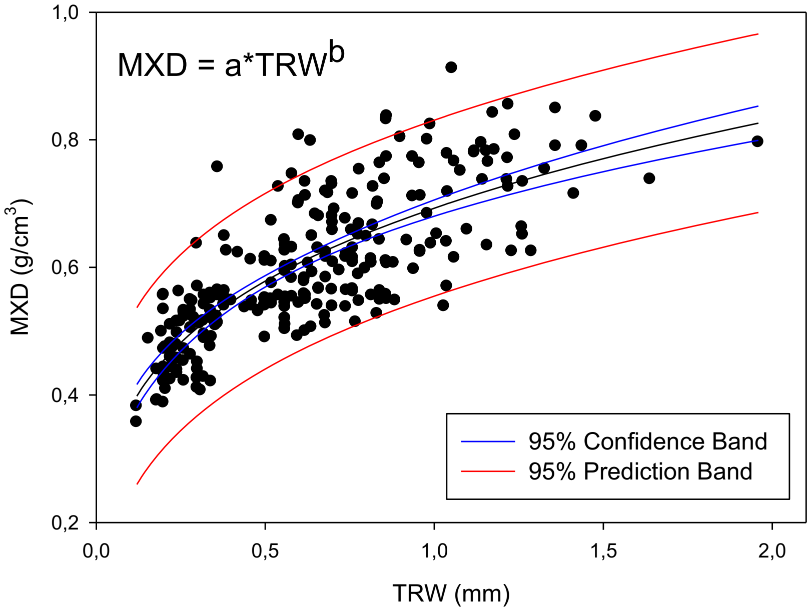

Figure 2. Relationship between tree-ring width (TRW) and maximum latewood density (MXD) of one tree sampled in Estany Gerber (GE). The solid black curve was fit according to the equation indicated in the upper left part of the figure.

Conclusions

Chapter 1

- Age-related changes in sapwood area drove basal area increment in mountain *P. uncinata* forests in the 20th century. Any potential climate-induced effect on basal area increment will be mainly controlled by sapwood production, which is mediated by tree age and altitude.

Chapter 2

- Altitude plays a major role affecting *P. uncinata* responses of tree-ring width indexes to climate at both site and tree scales. A stronger focus on individual tree responses would improve the ecological knowledge of the trees' vulnerability against climatic stressors.

Chapter 3

- A weaker response of tree-ring width variability to recent warming is observed, whereas summer drought is increasingly influencing tree growth in *P. uncinata* mountain forests.

Chapter 4

- At a synoptic scale, tree growth across the Mediterranean Basin is limited by drought or low water availability during the growing season.

Resum

Introducció general i objectius de l'estudi

Els arbres de la mateixa espècie que creixen al mateix lloc mostren un patró similar en les característiques dels seus anells de creixement al llarg del temps, el qual permet datar-los per comparació, mitjançant mètodes dendrocronològics. Aquesta assumpció es compleix sobretot en arbres d'àrees on el principal factor limitant de la formació dels anells de creixement és un clima de caràcter estacional, com és el cas d'individus vells localitzats dins o prop de límits de distribució altitudinals o latitudinals. Per tant, sovint els dendrocronòlegs duen a terme una selecció subjectiva de llocs i arbres a l'hora de construir cronologies mitjanes. Aquestes deriven de diferents series de creixement amb una sensibilitat climàtica suposadament elevada. Aquestes cronologies mitjanes persegueixen posar de relleu senyals climàtiques regionals comuns així com reduir el "soroll" no climàtic. Aquesta aproximació metodològica poblacional pot no capturar respostes del creixement a condicions ambientals heterogènies, les quals afecten d'una manera particular arbres de diferents grandàries, edats, espècies i trajectòries successionals, produint estimes de creixement esbiaixades. Encara que útil per a reconstruir patrons climàtics passats, aquesta aproximació dendrocronològica clàssica no ens dona un retrat precís de les respostes individuals dels arbres al canvi climàtic, que son el resultat d'interaccions múltiples entre inputs ambientals i respostes fisiològiques de l'arbre.

Característiques a nivell d'individu i de lloc que influencien el creixement de l'arbre.

Com hem dit, sovint el creixement i la productivitat dels arbres en boscos d'alta muntanya o ecotons latitudinals estan limitats per baixes temperatures i per un període curt de creixement. Per altra banda, el creixement dels arbres està essent afectat per l'escalfament global i canvis biogeoquímics relacionats com és l'augment de les concentracions atmosfèriques de CO_2. A Europa i Amèrica del Nord, mentre que àmplies àrees de boscos alpins de coníferes han mostrat increments en les taxes de creixement radial en les últimes dècades, altres estudis suggereixen que boscos boreals limitats per baixes temperatures no sempre mostren un increment del creixement sota condicions d'escalfament. A més a més, una pèrdua recent a nivell de lloc de la sensibilitat del creixement a l'augment de temperatures també ha sigut observada (veure capítol 3). Aquests patrons variats de creixement també apareixen entre arbres coexistents (capítol 2) i boscos propers entre ells (capítol 4), desafiant el nostre enteniment de les respostes del creixement a l'escalfament climàtic. La diversitat de respostes del creixement al clima entre arbres coexistents és degut en part a factors addicionals no climàtics com ara la disponibilitat hídrica local del sòl, el gruix de la capa orgànica d'aquest, la competició per la llum, la producció d'albeca i l'edat (capítol 1), l'altitud (capítol 2), etc. A més a més, la topografia complexa característica de la Conca Mediterrània prové d'efectes luv-lee i de l'orientació de la pendent o de la concavitat-convexitat de la microtopografia. Per tant, les respostes dels arbres al clima poden variar entre individus coexistents i aquestes respostes poden ésser afectades per factors de control no climàtics actuant a diverses escales espacials al llarg de l'àrea de distribució d'una espècie. Necessitem un millor coneixement de les interacciones entre les condicions de lloc i les característiques de l'arbre a escales regional i local per a comprendre com aquests factors poden modular les respostes individuals del creixement a l'escalfament climàtic (veure capítols 1 i 2). Considerem fonamental l'adopció d'aquesta aproximació per a un enteniment més ampli de les respostes a llarg termini dels boscos al canvi climàtic.

Característiques de les relacions creixement-clima a escala poblacional.

L'aproximació poblacional és útil com hem dit abans per a reconstruir patrons climàtics passats ja que reforça la senyal climàtica mitjana present en arbres de la mateixa espècie creixent al mateix lloc o regió, minimitzant les diferències individuals de creixement que constitueixen el "soroll" no climàtic. També hem destacat el control del creixement que exerceixen les baixes temperatures en boscos d'alta muntanya. No obstant això, la majoria de muntanyes de latituds mitjanes incloses a la Conca Mediterrània, com ara els Pirineus, estan també caracteritzades per dèficits periòdics d'humitat. Açò és degut a que el clima de la Conca Mediterrània pot alternar entre condicions àrides i humides provinents de distintes influències com ara mediterrànies, atlàntiques o continentals. Aquesta diversitat climàtica a macro i micro-escales enllaça amb el fet de que els patrons de creixement dels arbres al llarg de la Conca Mediterrània i durant les últimes dècades del segle XX han mostrat tendències diferents, sovint de signes oposats fins i tot derivant de llocs molt pròxims geogràficament (capítol 4). Aquesta elevada diversitat climàtica de la Conca Mediterrània implica també relacions creixement-clima complexes (és a dir, amb diferents influències de més d'un factor climàtic). De fet, l'inestabilitat temporal de les relacions creixement-clima, coneguda com a 'divergència', pot augmentar per tendències d'aridificació induïdes per l'escalfament climàtic, el qual disminuiria subseqüentment el control exercit per la temperatura sobre el creixement (capítol 3).

Dendroecologia dels boscos ibèrics de Pinus uncinata: aproximacions a nivells d'individu i població.

Pinus uncinata Ram. és una espècie longeva, de creixement lent i heliòfila que mostra una gran amplària ecològica en relació a la topografia (pendent, orientació, altitud) i al tipus de sòl. Es pot trobar en boscos subalpins dels Alps, els Pirineus i el Sistema Ibèric, assotada per les gelades d'hivern, les seues arrels penetrant la terra rocosa. Fins a l'any 2011, vàrem recollir mostres dendrocronològiques de 711 arbres de 30 llocs de *P. uncinata*, dels quals 27 llocs eren localitzats als Pirineus, un lloc a la prepirinenca serra de Guara i dos llocs amb poblacions relictes meridionals al Sistema Ibèric (províncies de Soria i Terol). Els boscos pirenaics de *P. uncinata* són generalment oberts, de baixa densitat i localitzats en indrets escarpats i elevats, formant grups aïllats prop del límit del bosc. El macroclima dels Pirineus està fortament influït per gradients est-oest i nord-sud amb condicions més mediterrànies (estius càlids i secs) cap a l'est i el sud, mentre que condicions continentals prevalen als Pirineus centrals. Les poblacions relictes de Soria i Terol i la prepirinenca serra de Guara estan sotmeses a condicions típicament mediterrànies. La temperatura mitjana anual i la precipitació total als llocs d'estudi oscil·laren entre els 2.0 i 4.9 °C i entre els 1200 i 2000 mm, respectivament, amb gener i juliol com a mesos més fred (mitjana -2.0 °C) i càlid (mitjana de 12.5 °C) respectivament.

L'objectiu general d'aquesta tesi és obtenir coneixement sobre la variabilitat del creixement de l'espècie *P. uncinata* a la Peninsula ibèrica i sobre les seues respostes al clima a escales d'individu i de població. Els objectius específics associats als diferents capítols de la tesi són els següents:

Capítol 1.

Analitzar les interaccions entre les característiques locals de lloc (p. ex. altitud, topografia) i les característiques intrínseques de l'arbre (p. ex. grandària, edat, àrea d'albeca) i avaluar com aquests factors modulen el creixement individual al llarg del càlid segle XX.

Capítol 2.

Determinar el grau d'importància de les característiques de lloc i les intrínseques de l'arbre com a factors de control de la variabilitat dels indexes d'amplària d'anell (TRW) i, en particular, de les seues respostes al clima.

Capítol 3.

Avaluar si les relacions creixement-clima canviaren al llarg de l'últim segle i, si és així, analitzar si aquesta divergència fou induïda per sequera fins i tot en boscos d'alta muntanya localitzats a prop del límit superior del bosc.

Capítol 4.

Establir en una perspectiva Mediterrània els patrons de creixement registrats a l'àrea de distribució de *Pinus uncinata* a la península Ibèrica, avaluant potencials patrons espacials en el creixement recent al llarg de la Conca Mediterrània.

Capítols

Capítol 1.

S'espera que el canvi climàtic faça augmentar el creixement dels arbres en boscos de coníferes de muntanya en regions fredes. No obstant això, durant el segle passat el creixement dels arbres ha mostrat respostes al clima de naturalesa inestable, relacionada amb l'edat i depenent de les condicions de l'indret on creixen. Malgrat això, la informació sobre els factors controladors d'aquesta resposta a nivell de lloc i d'arbre és insuficient. En aquest capítol vàrem avaluar si les susdites respostes canviants del creixement són més influïdes per les condicions de lloc, com l'altitud, o per factors a nivell d'arbre com la grandària i l'àrea d'albeca. Quantificàrem les tendències de creixement a nivell de lloc i d'arbre en boscos ibèrics de *Pinus uncinata* mitjançant dendrocronologia. El TRW fou convertit a increment d'àrea basal (BAI) per a avaluar les relacions entre creixement i les variables a nivell de lloc i arbre al llarg de tres períodes de temps (1901–1994, 1901–1947, 1948–1994) usant models d'equacions estructurals. Els arbres més vells es disposen a altituds majors, i la quantitat d'albeca decreix a mesura que envelleixen. Les tendències de BAI foren més baixes al període 1948–1994 que al període 1901–1947, és a dir, la taxa de creixement està disminuint, malgrat que els valors de BAI per als dos períodes mostren el patró contrari. L'àrea d'albeca i, en menor mesura, l'edat foren, positiva i negativament, respectivament, els principals factors controladors del Bai al llarg del segle XX, mentre que l'altitud jugà un paper menys important. Els nostres resultats manifesten la rellevància de les característiques individuals a nivell d'arbre com a factors moduladors de les respostes del creixement al clima. L'escalfament climàtic tindrà un menor efecte sobre el creixement radial en arbres de creixement lent ubicats a altituds elevades, en comparació amb arbres de creixement ràpid ubicats a cotes més baixes, els quals produeixen una major àrea d'albeca en termes relatius. Els arbres poden tornar-se relativament insensibles al clima a mesura que envelleixen i arriben a un llindar funcional associat amb la grandària i que comporta una reducció en la producció d'albeca.

Capítol 2.

Els arbres individuals, i no els boscos, responen al clima. No obstant açò, aproximacions a escala individual han sigut tradicionalment poc utilitzades en dendrocronologia per a monitorar retrospectivament o mesurar prospectivament les respostes del creixement radial dels arbres al clima. L'objectiu d'aquest estudi és adoptar aquesta visió individual per a analitzar retrospectivament la sensibilitat dels arbres a l'escalfament climàtic, i per a avaluar els factors potencials de control de les respostes del creixement al clima tant a escala de lloc com a escala d'individu. Mostrejàrem una xarxa de 29 boscos de *P. uncinata* i obtinguérem sèries de TRW de 642 arbres. El conjunt de dades analitzat inclou característiques individuals com a orientació, altitud, pendent, àrea basal, àrea d'albeca, altura de l'arbre i edat. Les respostes del creixement de l'arbre al clima foren avaluades relacionant índexs de creixement amb variables climàtiques usant dendrocronologia i models lineals mixtes. Regressions beta foren aplicats per a avaluar els factors potencials de control de les respostes del creixement al clima. Temperatures màximes de novembre més càlides durant l'any previ a la formació de l'anell augmentaren el creixement de *P. uncinata* principalment en llocs de cotes mitjanes, mentre que a cotes més elevades el creixement fou més depenent de l'efecte positiu de les temperatures de maig durant l'any de formació de l'anell. La precipitació de juny estimulà el creixement en llocs propensos a dèficit hídric com al límit meridional de l'àrea de distribució de l'espècie o en llocs amb molta pendent. Arbres creixent a altituds baixes i en llocs meridionals foren els més afectats negativament per condicions estiuenques càlides i seques. L'altitud fou el principal factor controlant la proporció de variabilitat del creixement explicada per el clima a escales de lloc i arbre. Tots dos (i) una aproximació a escala d'arbre per a quantificar les respostes dels índexs de creixement al clima i (ii) una caracterització detallada dels factors potencials de control d'aqueixes respostes individuals són requisits per a aplicar un marc d'enfocament individual en dendroecologia.

Capítol 3.

La relació creixement/clima de boscos d'alta muntanya teorèticament controlats per temperatura s'ha debilitat al llarg de les últimes dècades. Açò és probablement degut a nous factors limitants, com és un increment del risc de sequera per al funcionament i la productivitat dels ecosistemes a través de la Conca Mediterrània. A més, la disminució de la sensibilitat del creixement de l'arbre a la temperatura de primavera pot emergir en resposta a un increment de l'estrès per sequera. Avaluàrem aquestes idees a partir de l'anàlisi de la sensibilitat de la relació creixement/clima de les 1500 sèries mesurades de TRW i de les 102 de màxima densitat (MXD) provinents de 711 i 74 arbres, respectivament, els quals foren mostrejats a 30 boscos ibèrics d'alta muntanya de *P. uncinata*. Diferents estandarditzacions dendroclimatològiques i aproximacions amb períodes dividits foren utilitzats per a avaluar el comportament d'alta i baixa freqüència del creixement durant el segle XX en resposta a mitjanes de temperatura, precipitacions totals i índexs de sequera. Les variacions en TRW segueixen les temperatures estiuenques fins aproximadament el 1970 però divergeixen després, mentre que la MXD captura l'increment recent de temperatura bastant bé. Contrastant amb la divergència de baixa freqüència observada entre TRW i la temperatura estiuenca estigué l'estabilitat en la senyal d'alta freqüència fins el present. La sequera estival ha incrementat el seu control sobre el TRW al llarg del segle XX, encara que ha mostrat una tendència divergent amb la MXD després dels anys 70 del mateix segle. Els nostres resultats impliquen un debilitament de la sensibilitat a la temperatura en el creixement de *P. uncinata*, i revelen la importància de la sequera estival, la qual està recentment convertint-se en el factor limitant emergent de la formació dels anells en moltes parts de la Conca Mediterrània.

Capítol 4.

L'increment en les temperatures i els règims canviants de precipitacions defineixen la Conca Mediterrània com una de les àrees geogràfiques més sensibles al canvi climàtic. Junt a diversos efectes ecològics s'han observat disrupcions en la resposta del creixement al clima durant les últimes dècades. No obstant això, la topografia i la climatologia complexes de la Conca Mediterrània comporten patrons oposats en el creixement recent, els factors de control biòtics i abiòtics dels quals romanen sovint qüestionables. Compilàrem evidències dendrocronològiques de tendències recents de creixement posteriors a 1970 provinents de 1076 casos a 724 llocs estudiats de 75 publicacions a la Conca Mediterrània (30° a 46° N i 10° W a 40° E). Es posa de relleu un patró sinòptic on les tendències positives estan generalment ubicades en ambients amb clima relativament més fred i humit principalment al llarg de la zona nord-oest de la Conca, mentre que les tendències negatives sovint coincideixen amb llocs més xèrics situats cap a les regions del sud-oest i est. Aquest patró de respostes revela efectes tant beneficiosos com negatius del canvi climàtic sobre la funció i productivitat dels ecosistemes forestals pan-Mediterranis. Probablement esbiaixat per esforços selectius de mostreig cap a llocs d'altitud elevada i arbres vells situats als països del nord-oest de la Conca Mediterrània, emfatitzem la necessitat d'una distribució més uniforme dels llocs d'estudi i de les classes d'edat per a reflectir millor criteris ecològics en comptes de polítics i metodològics. Dades provinents de diferents fonts i tractaments resulten en nivells d'incertesa heterogenis a la hora d'assignar un signe a cada tendència, i ressalten la importància de l'accés lliure a dades dendrocronològiques per a permetre la compilació i estudi de noves xarxes de dades i la execució d'anàlisis addicionals.

Discussió global i conclusions

Factors de control del creixement a nivell d'individu (capítol 1).

A la xarxa de relacions entre les característiques d'individu i lloc, l'àrea d'albeca és el principal factor de control de les tendències decreixents recents trobades al BAI en boscos ibèrics d'alta muntanya de *P. uncinata*. Els arbres que produeixen més area d'albeca també mostren major BAI, i aquesta associació s'ha incrementat en les últimes dècades del segle passat. A més, el BAI incrementà a la primera meitat del segle XX a taxes més elevades que a la segona meitat del mateix segle. Açò pot estar degut al fet de que els arbres presenten una estabilització del BAI quan arriben a una fase senescent. Una relació negativa entre la edat i la taxa de creixement ha estat àmpliament documentada en diverses espècies; de la mateixa manera, l'efecte negatiu de la edat sobre el BAI coincideix amb observacions de nombrosos estudis que demostren com l'àrea d'albeca decreix a mesura que els arbres envelleixen. No obstant això, la influència negativa de la edat sobre el BAI ha incrementat segons els nostres SEMs, i pot estar determinat per canvis a l'àrea d'albeca; és a dir, arbres més vells produïren proporcionalment menys area d'albeca que els arbres joves a la segona meitat del segle XX.

Perquè està decreixent el BAI? Nosaltres proposem tres explicacions:

• Primer, l'increment de la longitud del sistema hidràulic a mesura que els arbres augmenten d'edat i acumulen biomassa pot estar una de les respostes. L'envelliment de les estructures conductives i la alteració de les xarxes hidràuliques d'arbres vells i peus grans pot contribuir a explicar una disminució acusada en la conductivitat hidràulica i la producció d'albeca a mesura que els arbres creixen i es fan vells, conduint per tant a tendències de disminució del creixement influenciades per l'albeca.

• Segon, les difícils condicions climàtiques presents a elevades altituds poden també explicar aquestes tendències de disminució del creixement influenciades per l'albeca. Les dures condicions ambientals d'aquets boscos d'alta muntanya (baixes temperatures de l'aire i del sòl, freqüents esdeveniments de gelades, elevada radiació i vents d'alta velocitat) són consistents amb el fet de que els arbres solen ser més vells a altituds més elevades degut a una reducció de les taxes de creixement radial i a un augment de la longevitat. També hem de recordar que els protocols dendrocronològics solen estar esbiaixats cap a un mostreig dels arbres més vells.

• Tercer, a mesura que incrementa la altitud, les temperatures de l'aire i del tronc de l'arbre disminueixen, produint un increment de la viscositat de l'aigua i per tant de la resistència al flux de saba. Açò, junt a les condiciones de vent de boscos d'alta muntanya que produeixen un efecte de dessecació, pot causar un increment de la producció d'albeca per a compensar aquest flux impedit de saba en boscos d'altituds elevades. Per tant, un augment de les temperatures al llarg del segle XX pot haver induït una disminució de la viscositat de l'aigua. Açò comporta un augment del flux de saba i una reducció de la producció d'albeca, produint un descens de les taxes de creixement.

Les nostres observacions suggereixen que:

- Qualsevol efecte potencial sobre el BAI induït per el clima estarà principalment controlat per la producció i la preservació d'albeca, que al seu torn està mediat per la edat de l'arbre i la altitud.

- Com els arbres de creixement lent ubicats a altituds elevades arriben a una major edat que els arbres de cotes més baixes i creixement més ràpid, esperem respostes del BAI diferenciades al llarg d'un gradient altitudinal i segons la edat.

- Una projecció més realista de les respostes futures del creixement i de la productivitat de boscos de muntanya a l'escalfament climàtic pot estar fortament afectada per característiques a nivell d'individu (com l'àrea d'albeca) i secundàriament per factors locals (com l'altitud) que modulen o esmorteeixen els efectes regionals de l'estrès climàtic sobre el creixement.

- Una vegada que els arbres arriben a un llindar funcional relacionat amb la edat o la grandària, lligat a una producció estancada d'albeca, es tornaran relativament insensibles a la variabilitat climàtica.

Respostes del creixement al clima a nivell d'individu (capítol 2).

Diversos estudis xilogenètics i avaluacions dendrocronològiques de les relacions creixement-clima indiquen que la formació de la fusta i la sensibilitat del creixement al clima poden dependre de la edat i estar modulats per les característiques del lloc. En el capítol 2 avaluàrem, seguint una aproximació individual, les respostes dels índexs de TRW (TRWi) al clima i com les característiques a nivell d'individu i a nivell de lloc poden influir sobre aquestes respostes.

Observem que les respostes dels TRWi al clima a escales d'espècie i de lloc es diferencien d'aquelles detectades a escala d'individu. A nivells d'espècie i de lloc els TRWi de *P. uncinata* augmenten amb condicions càlides durant el final de la tardor de l'any previ al de la formació de l'anell i durant la primavera de l'any del mateix any de formació, el que indica que el principal factor limitant dels TRWi en aquests boscos durant el segle XX han sigut les baixes temperatures. Elevades temperatures durant la tardor anterior a la formació de l'anell, quan la majoria del creixement vegetal ha cessat, contribueix probablement a augmentar la taxa de fotosíntesi i la producció i emmagatzematge de carbohidrats no estructurals que seran utilitzats per a la formació de fusta primerenca durant el pròxim període de creixement. En contrast, primaveres càlides afecten directament l'activitat cambial i poden fer avançar la represa del creixement després del període de dormància hivernal, i augmenten la producció de fusta.

A escala d'individu, la majoria dels arbres formen més fusta en resposta a temperatures màximes més càlides durant el Novembre previ, però alguns d'ells també reaccionen positivament a condicions humides durant el principi de l'estiu quan les taxes de creixement radial són normalment les més altes de l'any. Aquesta última observació és d'alguna manera inesperada ja que la majoria dels boscos mostrejats corresponen a boscos subalpins d'altituds elevades on el factor limitant del creixement és típicament la baixa temperatura. No obstant això, el haver considerat en el nostre estudi una xarxa tan àmplia de llocs permeté registrar el paper limitant de la baixa disponibilitat d'aigua a l'estiu sobre el creixement de *P. uncinata*, principalment en els llocs més xèrics de l'àrea de distribució de la espècie subjectes a influències climàtiques mediterrànies, és a dir, condicions més càlides i seques a l'estiu. Açò implica que aquests arbres estan probablement adaptats a estius secs però si l'escalfament climàtic condueix a condicions encara més àrides, els boscos de *P. uncinata* localitzats sobretot en llocs marginals (Prepirineus, sud del Sistema Ibèric) podrien mostrar un declivi del creixement i mortalitat, tal com ha sigut observat en altres límits xèrics de distribució. Més endavant parlarem sobre l'increment de la influència de la sequera sobre els índexs de creixement, detectat seguit un enfocament a escala de població (capítol 3).

El baix nivell de variància (3-33%) explicada per els models lineals mixtes usant predictors climàtics dels TRWi de *P. uncinata* a escala d'individu evidencia que el clima juga un paper secundari en el control de la variabilitat dels TRWi entre arbres coexistents, fins i tot en aquests ambients de clima extrem. De manera conseqüent, hem de considerar les característiques a nivell d'individu com ara l'àrea d'albeca (capítol 1) o les condiciones a nivell de lloc, com ara l'altitud, com factors importants de control de les respostes dels TRWi al clima.

A més, els individus amb les respostes més significants dels TRWi al clima, que poden representar una proporció petita del conjunt de la població, haurien de ser monitoritzats amb detall mitjançant mètodes ecofisiològics per a entendre de manera adequada els mecanismes que dirigeixen les respostes de l'arbre a l'escalfament climàtic.

L'altitud juga un paper principal influint sobre les respostes dels TRWi al clima a escales de lloc i d'arbre, en concordança amb treballs anteriors duts a terme al mateix ecosistema, i amb investigacions en coníferes d'ampla distribució com l'avet de Douglas. Açò suggereix que el decreixement de la temperatura de l'aire a mesura que ascendim en altitud és el principal factor de control dels TRWi a nivells d'arbre i de lloc, determinant l'altitud màxima a la que poden arribar les formes arbòries.

També observem en els TRWi un increment de la variabilitat explicada per el clima en la segona meitat del segle XX. Aquestes observacions recolzen altres estudis realitzats també en els Pirineus amb *P. uncinata*, que mostren la mateixa tendència cap a les últimes dècades. Una inestabilitat similar en les relacions creixement-clima fou trobada per Andreu *et al*. (2007) i relacionada amb condicions climàtiques canviants. Oferim ací una explicació ambiental alternativa per a aquest comportament inestable. L'escalfament climàtic s'ha intensificat ràpidament al llarg del nord-est de la Península ibèrica durant la primera meitat del segle passat, el qual podria haver millorat parcialment la limitació sobre els índexs de creixement exercida per les baixes temperatures imposades per el gradient altitudinal. Les nostres observacions recolzen la "relaxació" del gradient altitudinal de temperatura degut a un escalfament climàtic ràpid postulat per Tardif *et al*. (2003), particularment per a la primera meitat del segle passat. Més tard, l'altitud fou el principal factor de control del creixement en boscos de muntanya de *P. uncinata*, a pesar de que l'escalfament climàtic continuà però a una taxa més baixa que en la meitat de segle XX. Canvis en les associacions creixement-clima podrien també indicar relacions no linears entre el creixement i els factors de control climàtics (veure última secció). La pèrdua de les respostes a la temperatura en àrees fredes podria estar unit a alteracions en la distribució de carbó i en patrons intraanuals de creixement.

Respostes dels creixement al clima a nivell de població (capítol 3).

Al capítol 3 detectàrem una divergència de baixa freqüència entre la tendència decreixent de la sèrie de TRW (mitjanes poblacionals) des de la segona meitat del segle XX, i les temperatures creixents. Açò evidencia el debilitament de proxies teòricament sensibles a la temperatura, com ara el TRW, de capturar les tendències recents d'escalfament com ara les observades des dels anys 50. Aquest fenomen de divergència entre variables climàtiques i dendrocronològiques també ha sigut observat en altres boscos boreals i d'alta muntanya limitats per baixes temperatures. Contrari a la TRW, les tendències positives de la MXD a baixa freqüència segueixen la tendència positiva començada als anys 70. Açò concorda amb dades provinents de la serralada dels Alps, que suggereixen que la ocurrència d'un comportament divergent és més probable a la TRW que a la MXD.

El fenomen de divergència ha sigut atribuït a diverses causes incloent estrés per sequera induïda per altes temperatures, llindars creixement-clima no linears, efectes derivats de qüestions metodològiques, com ara els "end effects", o del desenvolupament de la cronologia, biaixos de les dades instrumentals o influències antropogèniques addicionals. Els nostres llocs mostrejats estan localitzats dins de la regió Mediterrània de sequera potencial, i per tant ens focalitzàrem en un possible efecte de l'estrés per sequera induïda per altes temperatures com a causa del fenomen de divergència ací encontrat.

En aquest sentit, la sequera està passant a estar un factor més limitant per al creixement dels boscos d'alta muntanya de *P. uncinata* en les últimes dècades, quan les sèries de TRW mostren correlacions estacionals més elevades amb el SPEI de juny-juliol. Aquests resultats indiquen que la sequera estival està influint de manera incremental la TRW al llarg del segle XX, el que concorda amb observacions en boscos d'altres muntanyes ibèriques. Açò pot estar degut a pèrdues potencials de la resposta positiva a la temperatura en els arbres quan un llindar funcional associat a temperatura és sobrepassat, el que comportaria un increment en la influència d'altres factors potencials com ara la humitat del sòl o la sequera.

D'altra banda, la sequera estival és cada vegada menys influent per a la MXD, específicament des dels anys 70. Quan fa massa calor i condicions de sequera per a que l'augment de la mida de les traqueides tinga lloc, la taxa de producció de traqueides disminueix i es forma una fusta més densa (MXD més elevat) degut a la formació de traqueides amb parets cel·lulars més gruixudes i lúmens més estrets. Aquests engruiximent i lignificació de les parets cel·lulars, duts a terme per les traqueides de la fusta tardana, milloren la força mecànica dels troncs però també permeten que les traqueides suporten tensions xilemàtiques més elevades degudes a un potencial hídric més baix. Específicament, el desenvolupament de la MXD està directament relacionada amb les condicions climàtiques durant la primavera i principalment durant el final de l'estiu i el començament de la tardor, quan la fusta tardana es forma. Durant la primera part del període de creixement, quan la fusta primerenca es forma, les variacions climàtiques afecten l'engruiximent radial de les traqueides, mentre que durant la ultima part del període de creixement el clima afecta principalment el procés d'engruiximent de les partes cel·lulars de la fusta tardana. En aquest sentit, per al subperíode 1930-1969, les correlacions més negatives de la MXD amb el SPEI foren trobades per al SPEI de Maig. Açò significa que condicions humides en primavera podrien augmentar la taxa de formació de la fusta primerenca, produint potencialment més traqueides i amb major amplària, de parets cel·lulars més fines i un retard subseqüent de la lignificació a l'estiu, produint una fusta tardana menys densa (és a dir, valors de MXD més baixos). La correlació positiva més alta per al mateix període correspon al SPEI de juliol, el qual suggereix que finals d'estiu humits aniran associats una producció de fusta tardana més densa per mitjà de l'augment de la lignificació i la síntesi de carbohidrats al final del període de creixement. A més, finals d'estiu humits no necessàriament han de derivar en la producció de lúmens més amples. En el subperíode 1970-2009, les correlacions positives més elevades entre la MXD i el SPEI es troben al gener considerant la sequera acumulada des del setembre previ (és a dir, escala de SPEI de cinc mesos); açò significa que condicions humides a la tardor i a l'hivern previs d'un any específic implicarien la producció d'una fusta tardana més densa durant el final de l'estiu de l'any següent. Aquest resultat és d'alguna manera inesperat, ja que significa que, apart de les condicions del final de l'estiu o de principis de la tardor d'un any específic, la MXD també pot estar influïda amb "retard" per les condicions climàtiques de l'any previ, com és normalment el cas de la TRW. La interpretació d'aquesta observació pot ser la mateixa que para la TRW, ja que condicions humides prèvies al període de creixement poden fer augmentar la síntesi i el emmagatzematge de carbohidrats que seran posteriorment utilitzats per a la lignificació i engruiximent de les cèl·lules de la fusta tardana en el següent període de creixement. Influències indirectes similars exercides per les condicions prèvies d'hivern també foren observades en poblacions xèriques de *Pinus halepensis*, que constitueixen els boscos típics mediterranis de cotes baixes. Les diferències observades entre els dos subperíodes referents a les respostes a la sequera podrien ser degudes a diferents intensitats d'estrés hídric d'un subperíode a l'altre, diferents condicions de temperatura o variabilitat climàtica (com hem dit abans, la primera meitat del segle XX fou climàticament menys variable que la segona meitat), o efectes indirectes o altres factors de control globals o locals com ara l'increment de les concentracions atmosfèriques de CO_2 i augment de la deposició de N.

Per a concloure, l'augment de les temperatures va comportar un increment de l'estrés per sequera en boscos pirenaics i ibèrics d'alta muntanya, com s'ha observat en altres boscos mediterranis de muntanya. Per tant, boscos d'altituds elevades que creixen limitats típicament per baixes temperatures estan tornant-se més limitats per la disponibilitat d'aigua. Podem estar sent testimonis de com s'està depassant un llindar fisiològic en termes de temperatura òptima per al creixement, reforçant el paper de la sequera com a factor limitant del creixement en boscos d'alta muntanya durant les últimes dècades. Però, com està responent el creixement dels arbres al clima en altres parts de la Conca Mediterrània? Són les nostres observacions i les tendències negatives recents de la TRW comparables amb altres regions?

Patrons biogeogràfics de les tendències recents del creixement a la Conca Mediterrània (capítol 4).

La intricada topografia i el clima divers, tots dos característiques de la Conca Mediterrània (CM), produeixen signes de tendència variats i a vegades oposats en variables dendrocronològiques com ara la TRW o la MXD, fins i tot entre llocs molt propers entre si. A pesar d'aquesta complexitat, els nostres resultats posen de relleu un patró actuant a escales sinòptiques, on la distribució de tendències positives en variables dendrocronològiques relacionades amb creixement o productivitat esta esbiaixada cap a àrees més humides i menys càlides, localitzades principalment cap al nord-oest de la CM. Les tendències negatives estan generalment disposades en àrees més xèriques i càlides, en àrees més al sud i al est de la CM. Aquestes observacions podrien indicar que, a pesar de la complexitat local climàtica i topogràfica característiques, a una escala global el creixement dels arbres al llarg de la CM està limitat per sequera o per baixa disponibilitat hídrica durant el període de creixement. Millores en la eficiència en l'ús de l'aigua (WUEi) pareixen ser insuficients per a compensar els efectes negatius de la reduïda disponibilitat hídrica sobre el creixement. Una reducció en la productivitat forestal deguda a limitació d'aigua podria tindre serioses implicacions referents al grau de segrest de carbó per els boscos ibèrics, afectant el cicle de carbó de la biosfera terrestre.

También mostrem un biaix dels mètodes de mostreig cap a llocs d'altituds elevades a escala de la CM, i açò és probablement el resultat de la empremta dels dendrocronòlegs, que tradicionalment han buscat els arbres més sensibles climàticament que en general creixen en ambients extrems d'altituds elevades. Per altre costat, els arbres més vells tendeixen a créixer a altituds més elevades degut a la menor pressió antròpica exercida (per exemple, tales) en comparació amb cotes més baixes durant les últimes dècades. A més a més, a altituds més elevades on les condicions climàtiques són severes la taxa de creixement és més baixa i els arbres son més longeus. Finalment, la majoria dels boscos millor preservats d'Europa es troben en muntanyes. Per tant s'assumeix que molts dels estudis dendrocronològics i les seues observacions estan també esbiaixats cap a una sobrerrepresentació d'arbres vells de creixement lent ubicats a altituds elevades. Emfatitzem la necessitat d'una distribució més uniforme dels llocs d'estudi i de les classes d'edat per a reflectir millor criteris ecològics en comptes de polítics i metodològics.

Perspectiva per a futures investigacions.

- En els mostreig dendrocronològic volíem obtenir una àmplia representació de la variabilitat poblacional, encara que mostrejàrem principalment individus grans i adults, que resultaren ser principalment individus vells. Incloent una bona representació de totes les classes d'edat (incloent plançons, individus vius i individus morts), de grandària i d'estatus social en estudis dendrocronològics futurs evitaria el biaixos més comuns a la dendrocronologia provinents de mostrejar els arbres més vells i grans. També necessitem una millor descripció dels arbres i registres més complets de dades ecològiques i de variables dendrocronològiques.

- Aquesta variabilitat ben mostrejada permetria també realitzar anàlisis més acurats de variables dendrocronològiques (per exemple TRW, MXD o àrea d'albeca) o variables de grandària i avaluar per tant la seua variabilitat a través d'un gradient altitudinal. Aquest enfocament també ajudaria a avaluar les relacions al·lomètriques entre variables, com les observades entre la taxa de creixement i la proporció *àrea foliar/àrea d'albeca*, o entre longitud i àrea basal de les branques. De fet, encara que les possibles diferències en la distribució d'edat o la grandària poden afectar el emmagatzematge de carbó en els boscos, aquests factors no han sigut explícitament representats en models de productivitat forestal a escala global.

- En els llocs mostrejats, els arbres més vells creixen a altituds més elevades (capítol 1). A més, quant més vells sigan els arbres (és a dir, arbres de les altituds més elevades), més alt serà el percentatge de variància dels índexs de creixement explicada per el clima (capítol 2). Açò implica que un mostreig estratificat per edats i per altitud seria útil per a separar diferents respostes dels índexs de creixement al clima i permetria una millora de la solidesa de les reconstruccions paleoclimàtiques.

- El fenomen de divergència entre la TRW i la temperatura trobat al capítol 3 hauria d'estar considerat en l'avaluació i el rendiment de reconstruccions climàtiques pirinenques que utilitzen proxies dendrocronològics basats en períodes curts de calibratge. Els arbres estan mostrant una sensibilitat cada vegada major a la sequera i una sensibilitat minvant a la temperatura en les últimes dècades fins i tot en aquests ecosistemes de muntanya on esperaríem una forta resposta a la temperatura. Açò implicaria que una reconstrucció climàtica pirinenca basada en relacions TRW-clima del present és qüestionable i hauria d'estar considerada acuradament. A més, després d'haver avaluat aquest fenomen de divergència a un nivell d'espècie, el nostre pròxim pas seria el desenvolupament d'un estudi a nivell de lloc de les senyals d'alta i baixa freqüència en les correlacions creixement-clima, el qual ens permetria extraure conclusions per a escales majors d'una manera més precisa.

- Els models d'equacions estructurals (capítol 1) i els models lineals mixtes (capítol 2) constitueixen mètodes lineals. Aquest enfocament lineal és correcte per a obtenir un coneixement simplificat dels mecanismes naturals. Però no podem oblidar que aquests mètodes no lineals poden no detectar potencials fenòmens no lineals que es troben també presents en la natura, per exemple les associacions no lineals entre l'altitud i les taxes de creixement radial o entre les àrees basal i d'albeca i basal. A més, la relació analitzada al capítol 1 entre el BAI i l'àrea d'albeca, encara que significant, es podria considerar que segueix una equació logarítmica més que lineal (veure el material suplementari del capítol 1). Quan representem l'àrea d'albeca front l'altitud per a *P. uncinata*, l'albeca generalment augmenta amb l'altitud per a superar l'augment de la viscositat de l'aigua, evitant d'aquesta manera un descens del flux de saba. Però hi ha un llindar coincidint amb l'altitud mitjana del límit del bosc als Pirineus (~2300 metres sobre el nivell de la mar) a partir del qual l'àrea d'albeca comença a disminuir (Fig. 1). Aquesta taxa de decreixement de l'albeca a partir del límit altitudinal del bosc pareix més ràpid que la taxa d'increment existent abans d'arribar a aqueix llindar. Al mateix temps l'edat i l'àrea basal es comporten de manera similar entre si (ja que els arbres més vells també són més grans; veure capítol 1), i també de manera similar a l'àrea d'albeca, és a dir, disminuint a partir del llindar del límit del bosc cap amunt. Per què l'àrea d'albeca i la edat pareixen disminuir des del llindar altitudinal del límit del bosc? Primer, a altituds més elevades que les del límit del bosc l'augment compensatori de la producció d'albeca pot cessar degut a que les baixes temperatures arriben a ser massa limitants per al creixement. Per tant, la conductivitat hidràulica disminueix, la producció de nous teixits és dificultada i l'acumulació de carbohidrats estructurals produeix un descens de la taxa fotosintètica per mitjà d'un mecanisme de retroalimentació negativa. Segon, el període de creixement serà més curt quant més elevada siga l'altitud; per tant la taxa de creixement radial es fa més petita, mentre que els anells interns deixen l'albeca i passen a formar part del duramen (és a dir, la proporció albeca:duramen disminueix de valor). Tercer, un increment de la limitació de la xilogènesis, la fotosíntesis i la conductivitat hidràulica imposat per la grandària de l'arbre en arbres vells, generalment localitzats a cotes altes, causaria una reducció més intensa del creixement i la producció d'albeca en comparació amb arbres més joves de cotes més baixes. Les relacions entre aquests mecanismes poden resultar en comportaments no lineals de l'àrea d'albeca i de la edat al llarg del gradient altitudinal. Métodes estadístics no lineals com ara els models additius generalitzats mixtes (GAMM) haurien de ser utilitzats per a analitzar de manera més profunda aquestes relacions, descrivint una imatge més acurada del sistema arbre-lloc-clima.

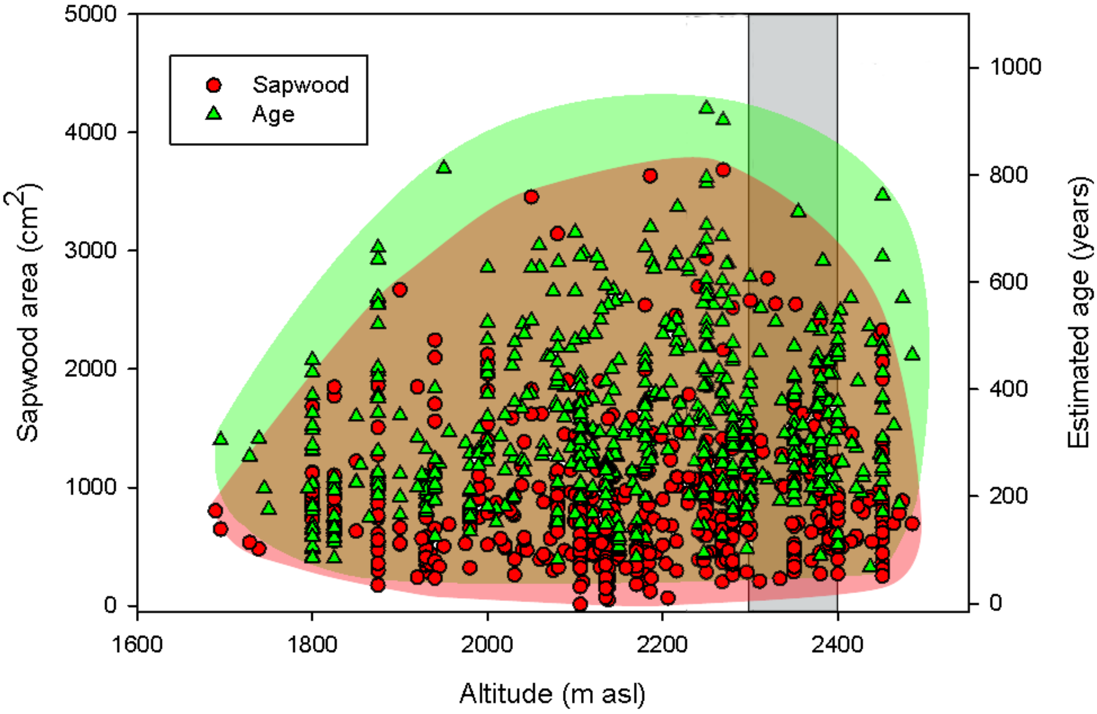

Figura 1. Relació entre l'àrea d'albeca, la edat i la altitud en els individus de *Pinus uncinata* mostrejats per a aquesta tesi (n = 700 arbres). L'àrea gris indica la ubicació altitudinal potencial del límit del bosc en els Pirineus (Ninot et al. 2008).

- Els capítols 3 i 4 evidencien la necessitat d'un mostreig de MXD més exhaustiu al llarg de la Conca Mediterrània. A altituds elevades, la MXD mostra una correlació significativa amb la temperatura per a la majoria del període estival, mentre que la TRW pareix respondre tan sols a les temperatures de principis de l'estiu; son necessàries per tant més investigacions sobre les possibles explicacions d'aquestes observacions. A més a més, les condicions climàtiques de començaments de l'estiu poden no ser rellevants en el control del creixement a finals de l'estiu, i viceversa. Hauríem d'intentar separar les senyals climàtiques contingudes en la TRW i en la MXD. El mètode per a realitzar açò podria basar-se en la eliminació de la relació entre la TRW i la MXD observada en anells estrets d'arbres creixent a altituds elevades, i una nova variable de MXD "lliure" de la influència de la TRW pot ser creada. La associació entre les cronologies de TRW i de MXD es fort, encara que no lineal (Fig. 2.). Podem utilitzar les equacions ajustades per a aquesta associació per a obtenir una cronologia modificada de una nova variable, MXD', d'acord amb la equació: MXD' = MXD/MXD_t, on la MXD és la densitat màxima de la fusta tardana en un anell amb una amplària particular (TRW), i on la MXD_t és el valor de MXD de la equació ajustada per a aqueixa particular amplària d'anell. Amb aquesta aproximació podem intentar (i) separar la senyal climàtica localitzada en la variabilitat de la TRW i la MXD i (ii) analitzar la resposta d'aquestos paràmetres a la variabilitat climàtica al llarg de l'any. Aquesta aproximació permetria unes reconstruccions climàtiques més estables ja que la temperatura pot tindre efectes diferents sobre el creixement radial en diferents subperíodes del període de creixement.

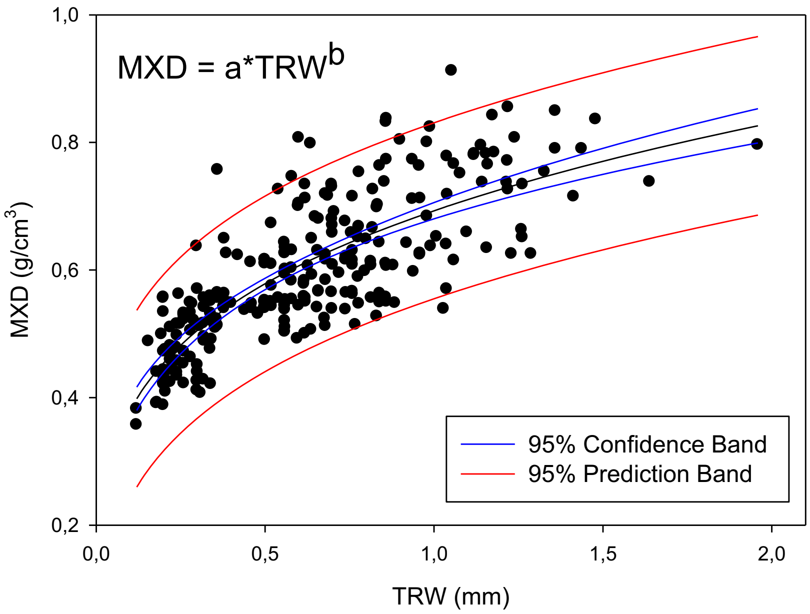

Figura 2. Relació entre l'amplària d'anell (TRW) i la densitat màxima de la fusta tardana (MXD) en un arbre mostrejat a l'Estany Gerber (GE). La línia negra sòlida fou ajustada d'acord amb la equació indicada a la part esquerra superior de la figura.

Conclusions

Capítol 1

- Canvis a l'àrea d'albeca relacionats amb la edat controlaren al segle XX l'increment d'àrea basal en boscos de muntanya de *P. uncinata*. Qualsevol efecte potencial del clima sobre l'increment d'àrea basal estarà principalment controlat per la producció d'albeca, que ve determinada per la edat de l'arbre i la altitud.

Capítol 2

- L'altitud juga un paper principal en la influència de les respostes dels índexs d'amplària d'anell de *P. uncinata* al clima a escales de lloc i d'individu. Un enfocament a nivell de les respostes individuals milloraria el coneixement ecològic de la vulnerabilitat dels arbres als factors climàtics estressants.

Capítol 3.

- S'observa una resposta més dèbil de la variabilitat d'amplària d'anell a l'escalfament recent, mentre que la sequera estival està influenciant cada vegada més el creixement dels boscos de muntanya de *P. uncinata*.

Capítol 4

- A una escala sinòptica, el creixement dels arbres a través de la Conca Mediterrània està limitat per sequera o per baixa disponibilitat d'aigua durant el període de creixement.

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