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Edurne Martínez del Castillo

# Bosques creciendo en su límite de distribución: cambio en la cubierta forestal y relaciones clima-crecimiento en el Parque Natural del Moncayo

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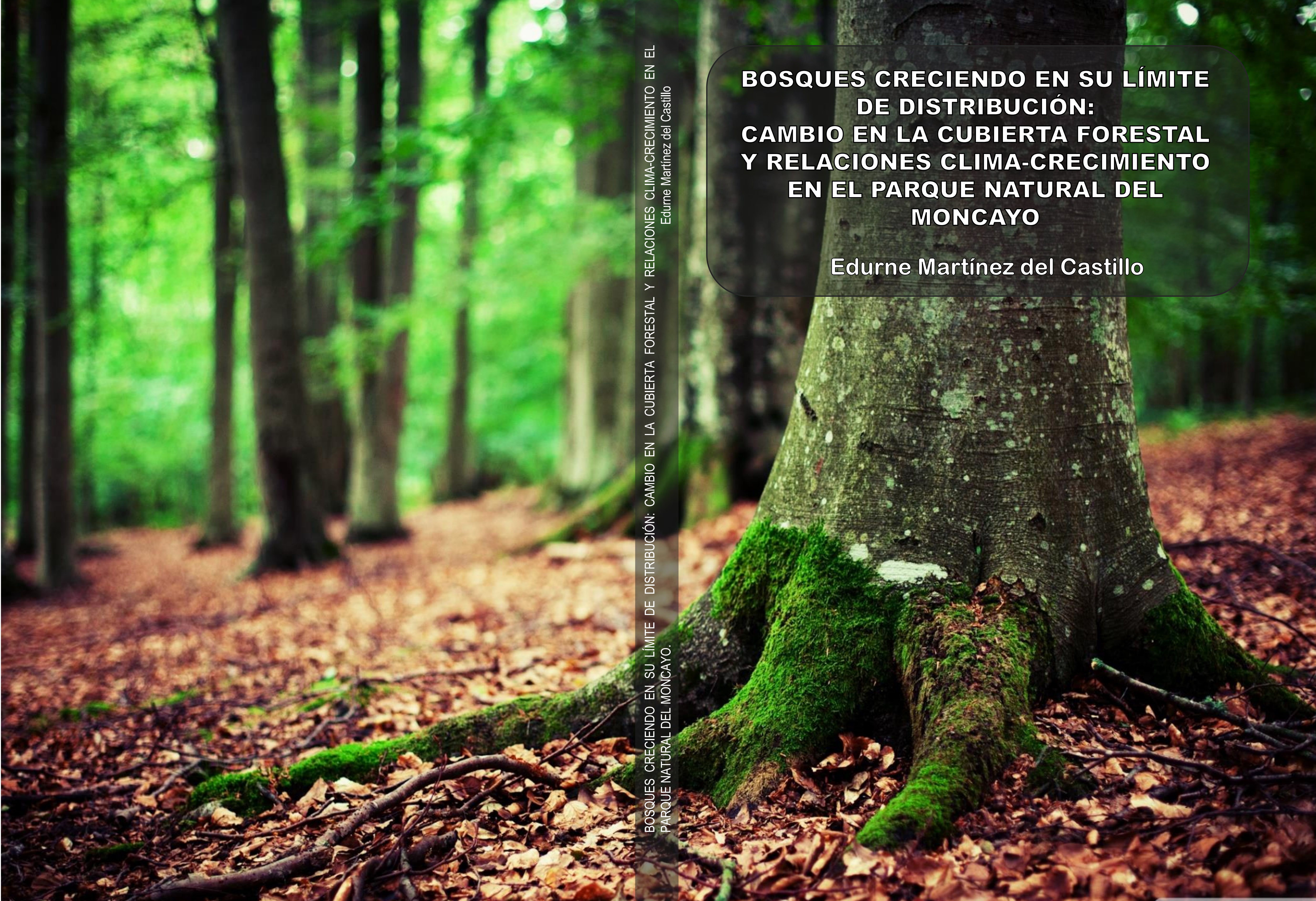

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FACULTAD DE FILOSOFÍA Y LETRAS
DEPARTAMENTO DE GEOGRAFÍA Y ORDENACIÓN DE TERRITORIO

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# TREE PERFORMANCE AT REAR-EDGE DISTRIBUTION: FOREST COVER CHANGE AND CLIMATE-GROWTH RELATIONSHIPS IN MONCAYO NATURAL PARK

MEMORIA DE TESIS PRESENTADA POR
EDURNE MARTINEZ DEL CASTILLO
PARA OBTENER EL GRADO DE DOCTOR POR LA UNIVERSIDAD DE ZARAGOZA

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Directores:
Dr. Martín de Luis Arrillaga
Dr. Luis Alberto Longares Aladrén

Departamento de Geografía y Ordenación del Territorio
Facultad de Filosofía y Letras
Universidad de Zaragoza

Tesis Doctoral

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# Tree performance at rear-edge distribution: Forest cover change and climate-growth relationships in Moncayo Natural Park

Memoria presentada por
Edurne Martínez del Castillo
Para la obtención del grado de doctor por la Universidad de Zaragoza

Los directores:

| Dr. Martín de Luis | Dr. Luis Alberto Longares |
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Los directores de la tesis doctoral, el Dr. MARTÍN DE LUIS ARRILLAGA, Profesor Contratado Doctor de la Universidad de Zaragoza y el Dr. LUIS ALBERTO LONGARES ALADRÉN, Profesor Contratado Doctor de la Universidad de Zaragoza.

CERTIFICAN

Que la memoria titulada “Bosques creciendo en su límite de distribución: Cambio en la cubierta forestal y relaciones clima-crecimiento en el Parque Natural del Moncayo" ha sido realizada bajo su dirección por Edurne Martínez del Castillo en el marco del Programa de Doctorado en Ordenación del Territorio y Medio Ambiente del Departamento de Geografía y Ordenación del territorio de la Universidad de Zaragoza.

Y para que conste y en cumplimiento de la normativa vigente, firman el presente informe en Zaragoza, a 11 de marzo del 2019,

Fdo. Dr. Martín de Luis

Fdo. Dr. Luis Alberto Longares

La Dra. María Teresa Echeverría Arnedo, coordinadora del Programa de Doctorado Ordenación del Territorio y Medio Ambiente del Departamento de Geografía de la Universidad de Zaragoza,

INFORMA

Que la presente Tesis Doctoral titulada "Bosques creciendo en su límite de distribución: Cambio en la cubierta forestal y relaciones clima-crecimiento en el Parque Natural del Moncayo", ha sido realizada por Edurne Martinez del Castillo, bajo la dirección del Dr. Martín de Luis Arrillaga y el Dr. Luis Alberto Longares Aladrén, y que la Comisión del citado Programa ha dado su conformidad para que sea presentada ante la Comisión General de
Doctorado de la Universidad de Zaragoza.

Y para que conste y en cumplimiento de la normativa vigente, firman el presente informe en Zaragoza, a 11 de marzo del 2019

Fdo. Dra. María Teresa Echeverría Arnedo
Coordinadora del Programa de Doctorado Ordenación del
Territorio y Medio Ambiente

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*A mi pequeña familia*

# RESUMEN

El cambio global afecta a los bosques en numerosas formas, poniendo en compromiso su situación actual en todo el mundo. En concreto, para el mundo mediterráneo se pronostican cambios sustanciales en las temperaturas, régimen de precipitaciones y recurrencia de eventos climáticos extremos que, unidos a los cambios en el clima que ya se han producido durante el último siglo, aumentan la vulnerabilidad de los bosques y ponen en peligro su supervivencia. Esto es especialmente relevante para aquellas especies forestales adaptadas a condiciones más frescas y húmedas, que encuentran en el mundo mediterráneo su límite de distribución debido a los condicionantes climáticos de la zona. La velocidad a la cual se producen los cambios en el clima hace necesaria la intervención antrópica para hacer frente a sus consecuencias mediante la gestión forestal, ya que los mecanismos naturales de adaptación de los bosques son procesos más lentos que el actual cambio global.

En esta tesis se propone un análisis espacial integrador mediante diversas técnicas orientadas a analizar tanto la distribución como el crecimiento del bosque persiguiendo como fin la aplicabilidad de sus resultados a la gestión y manejo forestal. El análisis se centra en las principales especies forestales presentes en el Parque Natural del Moncayo, como son el pino silvestre, el haya y el rebollo, que son especies muy importantes a nivel europeo debido a su valor ecológico y económico.

Los resultados obtenidos en la presente tesis ponen de manifiesto que la distribución espacial de estas masas forestales no es estable en el tiempo y está sujeta a cambios sustanciales que pueden ser detectados en un periodo relativamente corto de tiempo de poco más de dos décadas. Las especies están todavía inmersas en procesos de adaptación dinámica, relacionados principalmente con la situación de partida, con las prácticas de gestión forestal, con la competencia entre especies y con la adecuación al clima prevalente.

El hecho de que estas especies se encuentren en su límite de distribución no hace que las restricciones climáticas sean muy diferentes a las restricciones propias de cada especie. A grandes rasgos, estos limitantes son similares a los encontrados en otras regiones situadas a lo largo del rango de distribución, y por tanto son específicos de cada especie. Sin embargo, existen matices que restringen en mayor medida el desarrollo de estas especies en este límite de distribución. Además, determinados limitantes varían significativamente en función del gradiente altitudinal (i.e. climático), actuando en algunas zonas como potenciadores y en otras como inhibidores de crecimiento. En cambio, su situación de límite de distribución en el caso de las hayas y pinos silvestres sí que afecta enormemente a la duración del periodo de crecimiento, siendo muy diferente su efecto en estas dos especies y con sus matices dentro del gradiente ambiental de la zona de estudio. En el caso del haya las condiciones con carácter más mediterráneo influyen negativamente, restringiendo el periodo de crecimiento a poco más de dos meses, pero en el caso del pino se alarga considerablemente comparándolo con el crecimiento en la región eurosiberiana. Ambas estrategias son útiles para el desarrollo de la especie, pero al mismo tiempo podrían ser problemáticas en años determinados donde las condiciones climáticas sean desfavorables en los momentos críticos para cada especie.

El potencial de los resultados obtenidos en esta tesis en el terreno de la ordenación medioambiental es considerable, pudiéndose usar para planificar medidas de gestión forestal para cada especie orientadas a disminuir la influencia que el cambio global ejerce sobre ellas.

# SUMMARY

Global change affects forests in multiple forms, compromising its current situation around the world. Specifically, it has been forecasted substantial changes in the Mediterranean area related with climate, as temperature rising, changes in the precipitation patterns or recurrence of extreme climatic events. This predictions, joined to the current trends in climate of the past century, threaten the stability of forest ecosystems, increasing their vulnerability and endanger their survival. This fact is especially relevant for those species adapted to colder and wetter environments, which find in the Mediterranean area the limits of their distribution as a result of harsh climatic conditions. The actual rhythm of climatic change is too much faster that the mechanisms of forest adaptation to changes, therefore, human intervention (i.e. forest management) become necessary to ensure the preservation of this forest type in Mediterranean areas.

In this thesis, an inclusive and spatial analysis is proposed, using different techniques geared to analyze the forest distribution and growth. The final aim is to generate useful results for forest management purposes. The analysis if focused on the main forest species of Moncayo Natural Park, all of them important species at Europe level as European beech, Scots pine and Pyrenean oak.

The results of this thesis revealed that the spatial distribution of this species is not stable and the changes can be quantified in relatively short time periods as decades. The species are still

in a dynamic adaptation process, related with the previous situation, with the species competition, with the forest management actions and with the adaptation to the prevailing climate conditions.

Despite the species are growing at the edge of their distribution limits, the climatic constrains are similar to the climatic limitation on the core of the distribution or species-specific. However, there are some nuances that limit forest growth in this location. In addition, the importance of some climatic variables for forest performance varied significantly along the altitudinal gradient of the study zone, acting as an enhancer in a zone and as an inhibitor in other zone of different altitude. On the other hand, living at the edge of the distribution does affect tree growth duration, particularly in beech and pine, but in very different ways. In case of beech, the Mediterranean conditions affect negatively, limiting its growing period to two or three months, meanwhile in pines occurred the opposite; the duration of the growing period is longer compared with other pine forests in Centre and North Europe. Both adaptation strategies are subject to advantages but are also subjected to risks if the climatic conditions are unfavorable during critic periods for each specie.

The potential of the obtained results of this thesis to the environmental planning is remarkable, it could be used to design forest management actions for each specie geared to mitigate the effects of global and climate change.

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# INTRODUCCIÓN

# 1. Introducción

## 1.1. Los bosques y el cambio global

El cambio global y los bosques están íntimamente relacionados. Es evidente que el cambio global viene afectando a los bosques desde sus inicios, y de forma inversa, los cambios producidos en los bosques tienen su influencia en el devenir del cambio global. Éste cambio global es definido como una serie de grandes cambios ambientales relacionados con fluctuaciones climáticas y con la actividad humana (Vitousek 1994; Steffen et al. 2004) y engloba diversos componentes que a su vez están relacionados y pueden mostrar retroalimentaciones positivas o negativas complejas. Estos elementos son el cambio climático, cambios en ciclos biogeoquímicos, cambios de gestión y uso del suelo y cambios biogeográficos de distribución de organismos (Vitousek 1994). Todos estos componentes tienen su influencia en la distribución, composición, crecimiento y estado fitosanitario de los bosques, algunos de forma directa, como es el caso de las deforestaciones, y la mayoría de ellos de forma indirecta.

Los bosques, a su vez, son capaces de afectar e influir en el cambio global, principalmente mediante su influencia en el clima a través de las características físicas generadas en la superficie forestal (Steffen et al. 2004). Los bosques afectan los flujos de radiación en superficie, la temperatura, la humedad y sus dinámicas, por lo que cualquier modificación en la cobertura forestal puede cambiar las condiciones de la parte baja de la atmosfera, y por tanto, causar grandes influencias en el clima local y global (Pielke et al. 1998; Betts 2001). Un ejemplo de esto es la importancia de los árboles como un elemento clave en el ciclo de carbono; por un lado, atrapan y fijan el carbono a largo plazo mediante su crecimiento, y por otro, los procesos de destrucción del bosque como grandes incendios, explotación excesiva o deforestaciones, liberan grandes cantidades de $CO_2$ a la atmósfera.

Numerosos estudios analizan los efectos producidos en el clima debido a los cambios en los sistemas forestales (Schimel et al. 2001; Steffen et al. 2004; Graven et al. 2013; Green et al. 2017), donde la relación no es siempre negativa como se tiende a pensar, en la que la pérdida forestal conlleva a un aumento general de temperaturas y aumento en niveles de $CO_2$ que a su vez provocan una mayor pérdida forestal. Por una parte, la dirección de los cambios en la temperatura producidos por las deforestaciones históricas, varía espacialmente (Figura 1.1), de hecho, hay estudios que certifican que en grandes áreas, la perdida forestal se traduce en una disminución de las temperaturas debido a un aumento del efecto albedo de la superficie (Betts 2001).

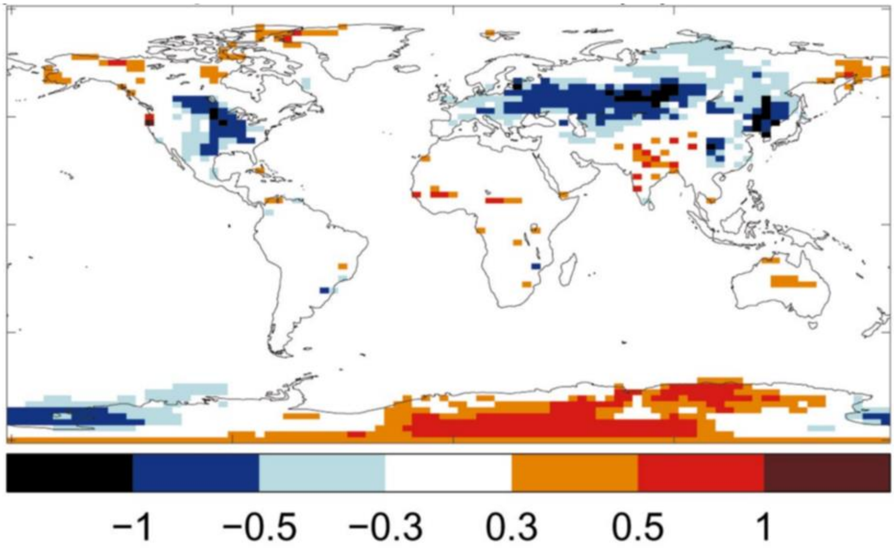


*Figura 1.1. Cambios simulados en la temperatura (ºC) de la superficie debido a deforestaciones históricas. Fuente: Betts 2001*

A nivel global, los bosques son considerados uno de los ecosistemas más importantes debido a la gran cantidad de biodiversidad que albergan y a los servicios medioambientales que ofrecen. No solo son importantes desde un punto de vista ecológico, sino que también poseen valores de uso directos e indirectos para la sociedad y la economía (FAO 1995). Ejemplos de uso directo son actividades como la extracción de madera, carbón, corcho, frutos o forraje; y el uso del bosque como lugar de esparcimiento o incentivo turístico. Entre los valores de uso indirectos se incluirían los relacionados con el medio ambiente en un sentido amplio, incluyendo la protección de cuencas frente la erosión que producen los árboles, la regulación de los recursos hídricos, protección de la fauna y flora asociadas o la función de reserva como sumidero de carbono.

Los bosques mediterráneos tienen numerosas peculiaridades debidas a múltiples condicionantes: la situación geográfica y la heterogeneidad de la topografía determinan la excepcional variedad de ecosistemas forestales, incluyendo especies forestales típicamente mediterráneas, pero también atlánticas, sub-atlánticas, eurosiberianas, montañas y alpinas (Vilà-Cabrera et al. 2018). Debido a esta configuración, la diversidad y riqueza ambiental de estos bosques es particularmente alta. En este contexto, los grandes cambios en el uso de la tierra como la sobreexplotación, las presiones de uso, la perdida de hábitats y la contaminación, son los principales factores que repercuten en el ambiente mediterráneo, conllevando procesos de degradación y por tanto, de perdida de funciones (Regato 2008).

En lo relativo al cambio en las condiciones climáticas que se lleva produciendo durante el último siglo, para la región mediterránea se pronostican cambios más notables en comparación con otras regiones. En concreto, un aumento de unos dos grados como promedio en la temperatura media durante el próximo siglo, y un cambio en el régimen de precipitaciones (IPCC 2013), sin embargo, el verdadero reto para los bosques será afrontar los eventos climáticos extremos asociados a estos cambios, como pueden ser sequias, olas de calor, heladas tardías o tormentas.

## 1.2. La gestión forestal para combatir los efectos del cambio global

Las especies forestales han evolucionado para adaptarse al entorno cambiante en el que se encuentran. Las poblaciones de especies ampliamente distribuidas, por lo general, tienen diferencias genéticas producidas para adaptarse al clima, a las condiciones del suelo y a los principales factores de perturbación como plagas o incendios, que existen en el lugar donde crecen (Alfaro et al. 2014). Otra forma de adaptación de los bosques es la migración natural mediante la cual las poblaciones van colonizando nuevos territorios y abandonando otros que ya no presentan condiciones óptimas para el desarrollo de la especie. Sin embargo, los procesos de adaptación genética y de migración natural son procesos lentos que tardan siglos en producirse y difícilmente pueden acelerarse para adaptarse al ritmo de cambio global y climático actual. Esto producirá un desacople entre la distribución actual de las poblaciones con respecto al clima para el cual se han adaptado, creando presiones fisiológicas que producirán un debilitamiento de los arboles frente a cualquier perturbación y pondrá en peligro su supervivencia (Sáenz-Romero et al. 2016).

Frente a esta problemática, se hace necesaria una intervención por parte del hombre para hacer frente a las consecuencias del cambio global por medio de la gestión forestal. Estas medidas de gestión pueden ser de mitigación, orientadas a afrontar las causas del cambio, o pueden ser medidas de adaptación, las cuales tratan de reducir sus impactos. Las primeras tratan de reducir emisiones derivadas de la degradación de los bosques o la deforestación, sustituir materiales y mejorar la función de los bosques como reservorios de carbono; mientras que las segundas engloban intervenciones destinadas a reducir la vulnerabilidad de los bosques (FAO 2016). Entre estas medidas de adaptación estarían las destinadas a, en la medida de lo posible, adaptar la distribución de las especies a lugares con condiciones adecuadas y/o sustituir especies forestales por otras más adaptadas a las nuevas condiciones. Estas prácticas de realineamiento de especies asistido por humanos han sido llamadas migración asistida, colonización asistida, reubicación asistida o migración facilitada (Pedlar et al. 2012; Dumroese et al. 2015; Koralewski et al. 2015; Sáenz-Romero et al. 2016).

Tanto para la planificación y diseño de medidas de gestión forestal, como para asegurar su efectividad a largo plazo, es necesario un profundo conocimiento del funcionamiento de las poblaciones sobre las que se va a actuar (Sáenz-Romero et al. 2016). En revisiones sobre los últimos estudios científicos que tratan sobre la gestión forestal en el ámbito Mediterráneo (Vilà-Cabrera et al. 2018), se pone de manifiesto la necesidad de estudios que combinen diferente información ambiental, con enfoques experimentales, modelado espacial y el uso de imágenes de satélite, con el fin de diseñar estrategias eficaces en el medio y largo plazo. El crecimiento de los árboles, cómo el clima condiciona ese crecimiento, la monitorización de la expansión, retroceso o sustitución forestal son elementos fundamentales para el diseño de medidas de adaptación. Con esto no solo se protegería el futuro de los bosques, sino que también se preservarían sus funciones medioambientales, socioculturales y económicas, tan valiosas para la sociedad.

### 1.3. Fuentes de información ambiental

Un análisis espacial integrador mediante el uso de diversas técnicas clave es necesario para la comprensión de los procesos de adaptación de las especies al cambio global y climático. Además, la combinación de estos elementos permite abordar la cuestión a diferentes escalas espaciales, que es necesario para que los resultados sean aplicables al territorio, entendido en un sentido amplio.

El estudio de la distribución espacial de las especies forestales y su evolución a lo largo del tiempo es abordable mediante la teledetección y el análisis de imágenes de satélite. La teledetección es, desde los años 70, una de las herramientas más útiles para el estudio extensivo de zonas forestales debido a una serie de ventajas intrínsecas a la observación espacial (Chuvieco and Chuvieco Salina 2010): la cobertura global y exhaustiva, observación multiescala, cobertura repetitiva, información sobre regiones no visibles del espectro, etc. El uso de la teledetección está ampliamente contrastado en multitud de estudios, entre los cuales destacan los de índole ecológica, como la generación de cartografía de paisaje, de ocupación y cambio de usos suelo o el estudio de la productividad de ecosistemas (Martínez del Castillo 2015).

En línea con lo anterior, la ecología del paisaje ha desarrollado métodos cuantitativos para medir el grado de cambio estructural de los bosques y paisajes forestales, que dan rigor a los análisis que relacionan los patrones espaciales del territorio con los procesos ecológicos, creando índices con los que cuantificar diferentes elementos del paisaje y su estructura (Naveh and Lieberman 1990; Farina 2006). Las ventajas del uso de estas técnicas para propuestas de planificación y ordenación medioambiental son notables ya que éstas se centran en la dimensión espacial de los procesos ecológicos y en la relación entre el medio ambiente natural y el medio ambiente antrópico como integrantes del mismo sistema (Carone and Simoniello 2006; Simoniello et al. 2015).

Por otra parte, para analizar los patrones espaciales y temporales de los procesos naturales y resolver cuestiones ambientales relacionadas con los bosques, se hace uso de la dendrocronología. Esta es una disciplina científica relacionada con el estudio de los anillos de los árboles. A través de la datación de esos anillos de crecimiento anual, se puede interpretar la información que contienen los diferentes factores que han influido en su crecimiento (Fritts 1972; Schweingruber 1988). Mediante el uso de estas técnicas, es posible hacer un seguimiento temporal del crecimiento de los árboles a distintas escalas, desde un seguimiento intra-anual, hasta el análisis de los registros de crecimiento que se han producido durante siglos.

El crecimiento intra-anual de los árboles o xilogénesis, es el principal proceso biológico a través del cual el carbón es secuestrado a largo plazo por los árboles (Cuny et al. 2015). El estudio de este proceso es adecuado para determinar la plasticidad fenotípica de las especies mediante el análisis de su variabilidad a lo largo de los años. Igualmente importante es el conocimiento de los momentos concretos en los que el crecimiento empieza o termina, ya que determinan la duración del periodo de crecimiento de las especies y, por tanto, la magnitud del mismo.

De forma complementaria, a través del análisis de la secuencia de crecimiento a lo largo de la vida del árbol y su interpretación conjunta con el clima del lugar, se puede obtener información sobre la sensibilidad climática y sobre la variabilidad espacial de la misma a lo largo del territorio. Para el establecimiento de las relaciones clima-crecimiento y su análisis espacial, es necesaria una red dendrocronológica densa y correctamente distribuida por el área de estudio, así como la existencia de datos climáticos de calidad para cada punto de muestreo dendrocronológico.

Por último, la aplicación de modelos estadísticos supone una herramienta útil para la predicción de una respuesta a partir de las variables dependientes. En este caso, los modelos de crecimiento nos ayudan a localizar los lugares donde las especies crecen más, señalando en el territorio aquellas áreas que son más óptimas para cada especie. De la misma manera, se puede modelar la predicción de las relaciones clima-crecimiento con el fin de obtener esta información de forma continua espacialmente. Esta información resulta tremendamente útil para la gestión forestal, ya que se puede inferir cómo afectan las condiciones climáticas a los arboles sin necesidad de muestrearlos.

## 1.4. Los bosques en su límite de distribución.

Los bosques encuentran su límite de distribución en zonas llamadas ecotonos, que son zonas de transición entre dos biomas vecinos que habitualmente contienen una mayor biodiversidad que las áreas adyacentes (Risser 1995b), ya que en ellas conviven especies de ambos biomas e incluso endemismos asociados a ese lugar concreto. Además, estas zonas son más sensibles a las variaciones y perturbaciones medioambientales, por tanto son zonas muy interesantes para el estudio de la vegetación en el contexto de monitorizar los impactos del cambio global (Risser 1995b; de Andrés et al. 2015).

En concreto, el objeto de estudio de esta tesis son especies forestales de distribución Eurosiberiana en uno de sus límites de distribución sur, situado en el Parque Natural del Moncayo, elegido como un lugar de especial interés por su vulnerabilidad como ecotono. Estas especies son el haya (*Fagus sylvatica* L.), el pino silvestre (*Pinus sylvestris* L.) y el rebollo (*Quercus pyrenaica* Willd.) (Figura 1.2).

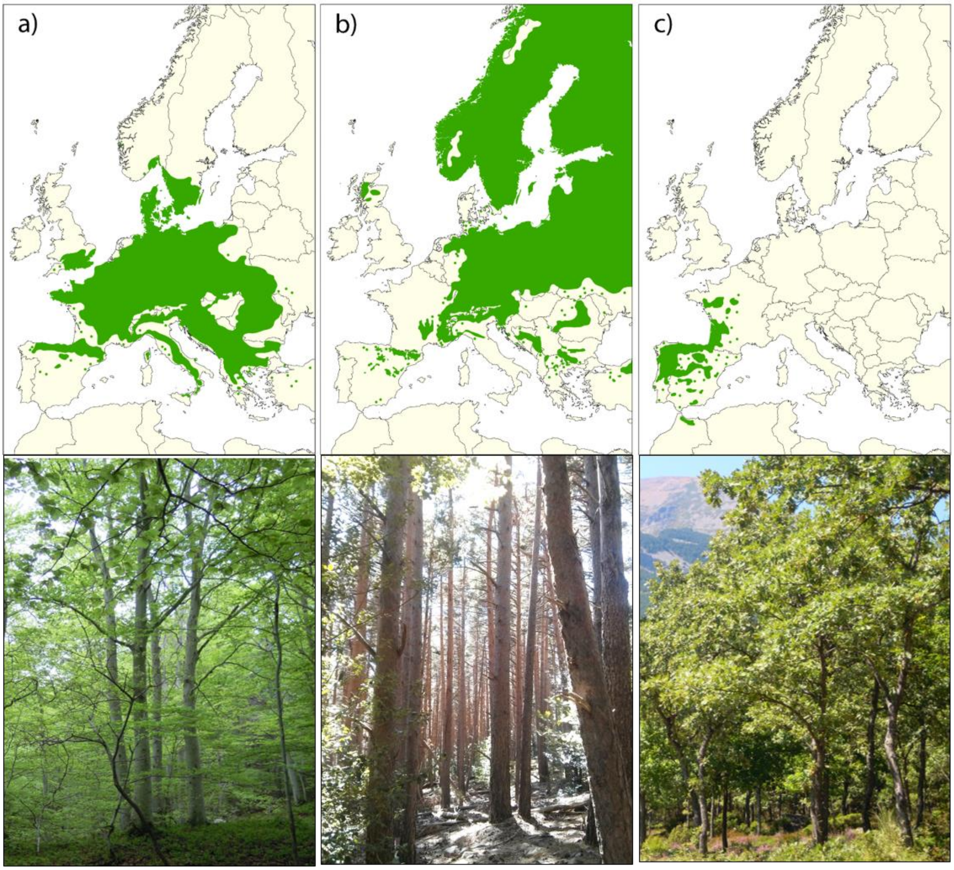


*Figura 1.2. Distribución espacial del haya (a), del pino silvestre (b) y del rebollo (c) en Europa occidental. Fotografías de las tres especies en la zona de estudio. Fuente: European Forest Genetic Resources Programme (Euforgen http://www.euforgen.org/distribution-maps).*

El haya es una de las especies frondosas más importantes y abundantes en Europa. Su distribución natural se extiende desde el sur de la península escandinava hasta Sicilia y desde el oeste de España hasta el noreste de Turquía en el este (Figura 1.2a). Esta especie requiere de unas condiciones húmedas y precipitaciones repartidas durante todo el año para su supervivencia, siendo vulnerable en condiciones de sequía (Geßler et al. 2007; Cavin and Jump 2016). En cuanto a las temperaturas, es bastante tolerante con el frío durante el invierno, pero sensible a las heladas tardías (Menzel et al. 2015). Las hayas son bastante eficaces, comparadas con otras especies arbóreas en la conservación de la capacidad productiva del suelo, debido a su sistema radicular y al alto contenido de potasio de las hojas (Houston Durrant et al. 2016a).

El pino silvestre es la especie de pino más ampliamente distribuida en el mundo, pudiéndose encontrarse en toda Eurasia (Figura 1.2b). Como ejemplo, la masa de pino silvestre de Siberia es la masa forestal mono-especifica más grande en todo el mundo (Houston Durrant et al. 2016b). Esta es una especie pionera, que puede colonizar rápidamente áreas alteradas con suelos pobres (Mátyás et al. 2004), y por ello ha sido usada como especie para reforestaciones. Tiene una gran resistencia a eventos de sequía y también al frio, pero no prospera en ambientes con alta contaminación atmosférica o en ambientes salinos (Houston Durrant et al. 2016b). Su característica madera rojiza o anaranjada tiene un gran valor económico y cultural en muchos países europeos, especialmente en el norte.

El rebollo tiene una distribución espacial más limitada comparada con las otras especies; se distribuye por el noroeste de la península Ibérica y oeste de Francia, en la región Atlántica, aun con alguna presencia de la especie en el ámbito mediterráneo en Cataluña, Andalucía incluso norte de Marruecos (Figura 1.2c). Es un roble de tamaño medio de copa irregular, a medio camino entre las especies de roble de ambientes templados y mediterráneos, adaptado a climas cálidos, aunque no a la sequía (Nieto Quintano et al. 2016). Es una especie importante en la silvicultura de la Península Ibérica, ha sido muy usada con fines ganaderos y para la obtención de leña, debido a su capacidad de rebrotar. Sin embargo, estos bosques se encuentran deteriorados de forma general, debido al cambio en los usos tradicionales y a los incendios forestales (Corcuera et al. 2006; Nieto Quintano et al. 2016). Es por eso que estos bosques están actualmente protegidos bajo la Directiva Hábitats (92/43/EEC) como bosques raros y/o residuales que contienen especies de interés comunitario.

# CAPITULO 2

# JUSTIFICACIÓN Y OBJETIVOS

## 2. Justificación y objetivos de la tesis

### 2.1. Contexto institucional

La presente tesis doctoral se enmarca en un proyecto de investigación ELENA (CGL2012-31668; Eventos climáticos extremos: caracterización, variabilidad espacio-temporal e impacto en los sistemas naturales) financiado por el del Ministerio de Economía y Competitividad y financiado con un contrato predoctoral para la formación de doctores (BES-2013-064453). El mismo organismo financió una estancia breve (EEBB-I-15-09810) disfrutada en la Universidad de Wageningen bajo la supervisión de la Dra. Ute Sass-Klaassen.

### 2.2. Justificación

Como se ha descrito en los primeros capítulos de esta tesis, los bosques se ven afectados por múltiples cambios derivados del cambio global, con especial incidencia del cambio en las condiciones climáticas y el cambio en el aprovechamiento y gestión antrópica. En concreto, los bosques de hayas, pinos silvestres y rebollos que se desarrollan en un ambiente más mediterráneo, y en situación de límite de distribución, pueden ser más vulnerables a los cambios, y se hace necesaria la gestión forestal para asegurar su óptimo desarrollo y supervivencia o en caso contrario, poder adecuar su distribución a las nuevas condiciones.

Para que las medidas de gestión forestal sean efectivas, se requiere un profundo conocimiento sobre la dinámica de las especies forestales en cuestión, haciendo necesario un análisis sobre los cambios en su distribución durante los últimos años al mismo tiempo que profundizar en el conocimiento sobre cómo crecen estas especies y sobre los factores que influyen en su crecimiento. Además, el desarrollo de un análisis espacial sobre la idoneidad climática para el desarrollo de cada una de las especies, es de gran interés para la zonificación y planificación de medidas de gestión orientadas a la conservación de estas masas forestales.

En resumen, la presente tesis doctoral trata de contribuir y enriquecer no solo esta parcela de la ciencia, sino al conjunto de la sociedad por medio de la transmisión y aplicación de los resultados científicos al manejo forestal.

## 2.2. Hipótesis

Las hipótesis de este estudio se detallan a continuación y están todas referidas al área de estudio, el Parque Natural del Moncayo.

i) La distribución de las masas forestales es fruto de la historia de usos antrópicos tradicionales y su posterior abandono, así como de diferentes intervenciones como reforestaciones, por lo tanto, esta distribución dista de la que ocuparían las especies de forma natural. Es de esperar que las especies estén equilibrando su distribución, extendiéndose en algunos lugares y retrayéndose en otros, por lo tanto, algunas especies están actualmente en proceso de colonización de nuevas zonas, aumentando su actual extensión, y otras se encontrarían en un proceso de retroceso.

ii) Las especies situadas en su límite de distribución son más sensibles a los factores climáticos que limitan su crecimiento y muestran su plasticidad fenotípica a este limitante adecuando su crecimiento a las variaciones de las condiciones climáticas que se producen cada año.

iii) Las diferentes especies forestales se ven influidas por diferentes limitantes climáticos en cuanto a crecimiento se refiere, y estos limitantes a su vez, varían a lo largo del gradiente climático presente en la zona de estudio. Además, la variación de estas relaciones entre clima y crecimiento están íntimamente relacionadas con la variabilidad climática de cada lugar, por tanto, estas relaciones pueden ser modeladas a lo largo del territorio.

iv) El conocimiento de la variabilidad del crecimiento de las especies a lo largo del gradiente climático puede ser modelado, pudiendo ser utilizado para generar una cartografía de idoneidad climática para cada una de las especies.

## 2.3. Objetivos

El principal objetivo de esta tesis es analizar y cuantificar el estado de las masas forestales en cuanto a distribución y crecimiento se refiere, identificando los condicionantes climáticos de cada una de ellas, con el fin de generar resultados que sean directamente aplicables a la ordenación medioambiental de un Espacio Natural Protegido, en este caso, el Parque Natural del Moncayo. Para la consecución de este objetivo general, se establecen una serie de objetivos específicos, detallados a continuación:

i) Cuantificar y analizar los cambios producidos en las cubiertas forestales en el periodo comprendido entre 1987 y 2010 y analizar los cambios en la estructura del bosque en relación a la fragmentación, conectividad y heterogeneidad.
ii) Analizar en profundidad la dinámica del crecimiento de las especies forestales más representativas del lugar, desde la xilogénesis (análisis del crecimiento intra-anual), hasta la variabilidad de crecimiento interanual, siempre con una visión espacial, donde se analizan las variaciones de crecimiento dentro del gradiente altitudinal que cada especie ocupa.
iii) Definir los elementos climáticos que influyen en el crecimiento de las especies y cuantificar las relaciones clima-crecimiento de éstas a lo largo del gradiente altitudinal.
iv) La creación de modelos para poder predecir de forma efectiva, tanto las relaciones clima-crecimiento, como el crecimiento potencial de las especies a lo largo de toda el área de distribución potencial que tiene cada especie dentro del Parque Natural.

v) Por último, se plantea como último objetivo la creación de mapas de idoneidad climática para el desarrollo de cada especie forestal como herramienta de gestión para el manejo forestal.

## 2.4. Estructura de la tesis

La tesis consiste en 9 capítulos: la introducción (capitulo 1), la justificación y objetivos (capitulo 2), el área de estudio (capitulo 3), metodología (capitulo 4), cuatro artículos de investigación (capítulo 5) y un capítulo final de conclusiones (capitulo 6).

Los cuatro capítulos de investigación han sido publicados en revistas internacionales pertenecientes al Q1 dentro de la rama catalogada como *Forestry*. Para su presentación en este documento, han sido formateados, manteniendo su estructura a excepción del área de estudio, que es común en todas ellos, detallada en el capítulo 3, y se mantiene el idioma en el que fueron publicados, en todos los casos es inglés.

El capítulo 5.1, fue publicado en 2015 en la revista *Applied geography* bajo el título *Evaluation of forest cover change using remote sensing techniques and landscape metrics in Moncayo Natural Park (Spain)*. En él se aborda el primer objetivo específico, analizando los cambios producidos en la cubierta forestal del Parque mediante análisis de imágenes de satélite y la aplicación de índices de Ecología del Paisaje.

El capítulo 5.2, fue publicado en 2016 en la revista *Frontiers in Plant Science* bajo el título *Living on the Edge: Contrasted Wood-Formation Dynamics in Fagus sylvatica and Pinus sylvestris under Mediterranean Conditions*. En él se aborda el segundo objetivo y se analiza el crecimiento intra-anual y la duración del periodo de crecimiento de las hayas y pinos silvestres en los límites altitudinales bajo y alto dentro del área de estudio.

El capítulo 5.3, fue publicado en 2019 en la revista *European Journal of Forest Research* bajo el título *Spatial patterns of climate-growth relationships across species distribution as a forest management tool in Moncayo Natural Park (Spain)*. En él, se identifican los factores climáticos que afectan al crecimiento de hayas, pinos y rebollos a lo largo del gradiente climático presente y se relaciona con la variabilidad climática de cada lugar, pudiendo modelar espacialmente las relaciones clima-crecimiento. En este capítulo se desarrollan el segundo, tercer y cuarto objetivo específico.

El capítulo 5.4, fue publicado en 2019 en la revista *Forest Ecology and Management* bajo el título *Modeling tree-growth: Assessing climate suitability of temperate forests growing in Moncayo Natural Park (Spain)*. En él se predice espacialmente el crecimiento potencial de cada especie forestal. Mediante la aplicación de modelos con base climática, se generan cartografías de idoneidad climática para el crecimiento de hayas, pinos y rebollos, completando así los dos últimos objetivos específicos de la presente tesis.

# CAPITULO 3

# ÁREA DE ESTUDIO

# 3. Área de estudio

## 3.1. El Parque Natural del Moncayo

El área de estudio en la cual se enmarca la tesis corresponde al Parque Natural del Moncayo, que forma parte del Catálogo de Espacios de la Red Natural de Aragón y que se localiza en el extremo centro-occidental de la provincia de Zaragoza (41°47′17″N, 1°50′18″O), en la comarca de Tarazona y el Moncayo (Figura 3.1).

Los límites del área de estudio coinciden con los límites del propio Parque Natural, figura mediante la cual este espacio está protegido y puede ser gestionado por la administración competente. El parque Natural tiene una extensión de 11.144 hectáreas y el rango de altitud varía desde los 850 m hasta los 2.314 m. Este territorio es uno de los espacios naturales protegidos más emblemáticos y característicos de la Red Natural de Aragón (Ley 12/2004, de 29 de diciembre). Desde su creación, este espacio ha sido sometido a diversos cambios en su catalogación, régimen de protección y extensión de territorio protegido. Fue uno de los primeros espacios protegidos declarados oficialmente en el territorio español, ya en 1927 fue catalogado como "Sitio Natural de Interés Nacional" para más adelante, en 1978, ser declarado "Parque Natural de la Dehesa del Moncayo". Posteriormente en 1998, alcanzó la denominación definitiva de "Parque Natural del Moncayo", bajo la ley 6/1998, de 19 de mayo, de Espacios Naturales Protegidos de Aragón.

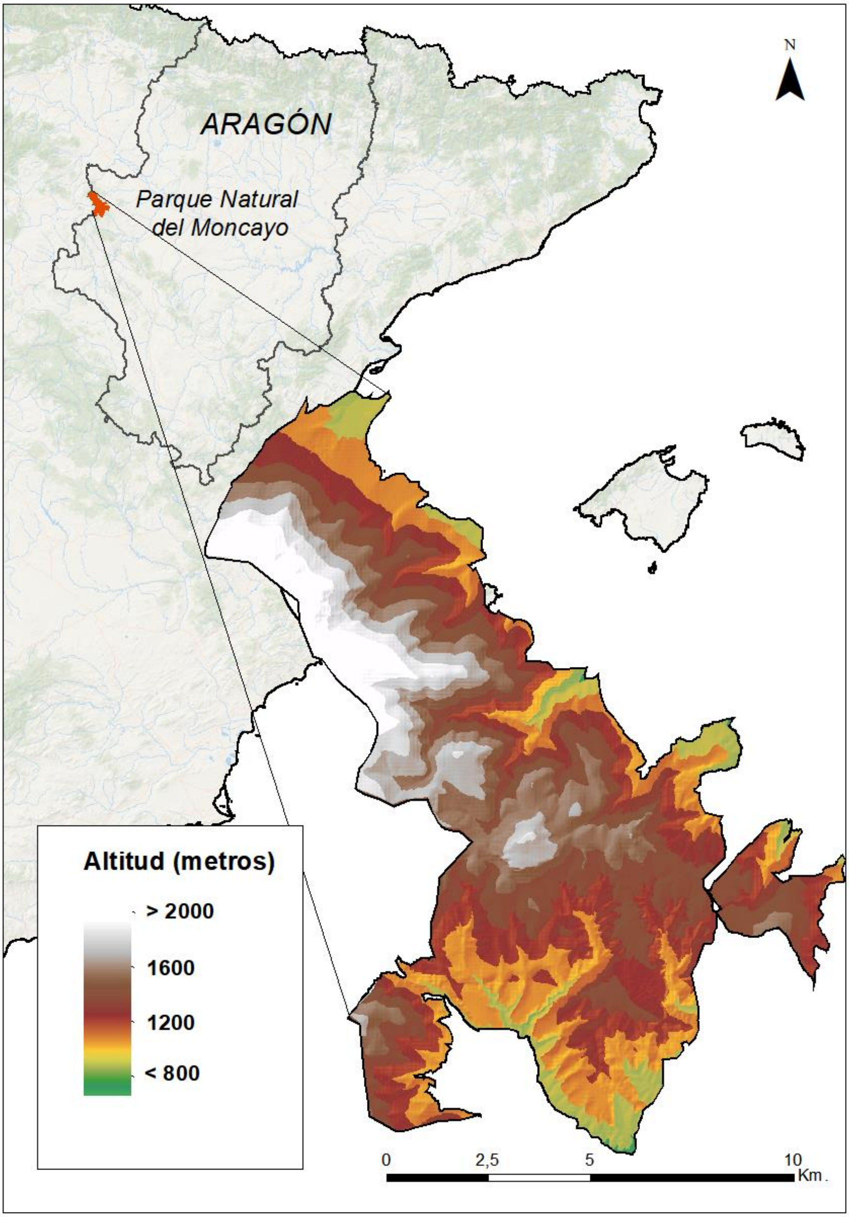


*Figura 3.1 Mapa de localización del Parque Natural del Moncayo y rango de elevaciones*

*Figura 3.2. Vista panorámica de la cara norte del macizo del Moncayo con el Barranco de Castilla en el centro, límite entre la provincia de Soria y Zaragoza*

Estas declaraciones han conllevado la ampliación en la superficie protegida, pasando de las iniciales 1.500 hectáreas del denominado "Monte del Moncayo" a las 9.848 hectáreas que alcanzaron protección en 1998, para alcanzar las actuales 11.144 hectáreas, que hoy forman parte del Parque Natural, tras su ampliación en 2007 a petición de los ayuntamientos de Talamantes y Purujosa. Además, en él confluyen otras figuras de protección como la de Lugar de Importancia Comunitaria (LIC) Sierra del Moncayo (LIC ES2430028) y Zona de Especial Protección para las Aves (ZEPA) Sierra del Moncayo-Los Fayos-Sierra de Armas (ZEPA 0000297). Además, han sido propuestos varios Lugares de Interés Geológico como: los Circos glaciares de San Miguel y San Gaudioso en Tarazona, Cueva Hermosa y Peñas Albas en Calcena o Cueva de los Rincones y el Barranco de Valcongosto en Purujosa.

En relación con las figuras de protección, la conservación de este espacio se ha visto reforzada con la aprobación de varias herramientas relacionadas con la gestión, encaminadas a la conservación de los valores que promovieron su inclusión en la Red Natural de Aragón. Así en el año 1998, se aprueba la primera de ellas, tras un intenso proceso de elaboración que concluye con el primer Plan de Ordenación de los Recursos Naturales (PORN - DECRETO 73/1998, de 31 de marzo (BOA 13/04/1998)) para el espacio, que servirá de base para el diseño y aprobación del Plan Rector de Uso y Gestión (PRUG - DECRETO 177/2014, de 4 de noviembre (BOA de 17/11/2014)) del Parque en 2002, actualizado en el 2014. Estos planes son revisados cada cierto tiempo con el objetivo de continuar las principales líneas de gestión del espacio protegido, en este sentido, los resultados de esta tesis pretenden aportar información útil para la gestión forestal de este espacio.

Bajo este contexto administrativo se engloba un territorio montañoso con carácter singular, de rasgos muy diferenciados del resto de relieves, morfologías y paisajes circundantes. Desde su especial configuración topográfica, siendo un macizo montañoso aislado entre los ambientes esteparios del centro de la Depresión del Ebro y los más continentalizados de la meseta castellana en su sector oriental, hasta su identidad como territorio fronterizo entre ecosistemas contrastados y refugio natural de elementos bióticos propios de ambientes eurosiberianos, frecuentes en cordilleras alejadas como la cantábrica o los pirineos. Por otra parte, su orientación, estructura geológica y composición litológica, le han dotado a lo largo del tiempo de rasgos favorecedores para la génesis y funcionamiento de procesos glaciares y periglaciares (Figura 3.3), que han dejado su huella a través de morfologías fácilmente reconocibles (Pellicer 2000). Además, su gradiente altitudinal tan acentuado ha definido sus rasgos climáticos a lo largo del tiempo y hoy en día es el principal factor de la distribución de la vegetación en altura, una vez que la influencia del hombre en el manejo de la cubierta vegetal va dejando paso a la dinámica natural.

*Figura 3.3. Circo glaciar de San Miguel*

Su situación hace que sea un espacio de transición entre el ambiente eurosiberiano y el más puramente mediterráneo matizado por el efecto de montaña, pudiéndose categorizar como ecotono. En estos espacios, conviven especies de ambos ambientes, así como endemismos, siendo zonas de elevada biodiversidad y también constituyendo muchas veces uno de los límites de distribución de las especies, lo que le otorga valores excepcionales desde el punto de vista biogeográfico y ecológico (Longares 2004). Estas características (carácter transicional, límite de distribución, singularidad y/o fragilidad de sus especies y comunidades) lo convierten en un espacio muy interesante para la detección de señales de cambio global a través del estudio de la respuesta de la vegetación al clima

## 3.2. La vegetación

El Moncayo tiene una gran disimetría entre sus vertientes; la soriana, de topografía tendida y orientación suroeste, y la zaragozana, fuertemente escarpada y con exposición nordeste. En esta última vertiente se concentran gran parte de los factores que generan variedad y diversidad en su composición vegetal: un marcado desnivel topográfico entre la depresión del Ebro y su cumbre, un fuerte gradiente altitudinal en cuanto a temperaturas y precipitaciones, una clara exposición a las influencias atlánticas, importantes diferencias edáficas y un largo historial de uso por parte del hombre. Ese fuerte gradiente altitudinal de temperaturas y precipitaciones provocado por la topografía, hace que la vegetación se encuentre escalonada en los llamados pisos de vegetación, inexistentes en otros puntos de similar latitud (Figura 3.4).

*Figura 3.4. Vista del Parque Natural del Moncayo desde el embalse de Lituénigo donde se aprecia la disposición de las comunidades vegetales en pisos de vegetación.*

En este sentido, se reconocen tres pisos de vegetación diferenciados, con discrepancias de la existencia o no de un cuarto piso, detallados a continuación (Longares 2004):

- Piso mesomediterráneo (Figura 3.5): es el más bajo de los pisos, llegando hasta los 1.000 m en la vertiente zaragozana y hasta los 1.200 m en la vertiente soriana, al ser esta más seca. Este piso está caracterizado por estar muy influido por la acción del hombre. Es constante la presencia de matorrales xerofíticos de sustitución con predominio de romero (*Rosmarinus officinalis* L.), tomillo (*Thymus vulgaris* L.) y aliaga (*Genista scorpius* L.) que ocupan el territorio potencial del coscojar (*Quercus coccifera* L.) hasta los 750 m y de la carrasca (*Quercus ilex* subsp. *Ballota* Desf.) entre los 600-1000/1300 m.

Esta última, al ganar altura, aparece combinada con quejigo (*Quercus faginea* Lam.) en algunos puntos, al mismo tiempo que en otros se encuentra mezclada con pinares fruto de diversas repoblaciones.

*Figura 3.5. Piso mesomediterráneo, vista desde el LIC Maderuela.*

- Piso supramediterráneo (Figura 3.6): la transición a este piso se produce a partir de los 900 m en la vertiente zaragozana y en torno a los 1.200 m en la soriana. En él se adentra el carrascal basófilo del anterior, aunque su área de distribución potencial se encuentra también ocupada por otras quercíneas, dominando entre éstas el rebollo (*Quercus pirenaica* Willd.), el cual aparece acompañado por el roble albar (*Quercus petraea* (Matts.) Liebl.) de forma puntual. Sobre este piso en la vertiente zaragozana se extienden las hayas

(*Fagus sylvatica* L.), siendo la banda ocupada por éstas donde se distinguen rasgos eurosiberianos de cierta similitud con el territorio vasco-cantábrico (Bolós, 1989). Esta especie está ausente en la parte soriana, siendo este hecho un indicador biológico de la menor humedad atmosférica de esta vertiente (Uribe-Echebarría, 2002). Por último, señalar que en este piso se encuentran además muy presentes las repoblaciones de pinar, en especial de pino albar (*Pinus sylvestris* L.) y, en las zonas más altas, de pino negro (*Pinus uncinata* Mill.).

*Figura 3.6. Piso supramediterráneo, vista donde se aprecia la sucesión de rebollo, haya y pino silvestre.*

- Piso oromediterráneo (Figura 3.7): la evolución hacia este piso se produce de forma paulatina en torno a los 1.600 m en la vertiente zaragozana y a los 1.700-1.800 en la soriana, donde el bosque comienza a perder importancia y da paso a los matorrales rastreros característicos compuestos por enebro (*Juniperus communis* L. *subsp. alpina* (Suter)) y piornales (*Cytisus balansae* subsp. *Europaeus* (G. López & C.E. Jarvis)) en sustratos silíceos y sabinares rastreros (*Juniperus sabina* L.) en suelos calcáreos.

*Figura 3.7. Piso oromediterráneo. Vista primaveral desde el pozo de San Miguel, localizado en la senda tradicional de ascenso a la cumbre del Moncayo.*

### 3.3. Las comunidades forestales

Las comunidades forestales que tienen mayor interés para el análisis son aquellas que tienen una mayor representatividad dentro del Parque Natural; dentro de las cuales destaca el hayedo. Esta formación encuentra en el Moncayo uno de sus límites de distribución meridional, por lo que desde el punto de vista biogeográfico se encuentra en el extremo de las condiciones ambientales adecuadas para su desarrollo. Este hayedo aparece sólo en la vertiente norte de la cordillera, entre 1.100 m y 1.700 m aproximadamente, ocupando una amplia zona en el interior del Parque Natural. Esa zona ocupada por el hayedo posee un clima local más húmedo no sólo por el predominio de las laderas umbrías, que reciben menos insolación, sino por estar expuesta al aire marítimo ascendente que genera frecuentes nieblas que ocupan este intervalo altitudinal (Figura 3.8).

*Figura 3.8. Niebla típica cubriendo la cima del Moncayo.*

La media de precipitaciones que se registran en este territorio, 980 mm anuales, no son suficientes en estas latitudes como para mantener esta formación boscosa, más aún cuando son frecuentes largos periodos sin precipitación, momento en el que las hayas se nutren de los frecuentes bancos de niebla (Villar et al. 1990; Longares 2004). Prueba de esta falta de precipitaciones y humedad son los troncos de las hayas, que mientras en otras regiones más húmedas están recubiertos de líquenes, aquí las cortezas están casi desnudas, presentando un aspecto grisáceo (Uribe-Echebarria 2002). Desde el punto de vista florístico, éste es un bosque muy pobre en especies (Figura 3.9), lo que probablemente se debe a que la competencia por el agua que se establece entre las raíces del árbol dominante y las de las plantas herbáceas hace difícil la vida de estas últimas (de Bolos 1989).

*Figura 3.9. Interior del hayedo.*

Otro grupo de especies forestales de interés son las pertenecientes al grupo de las quercíneas: el rebollo (*Quercus pyrenaica*), el roble albar (*Quercus petraea*) y la encina (*Quercus ilex* subsp. *ballota*). El rebollo es un árbol que a nivel mundial tiene un área de distribución muy pequeña, que va del norte de África al suroeste de Francia, con su máxima representación en la mitad occidental de la Península Ibérica (Nieto Quintano et al. 2016). En Aragón cuenta con algunas de sus mejores masas dentro del Parque Natural del Moncayo y entorno próximo, donde se encuentra a partir de los 900 m hasta los 1400 m de altitud. Esta interesante masa, cuya situación deriva del uso ganadero al que se sometió este territorio en forma de dehesa, que, una vez abandonado, permitió su regeneración, presenta problemas de envejecimiento dada la avanzada edad de los ejemplares que la componen (Uribe-Echebarria 2002). Esta situación ha hecho que los gestores del Parque Natural del Moncayo hayan promovido la realización de cortas selectivas para asegurar la persistencia de esta masa (Arrechea 2002). Tras el descenso del uso ganadero, el rebollo forma hoy extensos bosques en los tramos silíceos de la base del Macizo. Dichos rebollares y sus matorrales de sustitución, se extienden por las dos vertientes del macizo, ascendiendo más en altitud por la soriana (hasta unos 1.600 m) y menos por la aragonesa (hasta los 1.200 m), dado que esa cota está ampliamente colonizada por hayas y pinos.

El robledal de *Quercus petraea* es un bosque relicto, limitado actualmente como masa forestal al Monte de la Mata (Figura

3.10), dentro del Parque Natural. Esta reliquia de tiempos más húmedos que se dispersó otrora hacia tierras más meridionales, también ha sido altamente transformada por la explotación forestal privada a la que ha estado sometida, en la actualidad de una intensidad sensiblemente menor, sobreviviendo gracias a su gran capacidad de rebrote tras la tala.

*Figura 3.10. Monte de la mata en primavera.*

La encina se distribuye por las sierras de los alrededores del macizo del Moncayo, envolviendo a este por su base. Esta especie se adapta a suelos pobres y pedregosos y a condiciones de sequedad, tanto en aire como en el suelo, por lo que un aumento de estos bosques podría indicar una bajada generalizada en las condiciones de humedad de la zona (Figura 3.11).

*Figura 3.11. Encina creciendo bajo una gran roca con una curiosa inscripción.*

En la zona de estudio se observa como en la mitad septentrional del macizo, de naturaleza silícea, los encinares se sitúan inmediatamente por debajo del piso de los rebollares, fuera de los límites del Parque, mientras que en la mitad meridional está mucho más presente.

Finalmente, el resto de especies forestales que pueblan el Parque Natural del Moncayo de forma significativa son del genero *Pinus*, siendo todas ellas introducidas (Figura 3.12). Hacia 1920, las laderas del Moncayo presentaban una cubierta forestal muy escasa, por lo que se emprendió su repoblación con especies del genero *Pinus* (Pellicer 2000). Hasta entonces, no existía constancia alguna de presencia de pinos en esta zona (Uribe-Echebarria 2002), tan solo una conífera arbórea, el tejo (*Taxus baccata* L.), y varias arbustivas como enebros y sabinas del género *Juniperus*, vivían de forma espontánea en la zona. Entre estas repoblaciones destaca de forma especial las de pino albar (*Pinus sylvestris*) en zonas donde la especie dominante tendría que ser fagácea o quercínea. Esta especie está perfectamente adaptada desde los 900 m hasta los 1600 m, apareciendo por encima de este umbral ya solo en pequeños rodales, ganando peso la presencia de pino negro (*Pinus uncinata*). Estos últimos, fruto de un ensayo de replantación en altura en los años 60 lograron sobrevivir en los suelos relativamente profundos de la zona de morrenas, bajo los circos glaciares, donde hoy forman densos y oscuros pinares, asilvestrándose localmente en márgenes y taludes de pistas (Uribe-Echebarria 2002). Además de éstas, se realizaron repoblaciones con más especies de pinos, donde el pino negral

(*Pinus nigra* Arnold) fue la especie más utilizada, a pie de la montaña, donde además del negral también se empleó el pino carrasco (*Pinus halepensis* Mill.) y en las zonas de glacis con suelo arenoso, donde se utilizó el pino marítimo (*Pinus pinaster* Ait.).

*Figura 3.12. Vista del mosaico de pinares de repoblación entre los rebollares de la zona baja del Moncayo, con presencia de hayas en el primer plano.*

# CAPITULO 4

# METODOLOGÍA

## 4. Metodología

En este capítulo se expondrán de forma general las principales técnicas metodológicas utilizadas, que están descritas con mayor detalle en dentro de cada capítulo junto con los materiales utilizados.

### 4.1. Técnicas de teledetección e índices de ecología del paisaje.

Esta sección corresponde a la metodología aplicada en el capítulo 5, correspondiente al artículo *"Evaluation of forest cover change using remote sensing techniques and landscape metrics in Moncayo Natural Park (Spain)"*. En este artículo, se emplearon técnicas de Teledetección como la creación de neocanales y la clasificación supervisada para el análisis temporal de cambios en las cubiertas forestales.

El uso de la teledetección y sus técnicas para el estudio de temáticas de índole ecológica como la generación de cartografía de cambios en la ocupación del suelo está ampliamente contrastado, siendo numerosos los trabajos de investigación dedicados a la caracterización de la dinámica de la vegetación (Xie et al. 2008; Brink and Eva 2009; Kim et al. 2014; Devries et al. 2016). El uso de imágenes de satélite requiere de una corrección radiométrica para poder ser comparables entre ellas y ser usadas para crear productos intermedios de alto nivel como neocanales (Chander et al. 2009). La creación de neocanales (p.ej. índices de vegetación, transformada *tasseled cap* o componentes principales) implica la generación de nuevas bandas de información a partir de las ya existentes, reduciendo información redundante y obteniendo información no visible en los datos originales (Wright et al. 1980) (Figura 4.1).

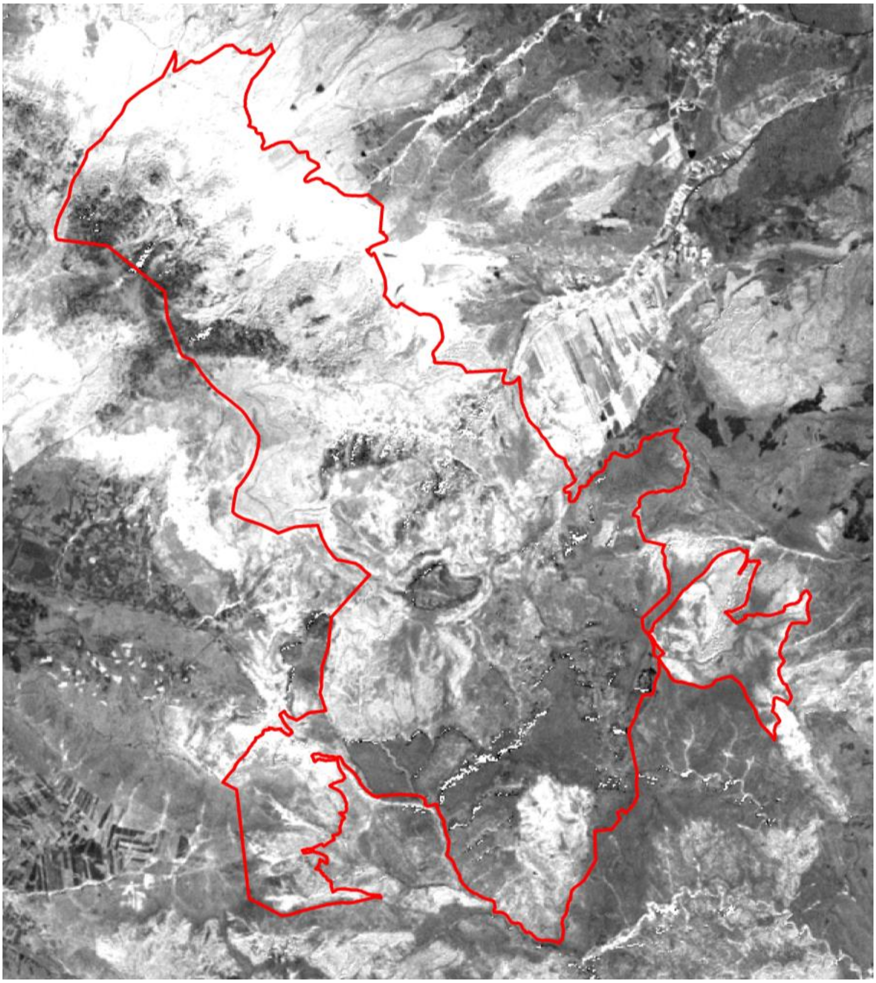


*Figura 4.1. Transformación Tasseled cap 2 "Greeness" de la zona de estudio. Esta capa está correlacionada con el vigor vegetal.*

La clasificación supervisada es un proceso mediante el cual se extraen clases o categorías diferenciadas en base a una leyenda predefinida a través de los datos obtenidos por los satélites (Xie et al. 2008). Es decir, es el proceso por el cual una imagen multibanda se convierte en otra imagen, del mismo tamaño y características de las originales, con la diferencia de que los niveles digitales que definen cada pixel no tiene relación con la radiancia detectada por el sensor, sino que se trata de una etiqueta que identifica la categoría asignada a este pixel (Chuvieco and Chuvieco Salina 2010). Se optó por clasificar las imágenes bajo el método supervisado, que parte de la premisa del conocimiento previo del terreno para la selección de las zonas de entrenamiento, el cual puede ser apoyado por la consulta de fotografías aéreas o cartografías auxiliares como mapas de ocupación del suelo o mapas forestales. Dentro de los métodos para llevar a cabo la clasificación, se utilizó el de máxima verosimilitud, que asume una distribución normal del patrón espectral de cada clase (Xie et al. 2008) y es comúnmente usado en la clasificación de cubiertas forestales. Finalmente, la clasificación fue mejorada con la aplicación posterior de lo que se conoce como clasificación experta, en la cual se aplican un conjunto de reglas con la finalidad de mejorar la distribución espacial de las cubiertas o solucionar errores conocidos, como ejemplo, no puede haber pixeles clasificados como vegetación de ribera aquellos que estén situados a más de 500 m de un rio o arroyo.

La aplicación de métodos cuantitativos en Ecología del paisaje se realiza mediante el uso de los denominados índices de paisaje. Los índices de paisaje aportan datos cuantitativos sobre la composición y la configuración de los paisajes, la proporción de cada cubierta del suelo o la superficie y la forma de los elementos del paisaje. Además, los índices de paisaje permiten la comparación entre distintas configuraciones paisajísticas de la misma área en distintos momentos temporales (Farina 2006). Los índices fueron seleccionados para caracterizar la fragmentación, conectividad y heterogeneidad del paisaje del área de estudio, que son tres conceptos básicos de la ecología del paisaje que permiten definir el patrón de una unidad paisajística y caracterizar los cambios producidos en la misma.

## 4.2. Estudios de xilogénesis

Esta sección corresponde a la metodología aplicada en el capítulo 6, correspondiente al artículo *"Living on the Edge: Contrasted Wood-Formation Dynamics in Fagus sylvatica and Pinus sylvestris under Mediterranean Conditions"*, donde se realizó un seguimiento de la xilogénesis de hayas y pinos en diferentes altitudes durante un periodo de tres años.

Los estudios de xilogénesis o de formación de madera consisten en monitorizar el crecimiento radial (secundario) de los arboles durante todo su periodo de crecimiento de forma sistemática, en este caso cada dos semanas. Para monitorizar el crecimiento de los árboles, se extraen muestras del árbol mediante un dispositivo trephor (Rossi et al. 2006a), llamadas comúnmente microcores, las cuales contienen madera, corteza y cambium vascular (Figura 4.2). El cambium es el meristema lateral que forma nuevas células, haciendo que el árbol crezca en grosor (Larson 1994).

*Figura 4.2. Muestreo con Trephor: detalle del microcore extraído, heridas producidas durante el muestreo ya cicatrizadas y fotografía microscópica de una muestra de Pinus sylvestris.*

La actividad cambial es la que asegura la vida perenne de los arboles mediante el cambio periódico de los tejidos del xilema y del floema (Plomion et al. 2001). El curso anual de la actividad cambial está íntimamente relacionado con las condiciones climáticas, como ejemplo, en regiones tropicales, los arboles pueden crecer durante todo el año de forma ininterrumpida, pero fuera de estas regiones, el crecimiento se produce durante unos meses, determinados por las condiciones ambientales tales como temperatura, precipitación, fotoperiodo y otras influencias (Begum et al. 2013).

Este tipo de estudios de monitorización de la xilogénesis ha aumentado durante las últimas décadas, estando la mayoría de ellos relacionados con analizar los impactos de los cambios en el clima sobre la duración y los momentos clave en relación al crecimiento de los bosques (Cherubini et al. 2003; Fonti et al. 2010; Rossi et al. 2013, 2016; von Arx et al. 2016). Actualmente, el uso de estas técnicas está extendido, habiendo múltiples trabajos previos enfocados en hayedos (Čufar et al. 2008b; Prislan et al. 2013; Kraus et al. 2016), pinos silvestres (Rathgeber et al. 2011a; Panayotov et al. 2013; Cuny and Rathgeber 2016), incluso en España (de Luis et al. 2007a; Linares et al. 2009; Camarero et al. 2010).

### 4.3. Dendroclimatología

Esta sección corresponde a la metodología aplicada en el capítulo 7, correspondiente al artículo "*Spatial patterns of climate-growth relationships across species distribution as a forest management tool in Moncayo Natural Park (Spain)*" y en el capítulo 8, correspondiente al artículo "*Modeling tree-growth: Assessing climate suitability of temperate forests growing in Moncayo Natural Park (Spain)*, en los cuales se trabaja con una red dendrocronológica distribuida por la zona de estudio.

### *4.3.1. Dendrocronologia*

La dendrocronología es una disciplina científica dotada de un conjunto de técnicas y métodos para datar los anillos de crecimiento anuales e interpretar la información que contienen con el fin de diferenciar los factores que han influido en su crecimiento. Como se ha visto en la sección anterior, el cambium es muy sensible a los factores ambientales, quedando registrados en las características físicas y químicas de los anillos (Fritts 1972). Estas características, como son el grosor del anillo, la proporción de madera temprana y tardía o la densidad, pueden ser medidas, creando una secuencia de datos anuales con los que se construyen las cronologías.

Para la extracción de este tipo de información se puede realizar mediante la extracción de testigos de crecimiento, también llamados cores (Figura 4.3) mediante el uso de barrenas de Pressler, no siendo necesario cortar el árbol para obtener la información

*Figura 4.3. Extracción de muestras con barrena Pressler. Detalle de muestras de Pinus sylvestris (arriba) y Fagus sylvatica (abajo) listo para ser datado y medido.*

En el Parque Natural del Moncayo se ha creado una densa red dendrocronológica, de un total de 49 puntos de muestreo, que recoge la variabilidad de ambientes sobre los cuales se desarrollan las especies objeto de estudio, tal y como se muestra en la Figura 4.4.

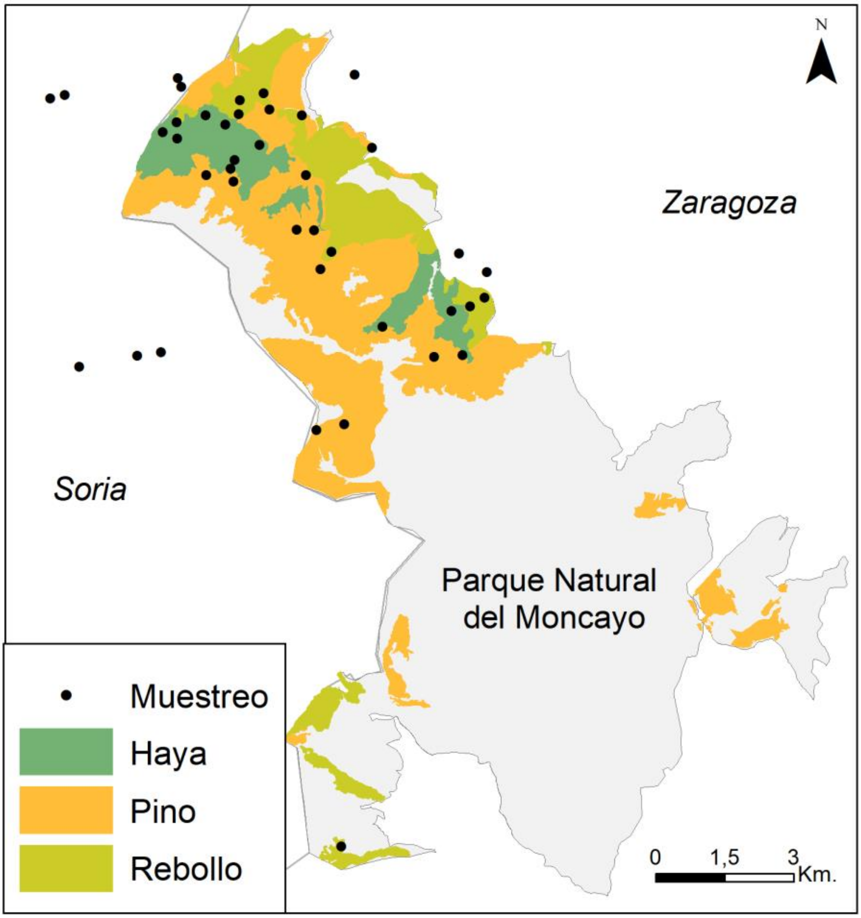


*Figura 4.4. Mapa localización de las cronologías recolectadas en el entorno del Moncayo. Las especificaciones de cada punto de muestreo están detalladas en la tabla S5.3.1 y S5.4.1.*

### 4.3.2. *Base de datos climática*

Para realizar un buen análisis dendroclimatológico es necesario contar con unos datos climáticos de calidad y referidos al lugar donde los árboles se desarrollan. Ante la dificultad de contar con estaciones meteorologías en cada punto de muestreo, y la no adecuación de los datos de estaciones cercanas, ya que están lejos y a una menor altitud, se optó por crear un grid climático diario de alta resolución espacial (200 x 200 m) y temporal (1951-2016) para el Parque Natural del Moncayo, usando el paquete de R *reddPrec* (Serrano-Notivoli et al. 2017c) basado en el método de reconstrucción desarrollado en Serrano-Notivoli et al. (2017a). Las variables climáticas utilizadas fueron precipitación, temperatura máxima y temperatura mínima, creando agregados mensuales, estacionales y anuales para el análisis.

### 4.4. Modelización y análisis estadístico

Esta sección corresponde a la metodología aplicada en el capítulo 7, correspondiente al artículo "*Spatial patterns of climate-growth relationships across species distribution as a forest management tool in Moncayo Natural Park (Spain)*" y en el capítulo 8, correspondiente al artículo "*Modeling tree-growth: Assessing climate suitability of temperate forests growing in Moncayo Natural Park (Spain),* en los cuales se usan diferentes modelos estadísticos para espacializar las relaciones clima-crecimiento en el primero de los casos, y para espacializar el crecimiento potencial de cada especie en el otro.

En el caso del capítulo 7, se utilizaron los Modelos Aditivos Generalizados (GAM), extienden el modelo lineal para acomodar las variables respuestas que no siguen una distribución normal, bajo un enfoque unificado (Hastie and Tibshirani 1986). Estos son modelos que incorporan regresiones no-paramétrica y la no-linealidad de las variables independientes.

En el caso del capítulo 8, se utilizaron los Modelos Lineares Mixtos Generalizados (GLMM), que son modelos de regresión lineal en los cuales las variables dependientes son combinadas de forma lineal y que incluyen además el efecto de factores aleatorios que permiten considerar en el análisis la variabilidad asociada al comportamiento individualizado de cada árbol.

# CAPITULO 5

# RESULTADOS

## 5. Resultados

A continuación, se presentan los resultados de la elaboración de esta tesis mediante los artículos que han sido publicados o están en proceso de revisión. La relación de autores, año de publicación, titulo, revista y detalles de la publicación se detallan a continuación:

- Martínez del Castillo, E., García-Martin, A., Longares, L. A., & de Luis, M. (2015). Evaluation of forest cover change using remote sensing techniques and landscape metrics in Moncayo Natural Park (Spain). *Applied Geography*, 62, 247–255. https://doi.org/10.1016/j.apgeog.2015.05.002

- Martínez del Castillo, E., Longares, L. A., Gričar, J., Prislan, P., Gil-Pelegrín, E., Čufar, K., & de Luis, M. (2016). Living on the Edge: Contrasted Wood-Formation Dynamics in *Fagus sylvatica* and *Pinus sylvestris* under Mediterranean Conditions. *Frontiers in Plant Science*, 7, 370. https://doi.org/10.3389/fpls.2016.00370

- Martínez del Castillo, E., Longares, L. A., Serrano-Notivoli, R., Sass-Klaassen, U.G.W. & de Luis, M. (2019). Spatial patterns of climate-growth relationships across species distribution as a forest management tool in Moncayo Natural Park (Spain). *European Journal of Forest Research*

https://doi.org/10.1007/s10342-019-01169-3

- Martínez del Castillo, E., Longares, L. A., Serrano-Notivoli, R., & de Luis, M. (2019). Modeling tree-growth: Assessing climate suitability of temperate forests growing in Moncayo Natural Park (Spain). *Forest Ecology and Management*, 435, 128–137. https://doi.org/10.1016/j.foreco.2018.12.05

## 5.1. Evaluation of forest cover change using remote sensing techniques and landscape metrics in Moncayo Natural Park (Spain).

### *5.1.1. Introduction*

An ecotone is a transitional area between two neighbouring biomes that contain different vegetation types (Risser 1995a). These areas contain more biodiversity than other adjacent areas. In addition, they are more sensitive to environmental disturbances and are, therefore, interesting locations for studies of vegetation dynamics. In the ecotones, many species are at their distributional limits; therefore, ecotones are regarded as a sensitive monitor of global climatic change (Risser 1995a; de Andrés et al. 2015).

Moncayo Natural Park is a mountain ecotone in a transitional zone between the Eurosiberian and Mediterranean biogeographical regions (Longares 2004). Within a small area, this hotspot contains an important assortment of vegetation types, such as beech, sessile oak, Pyrenean oak, Holm oak, Scots pine, European black pine, mountain pine, maritime pine, birch, gallery forests, junipers, other shrubs, mixed Mediterranean scrubs and mountain pastures.

This area, like the majority of Mediterranean mountains, has been highly influenced by resource exploitation over time because the Mediterranean landscape is one of the most modified places on Earth (Myers et al. 2000). However, the intense use of natural resources by rural societies until the first half of the 20th century has been followed by an important decrease in traditional uses since then (Lasanta et al. 2006; Heredia-Laclaustra et al. 2013). In the last three decades, land has been mostly abandoned in terms of human uses, and as a result, ecosystems have changed and evolved naturally (García-Ruiz et al. 1996). Some of these ecosystems have high natural values and protection through forest management actions, and a protection policy is necessary to guarantee the preservation of natural values. Forest ecosystems are especially important not only for sustaining biodiversity; they also have important functions from a social and economic point of view (Çakir et al. 2008). This area was declared to be an area of environmental protection in 1927 and renamed as a natural park in 1978 due to the importance of Moncayo mountain biodiversity and the presence of one of the southernmost sessile oak and beech forest stands in Europe. Thereby, the study of forest cover dynamics in an objective manner and with a replicable procedure in this area is necessary to evaluate whether management plans applied for natural conservation are working correctly.

The generation of land-cover cartography from satellite image processing is one of the most important and contrasted remote sensing applications. From this cartography, it is possible to obtain and analyse the spatial pattern of vegetation cover in a territory. This information has been used in the field of landscape ecology to study the territorial spatial pattern, which helps to understand many ecological processes with a strong spatial component. From the point of view of biodiversity conservation and sustainable development, considering these processes is a fundamental requirement for applying spatial management, for establishing administrative rules and for designing strategies for nature conservation

(Turner 2005). In addition, monitoring forest cover change through time to define the forest structure and dynamics has become increasingly important as a resource for forest management for determining the wealth of biodiversity (Baskent and Jordan 1996; Esbah et al. 2010).

Remote sensing techniques have many advantages over other traditional techniques based on field work or only in geographical information systems (GIS) such as a visualization of the global Earth surface; the acquisition of information in non-visible zones of the spectrum; and the use of different scales, high frequency and homogeneous information, historical records and low-cost information (Chuvieco and Chuvieco Salina 2010; Pôças et al. 2011a). Considering these characteristics, remote sensing has become one of the most powerful and useful tools for studying global processes such as global warming (Lillesand and Kiefer 1994; Chuvieco and Justice 2008). In this context, Landsat images have been used the most for determining forest cover and measuring forest cover change (Townshend et al. 2012). Detecting land cover change in mountainous areas using land-cover cartography from satellite imagery is the principal aim of studies such as Çakir et al., (2008), Keleş, Sivrikaya, Çakir, & Köe, (2008) or Pôças et al.,(2011), and the knowledge of these changes has been useful to forest management of protected areas (Jones et al. 2009; Kim and Daigle 2011; Shen et al. 2013).

Conversely, landscape ecology has developed a simple nomenclature (Forman 1995) and some quantitative indices to describe and analyse the landscape pattern (Haines-Young and Chopping 1996), which have permitted the quantification of the fragmentation, connectivity and diversity of landscapes–three basic concepts for describing landscape structure. The ability to quantitatively describe the structure is a prerequisite for the study of landscape function and change (McGarical and Marks 1994). Several studies evidence the value of these indices for the evaluation of protected areas, Mediterranean forests and mountainous areas (Lasanta et al. 2006; Geri et al. 2010; Cohen et al. 2011; Pelorosso et al. 2011). In this context, many studies using remote sensing techniques and landscape ecology metrics can be found in the literature (Başkent and Kadioğullari 2007; Keleş et al. 2008; Terzioğlu et al. 2009; Teixido et al. 2010; Pôças et al. 2011b).

The aim of this work is to describe and analyse land cover changes in Moncayo Natural Park from 1987 to 2010 through quantitative landscape indices over land cover cartographies of both years obtained with a supervised classification of four Landsat images. Despite the ecological value of this natural park, it has never been studied before under this perspective. The results of this study can be useful for evaluating the strategies for nature conservation designed by forest managers during the period evaluated, and they are also vital to future management.

### *5.1.2. Materials and methods*

#### 5.1.2.1. Satellite imagery and data processing

Landsat Thematic Mapper (TM) satellite imagery was used to map land cover, focusing on forest classes, and to obtain a spatiotemporal analysis. Two images were used in the land cover classification per year, one recorded on each of the following dates: 14th April (104 Julian Day (JD)) 1987, 4th August (216 JD) 1987, 18th June (199 JD) 2010 and 22th October (295 JD) 2010. All images were obtained from the U.S. Geological Survey (USGS) with a 1-A pre-processing level (geometric correction in UTM WGS84 projection). The spring and autumn images of each year considered were combined with the summer images in order to improve discrimination in the classification of deciduous species because the variation of the spectral response over seasons is crucial for distinguishing different classes of deciduous trees.

All image processing, classification and GIS analyses were performed using ERDAS Imagine™ 2011 image processing software and ArcGIS 10. First, radiometric calibration and normalization were applied to ensure that the land cover changes detected were not artefacts from atmospheric conditions, illumination geometry or sensor degradation over time but actually represented changes to surface conditions (Coops et al. 2010). Radiometric calibration is indispensable for comparing the values of images of different sensors, dates or climatic conditions. An appropriate radiometric correction is needed to create high-level intermediate products as well as essential for removing noise and increasing the interpretability of image data (Xie et al. 2008; Chander et al. 2009). A Minnaert method based on Colby's equation was used to perform radiometric correction (Colby 1991). In this process, the relative data on surface reflectivity given in digital numbers was transformed into an absolute form in reflectance values, applying a topographic normalization to compensate for the varying solar illumination associated with the irregular shape of the terrain.

Second, several transformations and ratios were applied to the transformed images to improve interpretability, to reduce redundant information and to extract information not readily visible in its raw form (Song et al. 2001). These transformations were NDVI (normalized difference vegetation index); PCA (principal component analysis) using only PC1, PC2 and PC3; and TCT (tasseled cap transformation) using TC1 (brightness), TC2 (greenness) and TC3 (wetness) of the summer images and TC2 and TC3 of the spring and autumn images. In addition, one extra band was created for each year with the aim of extracting the variation in greenness among seasons, the PC2 of the TC2 bands. Finally, all bands were rescaled to a common range and stacked in a new multiband of 23-band images (Table 5.1.1).

**Table 5.1.1**: Multiband list. In bold, bands considered for the supervised classification.

| Band | YEAR 1987 | YEAR 2010 |
|---|---|---|
| 1 | Band 1. 216 JD | Band 1. 199 JD |
| 2 | Band 2. 216 JD | Band 2. 199 JD |
| 3 | Band 3. 216 JD | Band 3. 199 JD |
| 4 | Band 4. 216 JD | Band 4. 199 JD |
| 5 | Band 5. 216 JD | Band 5. 199 JD |
| 6 | Band 7. 216 JD | Band 7. 199 JD |
| 7 | Band 4. 104 JD | Band 4. 295 JD |
| 8 | Band 5. 104 JD | Band 5. 295 JD |
| 9 | Band 7. 104 JD | Band 7. 295 JD |
| 10 | NDVI. 216 JD | NDVI. 199 JD |
| 11 | NDVI. 104 JD | NDVI. 295 JD |
| 12 | CP1. 216 JD | CP1. 199 JD |
| 13 | CP2. 216 JD | CP2. 199 JD |
| 14 | CP3. 216 JD | CP3. 199 JD |
| 15 | CP1. 104 JD | CP1. 295 JD |
| 16 | CP2. 104 JD | CP2. 295 JD |
| 17 | CP3. 104 JD | CP3. 295 JD |
| 18 | TC1. 216 JD | TC1. 199 JD |
| 19 | TC2. 216 JD | TC2. 199 JD |
| 20 | TC3. 216 JD | TC3. 199 JD |
| 21 | TC2. 104 JD | TC2. 295 JD |
| 22 | TC3. 104 JD | TC3. 295 JD |
| 23 | CP2 of both TC2 | CP2 of both TC2 |

### 5.1.2.2. Digital Classification

The classification was implemented over a subset of the Landsat images that included the entire area of Moncayo Natural Park. Digital classification was implemented following the supervised methodology with training, classification and verification stages (Lillesand, 2006). Nine classification classes were defined according to forest cover and other formations present in this area: *Fagus sylvatica* (European beech), *Quercus pyrenaica* (pyrenean oak), *Quercus ilex* (holm oak), *Quercus petraea* (sessile oak), *Pinus sp.* (*Pinus sylvestris*, *Pinus uncinata*, *Pinus nigra* and *Pinus pinaster*), mixed shrub (>1 m.), mixed scrub (<1 m.), pastures and bare ground.

Several areas of interest (AOI) were defined for each category in the training stage using regional forest cartography at a scale of 1:50.000 and a 0.5-m spatial resolution digital air photograph composition as ancillary data, among other documents such as vegetation maps from natural park cartography. In addition, a field work campaign was designed to visit the areas with more complicated vegetation spatial patterns. During the field work, over 200 georeferenced control points were established using a submeter GPS receiver at different locations. After a preliminary analysis was performed with these AOI, the number of bands was reduced in order to avoid redundant information. This analysis was conducted using a Euclidean spectral distance algorithm. As a result, only eight bands were used in the classification stage (Table 5.1.1). Several statistical analyses such as spectral signatures diagram, frequency histograms, contingence matrix and transformed divergence were computed to ensure the reliability of the classification.

In the classification stage, every pixel was classified into one of the classes previously defined by the criteria. The classification was implemented using the supervised maximum likelihood classification method, which assumes a normal distribution of spectral pattern for each class (Xie et al. 2008). After this stage, an expert system classification was applied to improve the results. This method requires good knowledge about the study area, the spatial and biological limitation of species and the spatial distribution of classes (Stefanov et al. 2001). Thus, in accordance with the literature on the area (Longares 2004), maps and field work, some topographical rules with biological sense were introduced for some classes to improve the categorical separation and, therefore, the classification accuracy. The following rules were applied: (i) pixels under 1000 m a. s. l. classified as "*Fagus sylvatica*" would be reclassified into "*Quercus pyrenaica*" because beech is not present in this region below this elevation, (ii) pixels upper 1400 m a. s. l. classified as "*Quercus pyrenaica*" would be reclassified into "*Fagus sylvatica*", (iii) "*Quercus petraea*" class is restricted to a specific hill because this oak is not present in other areas and (iv) pixels upper 2000 m a. s. l. cannot be classified as any forest class.

Because all of the maps are generalized representations of reality and contain some error, accuracy assessments were conducted to determine how accurately our classification portrayed land cover (Foody 2002). Accordingly, an accurate assessment of the output classification is essential for understanding the limitations of the final maps.

The error analysis was based on statistical validation comparing each classified image with control points. Control points were taken from different sources: (i) GPS ground-based points captured in field work campaigns, (ii) the third national forest inventory data set, and (iii) random points generated with ArcGis 10 software over the regional forest cartography at a scale of 1:50.000 used in the training stage. Therefore, the number of points per category used was more than the minimum number recommended for accuracy assessment (50 samples per category) (Congalton 1991). For the accuracy analysis for 1987, the points were checked over the 1985 aerial photography and points located in changing areas were deleted. Ultimately, 583 and 641 control points were used for the 1987 and 2010 images, respectively.

Accuracy was assessed using a confusion matrix for each land cover cartography, including three measures of accuracy: overall classification accuracy, producer's accuracy and user's accuracy. Producer's accuracy indicates the probability of a reference pixel being correctly classified, and it is a measure of omission error, whereas user's accuracy is the probability of a classified pixel actually representing that category on the ground (Keleş et al. 2008). The Kappa coefficients, which are frequently used and supported by many authors as the standard method for measuring the precision of digital classification (Foody 2002), were calculated as well.

Finally, a majority filter (7x7 pixel window) was applied to the classified images in order to improve the legibility of these cartographies because classified data often manifest a salt-and-pepper appearance due to the inherent spectral variability encountered by a classifier when applied on a pixel-by-pixel basis (Lillesand and Kiefer 1994).

### 5.1.2.3 Landscape indices

The quantitative methods of landscape ecology are based on the application of landscape metrics (McGarical and Marks 1994). These metrics display numerical information about landscape composition, configuration and dimension as well as allow comparisons of different times and even help to recreate future scenarios (Subirós et al. 2006). Consequently, landscape metrics are widely used in literature to study large natural areas, forest evolution, natural parks or urban expansion among others (Başkent and Kadioğullari 2007; Çakir et al. 2008; Keleş et al. 2008; Terzioğlu et al. 2009; Pôças et al. 2011a).

Landscape metrics can be applied at three different scales: landscape, class and patch level (McGarical and Marks 1994). In this study only landscape and class metrics were used because patch-level metrics are not useful for our purposes. Ten landscape metrics were calculated for both years using FRAGSTATS software (McGarigal et al. 2012) to characterize landscape heterogeneity, fragmentation and connectivity (Table 5.1.2). Landscape metrics selection was made based on criteria provided in the literature (Başkent and Kadioğullari 2007; Çakir et al. 2008; Keleş et al. 2008; Terzioğlu et al. 2009; Geri et al. 2010; Teixido et al. 2010; Cohen et al. 2011; Pôças et al. 2011b).

**Table 5.1.2.** Summary table of landscape metrics (All formulas available in McGarigal & Marks, 1995).

| Index | Acronym | Analysis Level | Landscape structure concept |
|---|---|---|---|
| Total landscape area (ha) | TA | L | fragmentation |
| Percentage of Landscape | PLAND | C | fragmentation |
| Class area | CA | C | fragmentation |
| Number of patches | NP | L/C | fragmentation |
| Patch density (#/100 ha) | PD | L/C | fragmentation |
| largest patch index | LPI | L/C | fragmentation |
| Patch Area (mean) | AREA_MN | L/C | fragmentation |
| Euclidean Nearest Neighbour Distance (Mean) | ENN_MN | C | Connectivity |
| Patch Cohesion Index | COHESION | C | Connectivity |
| Shannon's diversity index | SHDI | L | Heterogeneity |

All methodological steps are summarized in Figure 5.1.1.

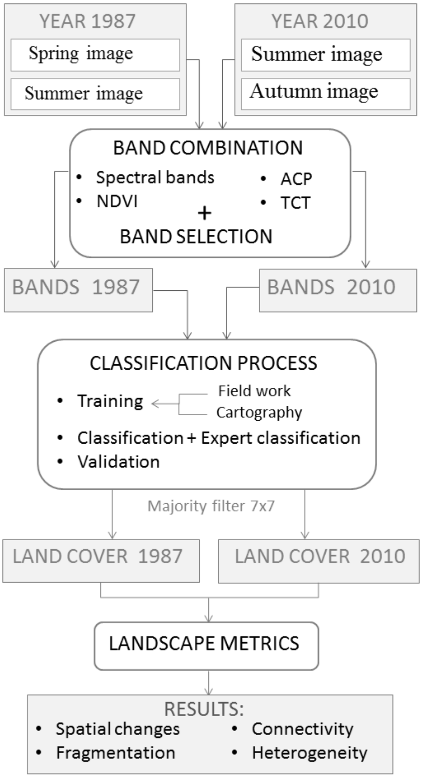


*Figura 5.1.1. Methodological scheme.*

### *5.1.3. Results*

#### 5.1.3.1 Accuracy assessment and digital classification

The overall accuracy of classification was 87.65% for the 1987 image and 84.56% for the 2010 image (Tables S5.1.1 and S5.1.2 in supplementary materials). These good results were confirmed by the Kappa coefficient (Table 5.1.3), reaching similar values: 0.86 and 0.82, respectively.

In terms of producer's accuracy all classes were above 80% with the exception of the pasture class in both years, the *Quercus ilex* class in 1987 and mixed shrub in 2010. The highest score is for the *Pinus* sp. class followed by the *Quercus pyrenaica* class in both years. User's accuracy scores were above 80% with the exception of the mixed shrub class for 1987 and the *Quercus pyrenaica* and mixed scrub classes in 2010. The best scores in user's accuracy were achieved by the *Fagus sylvatica* and pasture classes in both years (Tables S5.1.1 and S5.1.2 in supplementary materials). The Kappa coefficients were above 0.8 in all forest classes except for the *Quercus pyrenaica* class in 2010 (Table 5.1.3).

**Table 5.1.3.** Kappa's coefficient.

| KAPPA (K^) STATISTICS | Year 1987 | Year 2010 |
|---|---|---|
| *Fagus sylvatica* | 1.00 | 0.97 |
| *Quercus pyrenaica* | 0.84 | 0.75 |
| *Quercus ilex* | 0.82 | 0.83 |
| *Quercus petraea* | 0.98 | 0.93 |
| *Pinus sp.* | 0.95 | 0.87 |
| Bare ground | 0.81 | 0.78 |
| Mixed scrub | 0.82 | 0.76 |
| Pastures | 1.00 | 0.97 |
| Mixed shrub | 0.73 | 0.79 |
| Overall Kappa Statistics | 0.86 | 0.82 |

General vegetation spatial patterns are shown in classified maps (Figure 5.1.2). Moncayo Natural Park can be divided in two different parts in terms of vegetation. The northern part corresponds to higher altitudinal areas dominated by forest, whereas the southern part is dominated by mixed scrub and shrub.

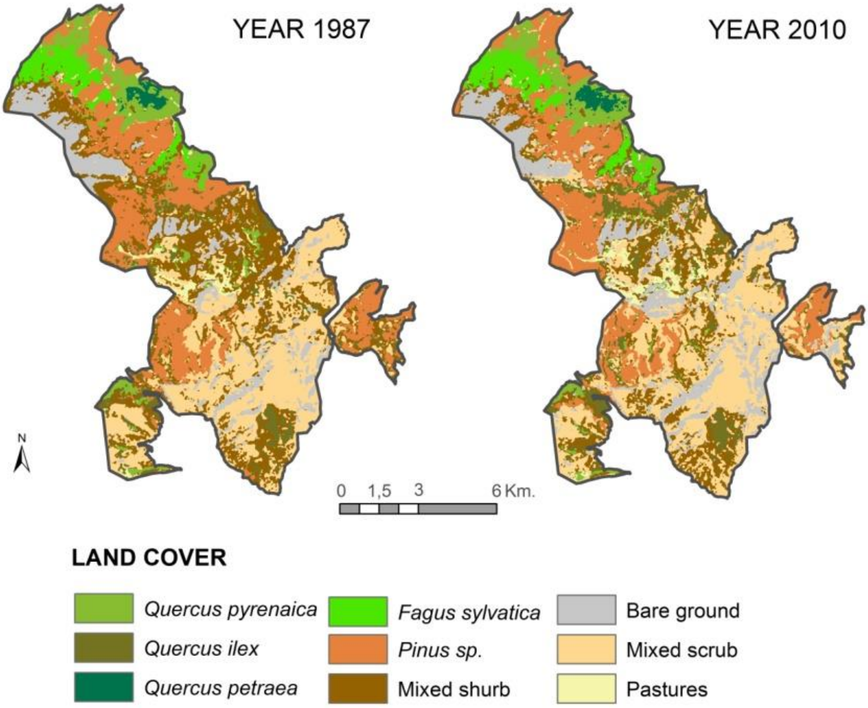


*Figura 5.1.2. Land cover type map of Moncayo Natural Park for the years 1987 (left) and 2010 (right).*

Total forested area was 37.8% of the territory in 1987, and 23 years later, it extended to 39.6%, increasing its surface by 1.7% (Table 5.1.4). Within the forested area, pines are the most expanded species occupying the large extension.

Notwithstanding these pines from old reforestations, currently, they are naturalized. Mixed shrub is the vegetation class with the greater changes.

**Table 5.1.4.** Landscape metrics at landscape level

| YEAR | TA | NP | PD | LPI | AREA_MN | SHDI |
|---|---|---|---|---|---|---|
| 1987 | 11226 | 3095 | 10.48 | 7.08 | 9.53 | 1.36 |
| 2010 | 11226 | 3677 | 12.46 | 5.44 | 8.02 | 1.38 |

### 5.1.3.2 Spatial analysis of forest structure

Landscape metrics provided valuable information about forest changes and specifically fragmentation, connectivity and heterogeneity measured at the landscape or class level.

At the landscape level the total number of patches increased from 3095 to 3677 between 1987 and 2010. As a consequence, patch density increased in the area (Table 5.1.5). In addition, the Largest Patch Index and Patch Mean Area decreased. As a result, these metrics indicate that the landscape has become more fragmented during this period. The last landscape level metric calculated showed that there is no important change in Shannon's diversity index, indicating that diversity or heterogeneity did not change over time.

**Table 5.1.5.** Total area per class and variation (ha)

| Classes | 1987 | | 2010 | | Variation (ha) |
|---|---|---|---|---|---|
| | ha | % | ha | % | |
| *Fagus sylvatica* | 460.63 | 4.10 | 498.99 | 4.44 | 38.36 |
| *Quercus pyrenaica* | 797.25 | 7.10 | 741.21 | 6.60 | -56.04 |
| *Quercus ilex* | 621.13 | 5.53 | 899.22 | 8.01 | 278.09 |
| *Quercus petraea* | 93.45 | 0.83 | 111.99 | 0.99 | 18.54 |
| *Pinus sp.* | 2280.93 | 20.31 | 2201.25 | 19.60 | -79.68 |
| Bare ground | 1142.12 | 10.17 | 1546.05 | 13.77 | 403.93 |
| Mixed scrub | 3037.28 | 27.05 | 3265.02 | 29.08 | 227.74 |
| Pastures | 210.31 | 1.87 | 289.31 | 2.57 | 79.00 |
| Mixed shrub | 2583.41 | 23.01 | 1673.47 | 14.90 | -909.94 |

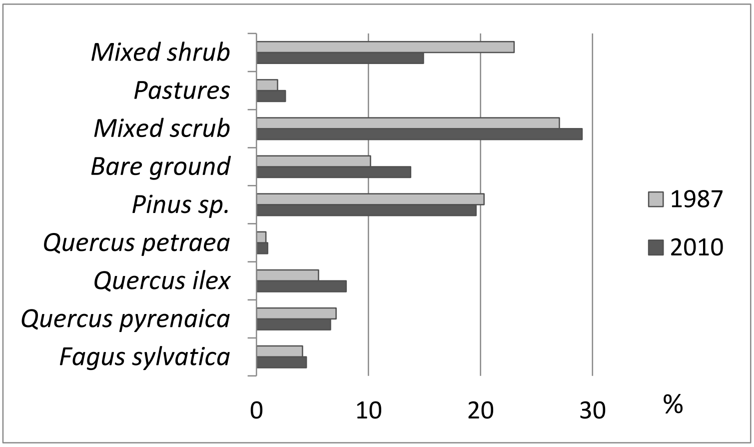


*Figura 5.1.3. Total area per class.*

At the class level, the metrics of area per class of land cover computed for each map are summarized in Table 5.1.5 and Figure 5.1.3. The results show the presence of each category and changes between years with mixed shrub as the class with the highest changes. The fragmentation indexes computed at the class level show significant changes within classes. However, the fragmentation gain is present in non-forest classes and in *Quercus petraea*; meanwhile, the other forest classes show a noticeable decrease in fragmentation (Tables 5.1.6 and 5.1.7). The Euclidean Nearest Neighbour Distance and Patch Cohesion Index reflect a widespread decrease in class connectivity. Among nine land cover classes, the most obvious change is the increased aggregation of *Quercus ilex*.

**Table 5.1.6**. Landscape metrics at the class level for 1987.

| | CA | PLAND | NP | PD | LPI | AREA_MN | ENN_MN | COHESION |
|---|---|---|---|---|---|---|---|---|
| *F. sylvatica* | 460.63 | 4.10 | 73 | 0.25 | 1.05 | 6.31 | 72.14 | 98.89 |
| *Q. pyrenaica* | 797.25 | 7.10 | 319 | 1.08 | 1.09 | 2.50 | 112.73 | 98.57 |
| *Q. ilex* | 621.13 | 5.53 | 642 | 2.18 | 0.31 | 0.97 | 83.71 | 94.75 |
| *Q. petraea* | 93.45 | 0.83 | 9 | 0.03 | 0.30 | 10.38 | 47.46 | 98.80 |
| *Pinus* sp | 2280.93 | 20.32 | 221 | 0.75 | 1.47 | 10.32 | 87.39 | 99.19 |
| Bare ground | 1142.12 | 10.17 | 317 | 1.07 | 1.51 | 3.60 | 106.75 | 98.28 |
| Mixed scrub | 3037.28 | 27.05 | 573 | 1.94 | 7.08 | 5.30 | 82.26 | 99.63 |
| Pastures | 210.31 | 1.87 | 181 | 0.61 | 0.18 | 1.16 | 183.97 | 96.39 |
| Mixed shrub | 2583.41 | 23.01 | 747 | 2.53 | 3.13 | 3.46 | 70.88 | 99.08 |

**Table 5.1.7.** Landscape metrics at the class level for 2010.

| | CA | PLAND | NP | PD | LPI | AREA_MN | ENN_MN | COHESION |
|---|---|---|---|---|---|---|---|---|
| *F. sylvatica* | 498.99 | 4.44 | 57 | 0.19 | 1.09 | 8.75 | 119.08 | 99.14 |
| *Q. pyrenaica* | 741.21 | 6.60 | 335 | 1.14 | 1.13 | 2.21 | 137.06 | 98.61 |
| *Quercus ilex* | 899.22 | 8.01 | 589 | 2.00 | 0.65 | 1.53 | 85.03 | 97.37 |
| *Quercus petraea* | 111.99 | 1.00 | 18 | 0.06 | 0.34 | 6.22 | 57.41 | 98.63 |
| *Pinus* sp | 2201.25 | 19.61 | 192 | 0.65 | 1.74 | 11.46 | 103.54 | 99.17 |
| Bare ground | 1546.05 | 13.77 | 554 | 1.88 | 0.83 | 2.79 | 112.52 | 97.98 |
| Mixed scrub | 3265.02 | 29.08 | 776 | 2.63 | 5.45 | 4.21 | 69.64 | 99.40 |
| Pastures | 289.31 | 2.58 | 284 | 0.96 | 0.20 | 1.02 | 166.24 | 96.12 |
| Mixed shrub | 1673.47 | 14.91 | 859 | 2.91 | 0.48 | 1.95 | 77.26 | 97.54 |

While all of the results of the indices used in this analysis provide a general view of forest structure, conditions and changes, we are aware of the inherent limitations of the use of Landsat imagery. The limitations are related not only with the accuracy of the digital classification but also with the spatial resolution of the Landsat sensor

### *5.1.4. Discussion*

#### 5.1.4.1 Digital classification and accuracy assessment

Accuracy assessment and map validation are necessary steps to determine cartography quality. Because it is not possible to generate a perfect classification maps, some level of error is expected, and attention must be paid to the limitations imposed by the user, region or sensor. Some omission errors (exclusion) were found in pastures and mixed shrub, and some commission errors (inclusion) were found in mixed scrub and mixed shrub, resulting in an underestimation of the former and an overestimation of the latter (Tables S5.1.1 and S5.1.2 in supplementary materials).

A spectral separability analysis within and between classes was performed during the classification process to ensure an adequate spectral discrimination of the classes defined. In this study, expert classification allows species classification in the case of deciduous trees; however, *Pinus* genera were not possible to separate into species.

#### 5.1.4.2 Spatial analysis in forest structure

The results of the digital classification show that the forested area changed over the last 23 years. In total, approximately 200 hectares were converted into forested area, signifying an annual forestation rate of 8.6 ha per year. This may be due to the combined role of two factors:

The first is related to forest management actions aimed at conserving and improving forested habitats. Management measures adopted by natural parks agencies or by forest managers are generally designed to protect the forest, improve its quality and increase forest surface. In particular, the main management actions applied over forest species in Moncayo Natural Park are described below (Table 5.1.8).

**Table 5.1.8.** Objectives and management actions applied over different species during the analysed period.

| Specie | Objective | Actions |
|---|---|---|
| *Quercus pyrenaica* | Improve quality and state of conservation. Enhance natural regeneration | Reduction of tree density conserving all tree sizes (Uneven-aged Management) |
| *Quercus ilex* | Improve forest structure | Reduction of tree density |
| *Pinus sylvestris* (reforested) | Improve *Fagus sylvatica* and *Quercus pyrenaica* regeneration | Low impact logging |
| *Pinus uncinata* (reforested) | Naturalize forest structure | Reduction of tree density |
| *Fagus sylvatica* | Improve natural regeneration | No actions applied |

Although the actions applied by managers are basically low impact logging for all species, these respond differently. The impact of the actions in pines are minimal in terms of forest expansion, however, *Quercus pyrenaica* forests are more sensitive to logging considering also the competition with *Fagus sylvatica* forests. Furthermore, *Quercus ilex* response with forest expansion. Overall the forest surface is increasing, and due to these actions, forest plantations of different species of pines are widely naturalized in the natural park. In other similar studies, the application of forest management policies lead in general to an overall forest surface increase (Cohen et al. 2011) even in zones affected by forest fires (Pôças et al. 2011a) or in regions with a strong logging pressure (Başkent and Kadioğullari 2007; Çakir et al. 2008). However, in some cases the natural forest surface decreased due to an increase of exotic plantations (Teixido et al. 2010) or due to forest cutting activities (Borrelli et al. 2013).

The second factor explaining the increase of forest cover in Moncayo Natural Park is related to the abandonment of extensive cattle farming, logging activities and wood exploitation by local habitants. These influences have been widely documented by other studies performed in mountainous Mediterranean areas in the second half of the 20th century. They show that the trend of forest expansion is mainly caused by the abandonment of traditional management practises such as grazing, burning and cutting (Morán-Ordóñez et al. 2011; Marull et al. 2014), also combined with land abandonment (Lasanta et al. 2006; Roura-Pascual et al. 2009; Arnaez et al. 2011; Heredia-Laclaustra et al. 2013).

Within forest species *Quercus ilex* experienced the greatest expansion as the largest losses in shrub surface were converted into a *Quercus ilex* formation. That large expansion may have been possible because in 1987 shrubs containing some young, shrub-sized *Quercus ilex* trees were already present. A further interesting change is the forest expansion of *Fagus sylvatica* at the expense of *Quercus pyrenaica* and pine forests. In addition, the prediction for future trends is more expansion of this species because huge amounts of young beech trees are growing inside the forests of other species due to its shade tolerance. In a few years, beech trees may surpass other trees in height and cause their decay (Ligot et al. 2013). The *Quercus petraea* forest shows a slight change in the period analysed, but it is not noticeable because this species can form hybrids trees with *Quercus pyrenaica* (Río et al. 2014). Mixed shrub is the vegetation class with greater changes, likely to be related to tree development in these areas; thus, shrub areas evolved into forested areas.

The results of the landscape metrics analysis provide a global understanding of key trends of forest structure. The fragmentation can be determined by using the following metrics: number of patches, patch density, largest patch density or mean patch area. The general increase in number of patches as well as patch density and the decrease of LPI clearly indicate that landscape fragmentation increased during the period. However, the class results show that fragmentation decreased in the forest classes with the exception of *Quercus petraea*. These results are comparable with the results of other forests where the fragmentation is decreasing regardless of the gain or loss of forest (Keleş et al. 2008; Geri et al. 2010). Nevertheless, there are more examples of forest fragmentation increasing in similar areas during the period studied (Başkent and Kadioğullari 2007; Keleş et al. 2008; Teixido et al. 2010; Cohen et al. 2011; Pôças et al. 2011b). The differences between fragmentation of the forest and the landscape may be because the landscape results are strongly conditioned by the extension and changes in mixed shrubs.

The connectivity indices indicate a general decrease in connectivity, which is the general pattern within the classes, despite the increase in aggregation level in *Fagus sylvatica* and *Quercus pyrenaica* forests. In other similar areas in north-western Spain (Vila Subirós et al. 2009; Marull et al. 2014), connectivity was measured with the same metrics, and the results show an increase in forest connectivity due to trends towards the predominance and homogenization of forest.

Finally, heterogeneity (measured using Shannon's diversity index (SHDI) for all landscapes) remains without significant changes over the last 23 years. However, in other nearby mountain landscapes, heterogeneity has changed in both directions. In Alta Garrotxa in Spain, the heterogeneity decreased from 1.66 to 0.52 in a 50-year period (Vila Subirós et al. 2009) due to different management actions on the forest. On the contrary, in two mountain areas in the pre-Pyrenees (Alquezar and Lierp valley), the heterogeneity increased due to crop abandonment and reforestation (Heredia-Laclaustra et al. 2013). These results clearly indicate that forest management plays a significant role in the increase, maintenance or decrease in forest structure and landscape patterns.

### *5.1.5. Conclusion*

From ecological and economical points of view, the use of remote sensing techniques, GIS and landscape ecology indices to monitor the composition, structure and evolution of forest ecosystems has become more important over the last few years. In the case of natural protected areas, managers need precise information about spatial and temporal forest configuration in order to monitor the effect of applied actions or to apply appropriate conservation measures. This study shows the potential of the techniques used to provide accurate measurements that can be reproduced in other areas.

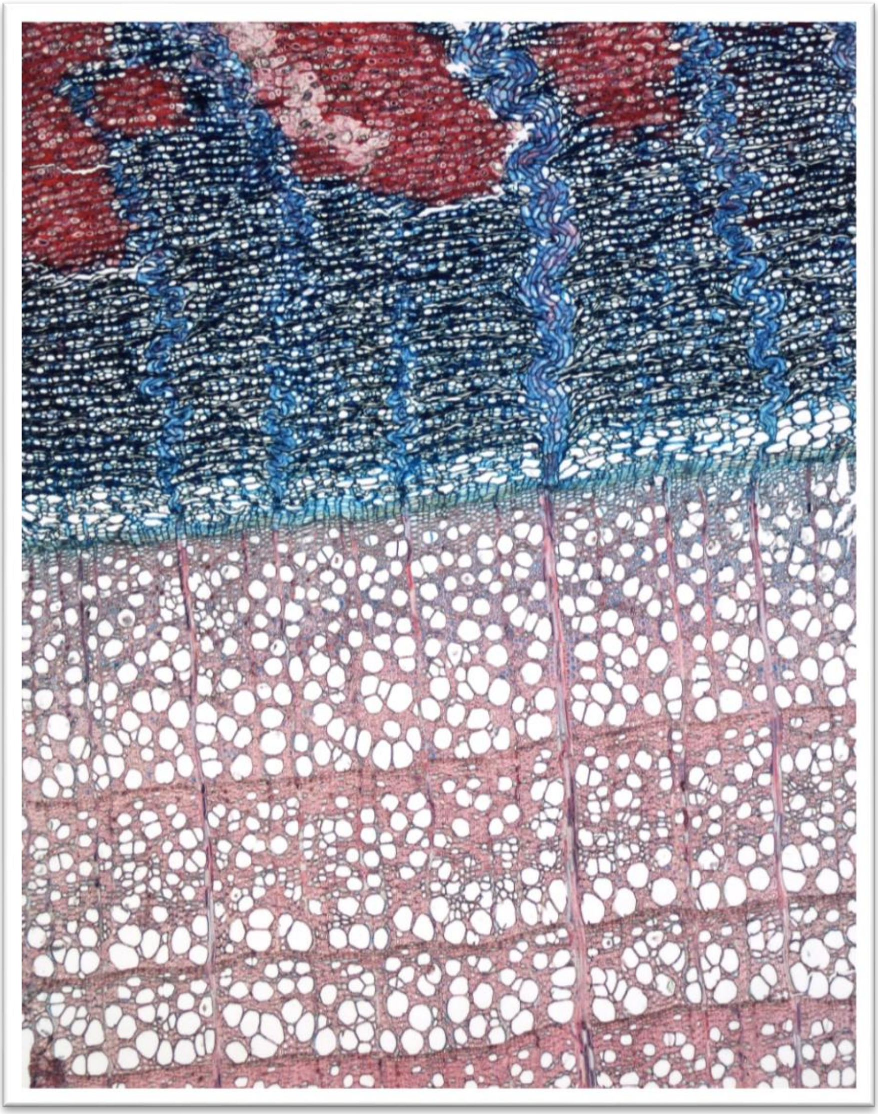
The use of Landsat imagery to discriminate vegetation at the species level is a challenge but is possible with additional information, as shown by Xie et al. (2008) and in the current study. In this respect, it is important to highlight that post-process expert classification based on solid knowledge of the study area improves the species classification, correcting some known errors and, consequently, obtaining results more faithful to reality.

Focusing on the results obtained in this work and summarizing them, we observed several changes in forest surface and structure which can be explained by the abandonment of traditional uses and triggered by protection of the region as a natural park. The increase in forest surface and the decrease of fragmentation are good evidence of the application of proper forest actions given that one of the aims of natural park management policy is to preserve and recover forest ecosystems.

Focusing on the different species, forest managers should consider modify slightly the weight of the actions among the species, in order to achieve their objectives. Applying over pines a higher logging pressure, should lead to an increase forest surface for *Fagus sylvatica* and *Quercus pyrenaica*. The logging pressure in pines should be applied especially in the borders to promote the other species regeneration without any fragmentation increase. The reduction of tree density for *Quercus pyrenaica* should be reconsidered since the specie is losing its surface.

In conclusion, this study was able to highlight critical information about forest structure and dynamics over a period in spatial and quantitative ways, reaffirming the value of the landscape metrics approach for management purposes. The findings revealed that overall changes can be quantified, and this type of approach is needed by managers to assess their actions.

## 5.2. Living on the edge: contrasted wood-formation dynamics in *Fagus sylvatica* and *Pinus sylvestris* under Mediterranean conditions



### *5.2.1. Introduction*

A forest community can prosper only on sites where the environmental conditions are within the niche volumes of each species (Reed and Clark 1978). The distribution of different species is limited by a combination and interaction of biotic and abiotic factors (Mcinerny and Etienne 2012); outside such conditions, the species cannot survive (Kearney 2006).

The widespread forest species European beech (*Fagus sylvatica*) and Scots pine (*Pinus sylvestris*) have both high ecological relevance and economic values. European beech forests are spread all over central Europe, from central Poland, the south of Scandinavia and British Isles to the southernmost locations in the mountain ranges of Greece, Italy and Spain (Jalas and Suominen 1973). Scots pine forests are distributed from the Alps to northeast Europe, covering all Scandinavia and Russia beyond 55º northern latitude (Jalas and Suominen 1976). In the Mediterranean region are isolated patches of both species, climatically constrained by the warmer and drier conditions compared to the greater part of Europe. In these areas, extreme climatic events, such as summer droughts, heat waves or late frosts, restrict forest expansion on the edge of the distribution limit, leaving some populations isolated in mountain shelters.

Climate not only affects forest distribution but also tree growth. The study of cambial activity and tree-ring formation provides valuable information for understanding how trees respond to different climatic conditions (De Luis et al. 2011a; Gričar et al. 2014). In temperate ecosystems, climatic variability leads to an annual periodicity of cambial activity, with winter dormancy and an active period during the growing season.

Monitoring wood formation at the edge of a species' distribution is therefore especially relevant, since these trees are most sensitive to limiting climatic factors and respond most distinctively to any change (Fritts 1972; Gruber et al. 2010; González-González et al. 2014). Knowing how these species grow may help to predict the distribution of tree species in the context of the expected climate change scenarios (De Luis et al. 2011a). In particular, more extreme climatic conditions are expected to affect tree-species' distribution (Richter et al. 2012; Eilmann et al. 2014).

Although the wood-formation patterns of *Fagus sylvatica* and *Pinus sylvestris* have been studied on different sites in Europe, studies along the western - southern distribution limits are still missing. Rossi et al. (2013) and Cuny et al. (2015) , in comprehensive studies, compiled data on cambium phenology and wood-formation dynamics for several conifer species, including *Pinus sylvestris,* growing in different biomes. In Austria, *P. sylvestris* trees growing at xeric and dry-mesic sites were studied by Gruber et al. (2010), Oberhuber et al. (2011) and Swidrak et al. (2014). Similar studies were performed by Rathgeber et al. (2011a) and Cuny et al. (2012, 2014) in France, as well as by Jyske et al. (2014) and Seo et al. (2011) in Finland. These studies highlighted the plasticity of tree-ring formation of *P. sylvestris* in response to contrasting climatic conditions. Different key phenological dates showed distinct variability among study sites and years. It was shown that trees at northern sites initiate tree-ring formation later than trees at southern sites.

Compared to *P. sylvestris*, there is less information available on *F. sylvatica*. Cambial productivity of this species has been monitored at different sites and during several growth seasons in Slovenia by Čufar et al. (2008b) and Prislan et al. (2013) and also in Romania (Semeniuc et al. 2014). In addition, other studies have been performed for one growing season in the Netherlands (van der Werf et al. 2007), France (Michelot et al. 2012), Czech Republic (Vavrčík et al. 2013) and in north Germany (Schmitt et al. 2000). Previous studies indicated the importance of photoperiod and leaf phenology for the onset of xylem production, and the influence of climatic conditions in June, which was proved to be the most important month for wood formation (Čufar et al. 2014a). Studies performed during several years showed that year-to-year variations in tree-ring formation can be explained by climatic conditions or environmental factors, although in some cases the relationship between variation in xylogenesis and weather conditions can be very complex (Prislan et al. 2013).

In order to better understand the growth adaptations and limitations of *F. sylvatica* and *P. sylvestris* at one of the Mediterranean edges of their distribution, we studied the dynamics of xylem-growth formation at one of the southernmost sites of the two species during three years.

Cambium phenology (onset and cessation of cambial cell production) and the timing of xylem formation was compared between the two species and sites to evaluate the adaptation strategies under different environmental conditions. The duration of the xylogenesis were compared with those from other studies of the same two species performed all over Europe

### *5.2.2. Methodology*

#### 5.2.2.1. Sample preparation

The sampling of tissues for xylem-formation monitoring was performed biweekly from mid-March until late November from 2011 to 2013. At each sampling date, six trees were randomly selected per species and site in a sampling plot of around 50 m$^2$. The selected trees were similar, healthy and dominant, with a stem diameter at breast height of 40-55 cm and an age of around 80 years for *P. sylvestris* and 35-50 cm and 120 years for *F. sylvatica*. From each tree, two microcores containing phloem, cambium and the last formed xylem growth ring were collected at breast height with a Trephor tool (Rossi et al. 2006a). The sample had a diameter of 2 mm and was up to 15 mm long. The sampling followed a helical arrangement around the stem to avoid wound effects from previous samplings, with sampling locations separated by at least 10 cm. After sampling, the microcores were immediately transferred in Eppendorf microtubes filled with formaldehyde-ethanol-acetic acid (FAA) fixative solution for one week and later stored in 70% ethanol.

The microcores were processed following the protocol described by Rossi et al. (2006). The microcores were first dehydrated in a graded series of ethanol (70 %, 80 %, 90 % and 100%) and infiltrated with D-limonene and paraffin using a Tissue Processor Leica TP1020. After infiltration, samples were embedded in paraffin blocks. Transverse sections of 8-10 μm thickness, depending on the species, were cut with a Leica RM 2245 rotary microtome. The sections were afterwards stained with safranin and astra blue (Gričar et al. 2007; van der Werf et al. 2007; Prislan et al. 2013), mounted in Euparal and examined with a Nikon Eclipse E800 light microscope equipped with polarized light mode.

#### 5.2.2.3. Xylem phenology measurements and data processing

For *F. sylvatica*, the width of the cell layers in the cambium was measured with the NIS Elements BR3 image analysis system. Moreover, the width of growth-ring increments and also the width of tissues containing xylem cells in various differentiation phases were measured, i.e., post-cambial growth (enlarging cells), cells undergoing secondary wall thickening and mature cells. For *P. sylvestris*, the cambial cells were counted as well as the xylem cells in the three different aforementioned phases.

Cambial activity was identified and interpreted within the context of the multi-seriate concept, that the vascular cambium comprises both the cambial initial cells and xylem and phloem mother cells (Plomion et al. 2001). Thin-walled cambial cells were identified based on their small radial dimensions compared to xylem and phloem cells in the enlarging phase (post-cambial growth), with larger radial dimensions. The polarized mode of the light microscope enabled the discrimination between enlarging cells and secondary wall-thickening cells as described in Rossi et al. (2006b).

The number of cells and the width of tissues in each phase varied between and within trees due to the variation of the tree-ring width around the tree circumference. The number of cells in the previous xylem ring was therefore counted for *P. sylvestris* to normalize the measurements according to Rossi et al. (2003). In the case of *F. sylvatica*, the normalization formula was adapted using width measurements instead of cell number, as described in Prislan et al. (2013).

Extreme values were filtered and xylem-formation dynamics was analysed with the Gompertz function (Rossi et al. 2003). Cambium phenology and timing of xylem formation were assessed using R package CAVIAR (Rathgeber et al. 2011b, a). We defined: beginning and end of the enlarging phase (bE, cE), beginning and end of the thickening phase (bW, cW) and beginning of cell maturation phase (bM). All the dates were computed with a dedicated function using logistic regressions. Differences in the different xylogenesis phases were determined applying repeated measurements ANOVA analysis (De Luis et al. 2011a; Prislan et al. 2013). The effects of fixed factors such as species and sites and the effect of time were evaluated. The total duration of the xylogenesis period was calculated by subtracting the beginning of the enlarging phase from the cessation of the thickening phase. Mean xylogenesis duration was calculated to compare the results with other studies.

### *5.2.3. Results*

#### 5.2.3.1. Wood formation

In all years, locations and species, the cambium was still dormant on the first sampling date in the last week of March. Despite site and annual variations in weather conditions, the different xylogenesis phases followed a common pattern during the growing season. The cell enlarging and cell-wall thickening curves follow a characteristic bell shape, while the cell maturation curve follows a sigmoid shape (Figure 5.2.1).

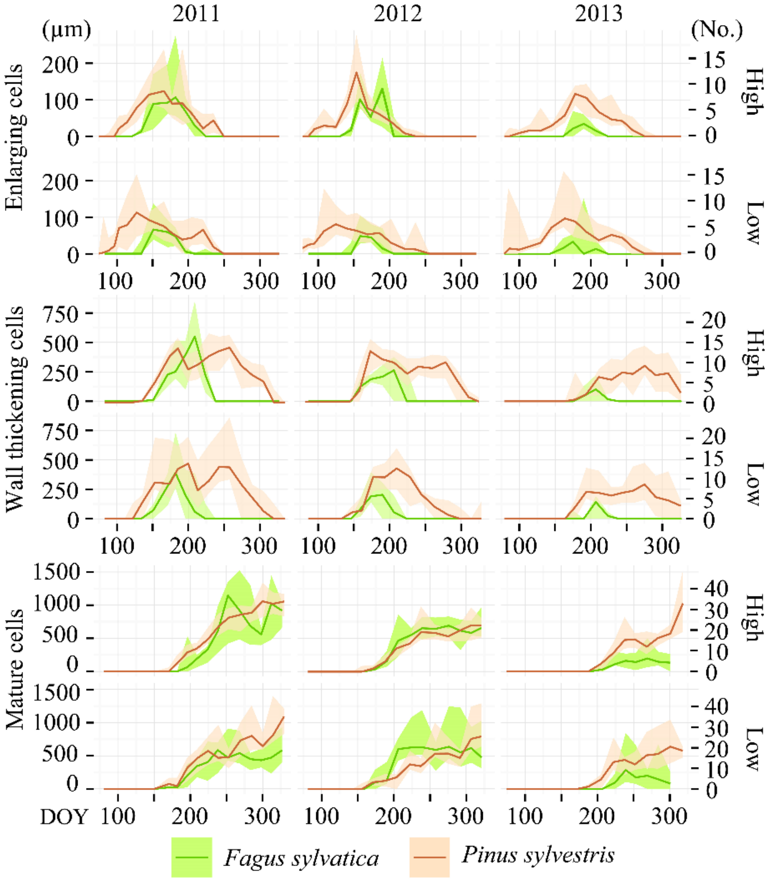
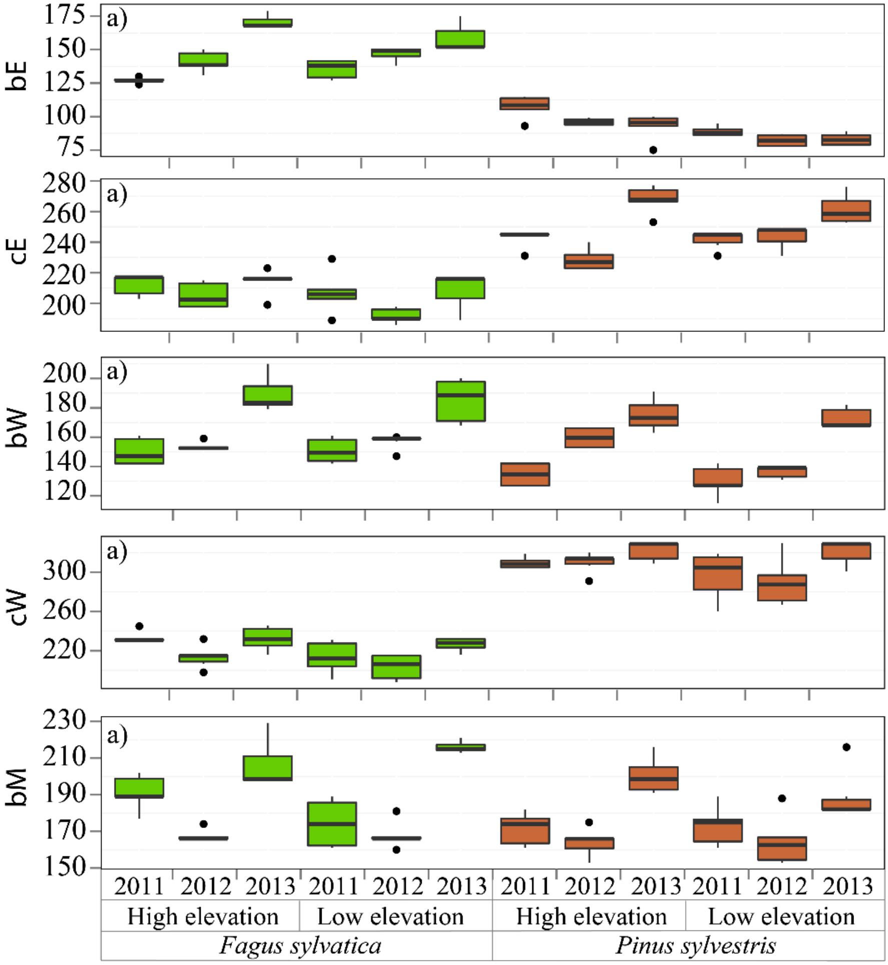


*Figura 5.2.1. Seasonal dynamics of xylogenesis phases in 2011, 2012 and 2013. Amount (number for Pinus sylvestris and width of tissue for Fagus sylvatica expressed in micrometers) of enlarging cells, cells undergoing secondary wall formation and lignification, as well as mature cells in the currently formed growth rings on Moncayo low and high elevation sites. The lines represent the median and the dashed area the range between the 90th and 10th percentiles.*

Overall, the onset of cell enlargement in *P. sylvestris* occurred between the last week of March and the first week of April, followed by the onset of the wall-thickening phase around two months later. The beginning of cell maturation occurred around the summer solstice, before the enlarging of cell ends in early September. Over more than two months, the currently forming tree-ring contained cells in different developmental stages. Completely mature xylem growth rings were observed in the first half of November. Xylem-formation dynamics patterns differed between *F. sylvatica* and *P. sylvestris*. In *F. sylvatica* the onset of enlarging and wall-thickening phases occurred in the second half of May and in June, respectively. The beginning of the maturation process occurred from the last week of June to mid-July, followed by an immediate ending of the enlarging phase. Finally, the xylogenesis ended around mid-August.

#### 5.2.3.2. Phenology of xylem formation

The critical dates for the xylogenesis of *P. sylvestris* and *F. sylvatica* were summarized on three levels, shown in Figure 5.2.2. Dates significantly differed between the two species (ANOVA bE, cE, bW, cW: $p<0.001$; bM: $p=0.005$). The cell enlargement started first in *P. sylvestris,* around 31 March (DOY 90) and fifty days later, around 20 May (DOY 140) in *F. sylvatica*. Cessation of cell enlargement was observed between 9 July and 6 August (DOY 190-218) for *F. sylvatica* and in *P. sylvestris* between 10 August and 1 October (DOY 222-274). Cell-wall thickening and lignification began up to ca. one month earlier and ended around three months later in *P. sylvestris* than in *F. sylvatica*. The first mature cells were observed around 25 June (DOY 176) in *P. sylvestris* and around 7 July (DOY 188) in *F. sylvatica*.


a)
bE
175
150
125
100
75
cE
280
260
240
220
200
bW
200
180
160
140
120
cW
300
260
220
bM
230
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2011
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Fagus sylvatica
Pinus sylvestris

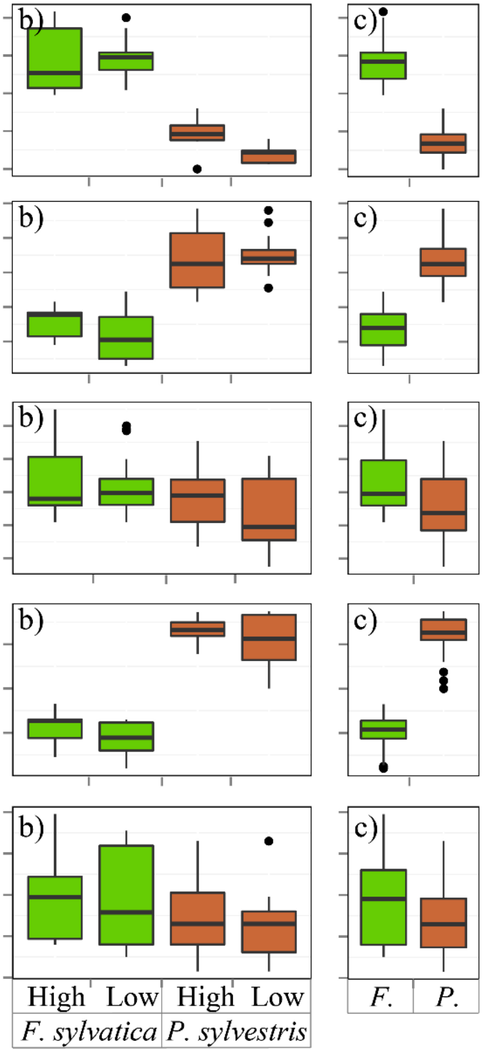


*Figura 5.2.2. Beginning and cessation of the cell enlargement (bE, cE) and cell-wall thickening phase (bW, cW) and beginning of maturation (bM) grouped by (a) sites, species and years, (b) sites and species and (c) species. The central lines indicate the median value, vertical hinges indicate the first and third quartiles, error bars indicate the 95% confidence interval of the median and dots indicate values beyond the 95% confidence interval threshold.*

The beginning of the enlargement phase was highly variable and significantly different among the years for both species at both high and low elevations (ANOVA species*site: *p*<0.001). In *F. sylvatica,* it began between 7 May and 20 June (DOY 127-171), with noticeable differences within years (Figure 5.2.2). In *P. sylvestris,* cell enlargement began between 23 March and 17 April (DOY 82-107). Although the variability was lower in the latter species, in 2011 there was a delay in the beginning of cell enlargement. Focusing on the elevation differences, cell enlargement started earlier at lower elevation in the *P. sylvestris* than in *F. sylvatica*. The end of this phase highly varied among years, whereby higher variability was observed between the years then among the sites for each species (ANOVA site: *p*=0.31).

The onset of the secondary wall formation was highly variable (Figure 5.2.2); in all cases the cell-wall thickening phase started earlier in 2011 and later in 2013, followed by the same temporal pattern (within-subjects ANOVA time*species*site: *p*=0.561). (Figure 5.2.2). The first mature cells (5%) were formed earliest in *P. sylvestris* at low elevation in 2012 (around June 4, DOY 155), and in 2011 (around 11 June, DOY 162) for *F. sylvatica*.

#### 5.2.3.3. Duration of the growing season

The total duration of the xylogenesis of *F. sylvatica* was significantly shorter than in *P. sylvestris* (ANOVA species: *p*<0.001) (Figure 5.2.3). The cell production period during the three study years took 48 to 75 days for *F. sylvatica*, in contrast to *P. sylvestris*, with a growing period lasting from 140 to 170 days. Trees growing at low elevation had a longer growing period in the case of *P. sylvestris*, whereas the growing period of *F. sylvatica*, in contrast, was shorter at low elevation than at high elevation.

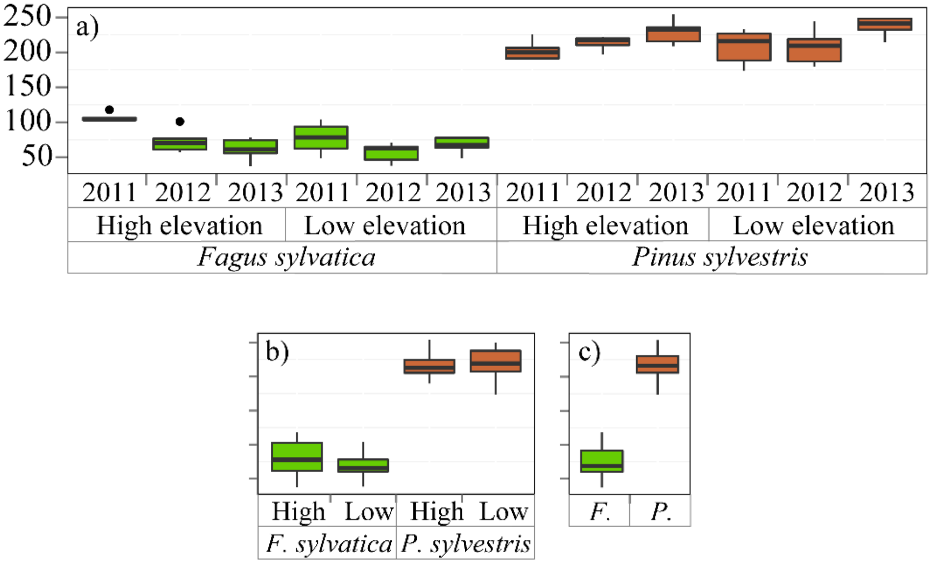


*Figura 5.2.3. Xylogenesis duration grouped by (a) sites, species and years, (b) sites and species and (c) species. The box chart legend is as in Figure 5.2.2.*

The mean duration of the xylogenesis was compared with other studies all over Europe (Table 5.2.1 and Figure 5.2.4). In *P. sylvestris*, the duration of xylogenesis was shorter at high latitude and longer at low latitude, with a range of 49 days in Finland (Seo et al. 2011) to 217 days in Spain. In contrast, wood formation process in *F. sylvatica* was longer at high latitudes, over 163 days in the Netherlands (van der Werf et al. 2007) and only 67 days in Spain. In both species, the average duration of the xylem formation follows a linear pattern along the latitudinal range; however, whether it is directly or inversely proportional to the latitude depends on the species (Figure 5.2.5).

**Table 5.2.1.** Mean xylogenesis duration values of *Fagus sylvatica* and *Pinus sylvestris* from various wood-formation studies in Europe.

| Species | Country | m a.s.l. | Long. | Lat. | Mean xylo. duration (days) | Reference |
|---|---|---|---|---|---|---|
| *Fagus sylvatica* | Spain | 1560 | -1.82 | 41.79 | 80 | This study |
| | Spain | 1180 | -1.81 | 41.80 | 67 | This study |
| | Slovenia | 400 | 14.66 | 46.00 | 113 | (Čufar et al. 2008a) |
| | Slovenia | 400 | 14.66 | 46.00 | 153 | (Prislan et al. 2013) |
| | Slovenia | 1200 | 14.80 | 46.26 | 122 | (Prislan et al. 2013) |
| | Romania | 850 | 25.55 | 47.48 | 122 | (Semeniuc et al. 2014) |
| | France | 120 | 2.66 | 48.41 | 115 | (Michelot et al. 2012) |
| | Czech Rep. | 630 | 16.70 | 49.46 | 116 | (Vavrčík et al. 2013) |
| | Netherlands | 50 | 5.71 | 51.98 | 163 | (van der Werf et al. 2007) |
| *Pinus sylvestris* | Spain | 1560 | -1.82 | 41.79 | 215 | This study |
| | Spain | 1180 | -1.81 | 41.80 | 217 | This study |
| | Austria | 750 | 10.84 | 47.23 | 137 | (Gruber et al. 2010) |
| | Austria | 750 | 10.84 | 47.23 | 160 | (Gruber et al. 2010) |
| | Austria | 750 | 10.84 | 47.23 | 170 | (Oberhuber et al. 2011) |
| | Austria | 750 | 10.84 | 47.23 | 172 | (Swidrak et al. 2014) |
| | France | 643 | 7.15 | 48.48 | 189 | (Cuny et al. 2012, 2014) |
| | France | 270 | 6.32 | 48.74 | 199 | (Rathgeber et al. 2011a) |
| | Finland | 60 | 25.00 | 60.20 | 91 | (Jyske et al. 2014) |
| | Finland | 120 | 25.60 | 61.20 | 79 | (Jyske et al. 2014) |
| | Finland | 181 | 24.30 | 61.90 | 73 | (Jyske et al. 2014) |
| | Finland | 110 | 27.30 | 62.40 | 63 | (Jyske et al. 2014) |
| | Finland | 140 | 26.40 | 66.20 | 64 | (Jyske et al. 2014) |
| | Finland | 140 | 26.70 | 66.30 | 63 | (Seo et al. 2011) |
| | Finland | 390 | 29.40 | 67.50 | 54 | (Jyske et al. 2014) |
| | Finland | 300 | 27.40 | 68.30 | 49 | (Seo et al. 2011) |

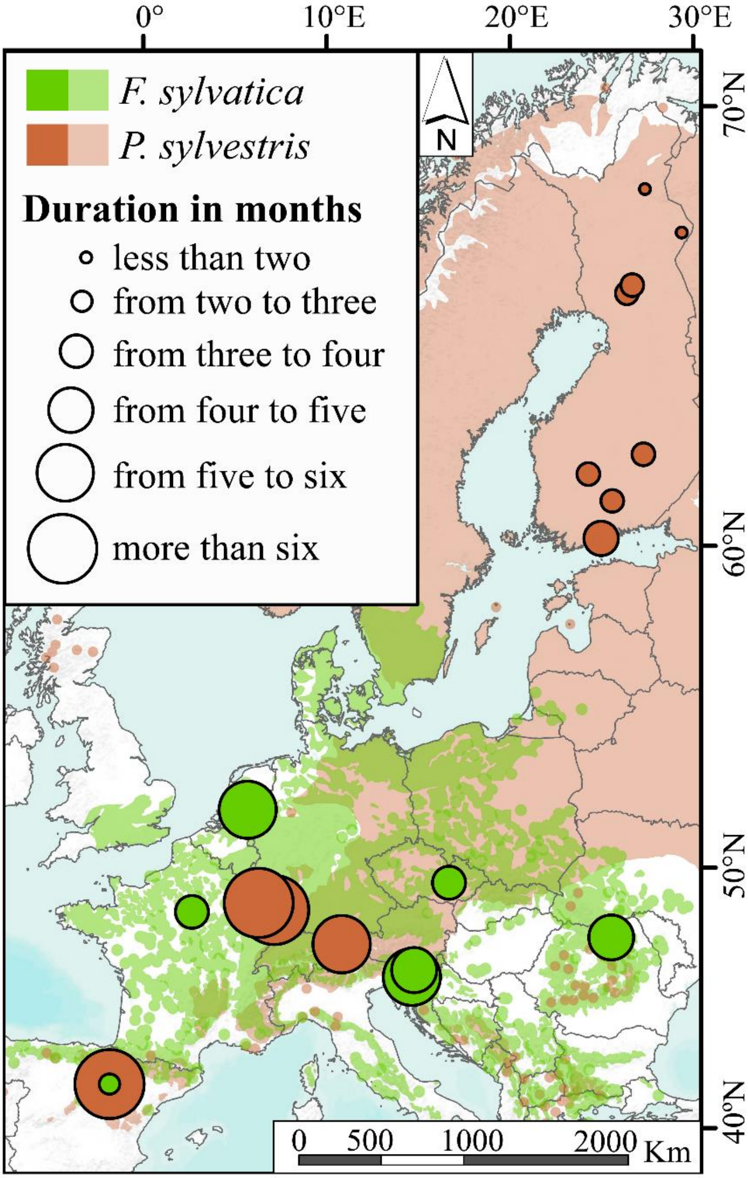


*Figura 5.2.4. Xylogenesis duration of Fagus sylvatica and Pinus sylvestris in Europe.*

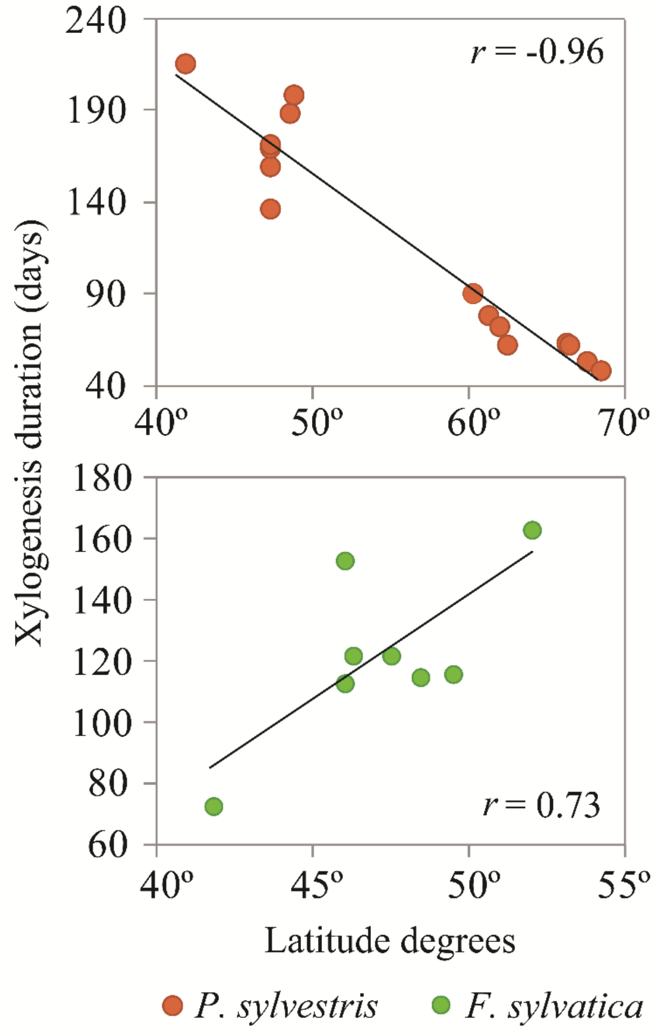


*Figura 5.2.5. Xylogenesis duration variations by latitude. The black lines represent linear regressions: (P. sylvestris) $y = -6.25x + 470.14$, $p < 0.001$; (F. sylvatica) $y = 7.28x - 222.56$, $p = 0.010$.*

### *5.2.4. Discussion*

#### 5.2.4.1. Dynamics of xylogenesis

Tree growth is largely affected by different climatic conditions, which become more limiting in adverse climatic conditions, such as in a Continental Mediterranean climate (Camarero et al. 2010; De Luis et al. 2011a; Pasho et al. 2012). Different tree species are differently affected by climate: e.g., evergreen or deciduous species, or early-successional or late-successional species. In this context, previous studies suggest that evergreen species adapt better to Mediterranean environmental and climatic conditions than deciduous species (Blumler 1991), while early-successional species adopt riskier life strategies (Körner and Basler 2010), making them more adaptive but also more vulnerable to the highly variable Mediterranean climate. These differences may trigger a different phenology of xylem formation. Our results suggest that *F. sylvatica* and *P. sylvestris* respond differently to local Mediterranean conditions. Accordingly, the phenology of xylem formation was significantly different between the two species, the period of all *P. sylvestris* developmental phases being significantly longer.

Our results demonstrate that Mediterranean climate has less impact on *P. sylvestris* than on *F. sylvatica*, despite this early-successional condition. The *Pinus* genus has been established as very plastic and capable of adapting its growth to changing climatic conditions (Camarero et al. 2010; De Luis et al. 2011a; Novak et al. 2013; Vieira et al. 2014) and the bimodal growth pattern as an adaptation to Mediterranean climate has been frequently described (Camarero et al. 2010; Campelo et al. 2015). Specifically, *P. sylvestris* has recently been determined as a plastic species in the Mediterranean area (Sánchez-Salguero et al. 2015).

Several studies performed on *F. sylvatica* under Mediterranean conditions have highlighted the growth limitation due to summer high temperatures and drought (Robson et al. 2013; Rasztovits et al. 2014; Chen et al. 2015; Rozas et al. 2015). In addition to climatic constrictions, *F. sylvatica* trees are more limited during the year in terms of plasticity because, with the activation of a leaf senescence mechanism, trees inexorably enter a dormant period. Despite this, our results reveal differences in the altitudinal gradient in agreement with the results shown in Prislan et al. (2013): who found similar patterns but different timing in two *F. sylvatica* forests with different climatic regimes.

The most striking result of the present study is the great differences in growth patterns among the years, highlighting a plastic response of radial growth in *F. sylvatica,* similarly as in *P. sylvestris.*

#### 5.2.4.2. Occurrence of xylem phenology

High variability in xylem phenology between years and sites demonstrates high plasticity of the species. The timing of different developmental phases significantly varied between the two species. Even though the variability of the critical dates was high among years and sites, the most remarkable disparity was found between the two tree species.

Xylogenesis, starting with cambial division and cell enlargement, is triggered by an increase in air temperature in spring. Several studies have demonstrated this positive relationship (Rossi et al. 2008; Vieira et al. 2014), which has also been supported by stem heating experiments (Gričar et al. 2007; Begum et al. 2010). Under the same climatic conditions, we showed a difference in the onset of xylogenesis between the two species of over 50 days, especially in 2013, when the difference was about 72 days at both elevations. These differences suggest that climatic conditions for the onset of xylogenesis are species-specific. Moreover, the same weather conditions resulted in a completely different response of the tree species in terms of the temporal dynamics of xylogenesis, as can clearly be seen in 2011, when *F. sylvatica* started earlier than in the other two study years, while *P. sylvestris* showed the latest onset of growth in the same year.

The end of the cell-wall thickening phase seems to be a key date, since it defines the end of xylogenesis. Overall, the thickening phase in *P. sylvestris* continued until mid-November, whereas in *F. sylvatica* it ceased in mid-August, i.e., about three months earlier. Mild temperatures during early autumn may result in an extension of the growing period for *P. sylvestris* but not for *F. sylvatica,* since by that time leaf senescence has also already started. Cessation of cell-wall thickening was first observed in the lower part of the mountain in both species, as was similarly reported by Moser et al. (2009) and Oladi et al. (2011). This indicates that the end of xylogenesis is possibly influenced by temperature as well as the length of the photoperiod, as proposed by Plomion et al. (2001).

A common pattern is an evident delay in all developmental phases in 2013, except the beginning of wood formation in *P. sylvestris*. This may be explained by the late frost that occurred in 2013, after the onset of cell enlargement in *P. sylvestris*. This event presumably affected the temporal dynamics of wood formation in both species, although with different magnitudes. Menzel et al., (2015) showed that spring late frost events cause considerable damage in *F. sylvatica*. Nonetheless, a more detailed study of the climatic-growth relationship would be needed to confirm this hypothesis.

#### 5.2.4.3. Growing-season length under Mediterranean conditions

Although both species are growing at their southern distribution limit and, consequently, their radial growth is somewhat constrained, the duration of the growing period of the two species significantly varied. The duration of xylogenesis highlights the differences between the species; it was two months for *F. sylvatica* and more than five months for *P. sylvestris*. Because of the early start and late end, *P. sylvestris* on Moncayo showed the longest xylogenesis duration in this species recorded in the various studies to date. Moreover, the shortest xylogenesis duration for *F. sylvatica* was also captured on this mountain.

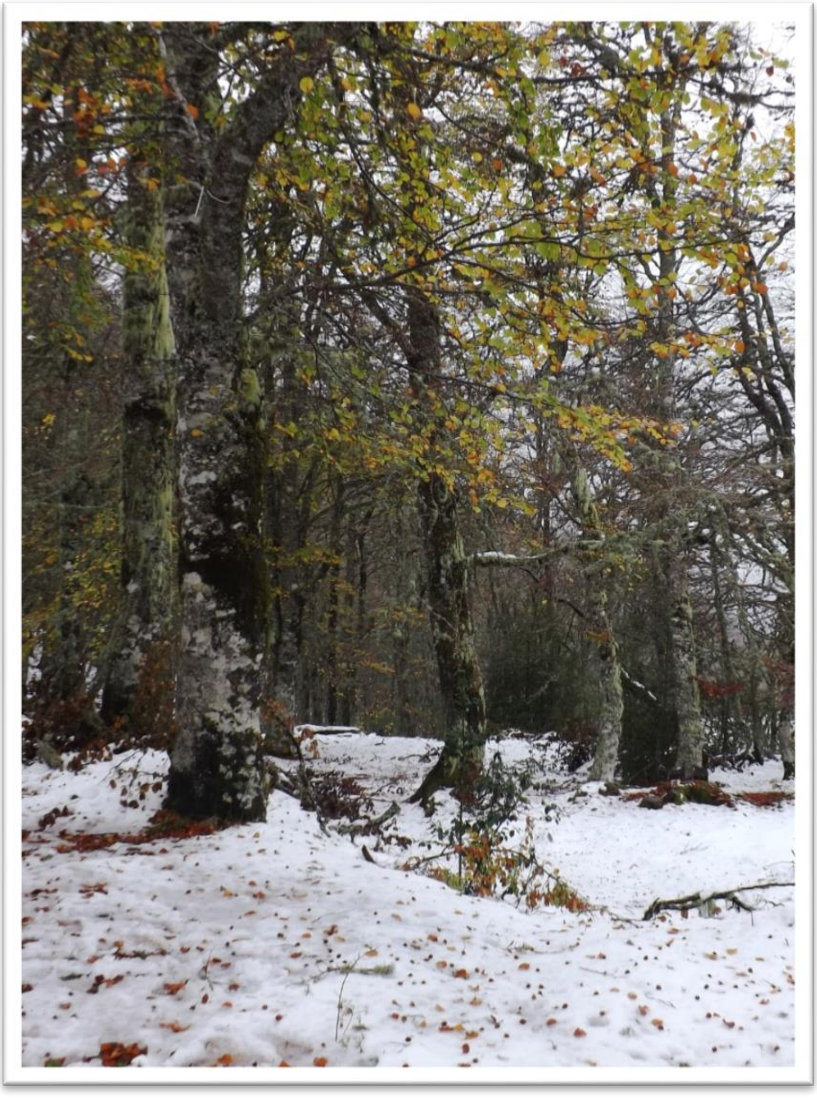
Cambial resumption in *P. sylvestris* occurred earlier than on numerous Central European sites (Gruber et al. 2010; Oberhuber et al. 2011; Cuny et al. 2012, 2014; Swidrak et al. 2014), which could be explained by the warmer spring in Moncayo. These results are also in accordance with observations of Rossi et al. (2013) on various sites and Jyske et al. (2014) in Finland. On the other hand, the end of xylogenesis occurred later at Moncayo and resulted in a longer duration of xylogenesis than in other places in central and northern Europe. An extension of the growing season has also been described for other pine species, such as *Pinus halepensis* (De Luis et al. 2011b) or *Pinus pinaster* (Vieira et al. 2014). The extension of xylogenesis could be caused by the Mediterranean mild temperatures, despite water restrictions. However, in *F. sylvatica*, the results showed the opposite response, the beginning was later than in colder locations in Europe, such as in France (Michelot et al. 2012), Slovenia (Čufar et al. 2008b; Prislan et al. 2013), Romania (Semeniuc et al. 2014), Czech Republic (Vavrčík et al. 2013) and the Netherlands (van der Werf et al. 2007). This indicates that warmer and drier conditions at Moncayo negatively affect the duration of xylogenesis in *F. sylvatica*.

### *5.2.5. Conclusions*

It appears that the temporal dynamics of xylogenesis is considerably different in *F. sylvatica* than in *P. sylvestris* growing at the edge of their southern spatial distribution. This shows that intra-annual radial growth patterns in the studied species are differently affected by the Mediterranean conditions. The annual variation of the critical xylogenesis dates indicates a high species-specific plasticity for adapting to changing climatic conditions. As a result, the period of xylogenesis in *F. sylvatica* was around two months, while for *P. sylvestris* it was more than five months. Our findings are in accordance with our hypothesis of contrasting growth strategies and adaptations of the two species at the edge of their spatial distribution.

Furthermore, we compared our observations with those of other authors working on the same two species in different climatic environments, especially along a latitudinal range. A clear north-south trend was found in the xylogenesis duration over the distribution range of both species. *P. sylvestris* showed a positive xylogenesis duration trend on southern locations. *F. sylvatica,* in contrast, showed a shorter xylogenesis duration in the south of Europe than that shown in northern locations. These findings demonstrate that a deciduous and late-successional species such as *F. sylvatica* is negatively affected by Mediterranean climatic conditions, resulting in a shorter xylogenesis, whereas in the evergreen and early-successional *P. sylvestris,* xylogenesis is shown to be longer in Mediterranean environments.

## 5.3. Spatial patterns of climate-growth relationships across species distribution as a forest management tool in Moncayo Natural Park (Spain)



### 5.3.1. Introduction

Climate is one of the main abiotic factors that defines and limits the natural distribution of tree species (Mott 2010). Therefore, it is expected that predicted climate change (IPCC 2013) will have a significant impact on the distribution of species (Pearson and Dawson 2003).

Tree species often exhibit physiological adaptations along climatic gradients, adapting to the specific climatic and site conditions (Sáenz-Romero et al. 2016). Alternatively, species can migrate in response to climate changes. However, both functional adaptation and migration are slow processes for long-lived organisms, such as trees, and likely do not keep pace with the actual change in environmental conditions (Sáenz-Romero et al. 2016).

Management of natural protected areas and commercial forests requires long-term strategies and practical guidelines to facilitate management decisions in response to climate change (Nabuurs et al. 2017; Walentowski et al. 2017; Loran et al. 2018). Assisted migration is an important tool to adjust species distributions to changing climate conditions and mitigate its effects. However, implementing assisted migration requires knowledge of climate-growth relationships (CGRs) within a species' range to ensure the success of the reforestation plan.

Tree-ring research is a powerful tool to assess the dynamics of climate-growth relationships, including reactions to extreme climate events (Fritts 1972) throughout long time periods. Using a tree-centered approach opens the possibility to understand tree function under specific climate and site conditions (Sass-Klaassen et al. 2016). This comes with the limitation that the gained information represents individual tree populations growing under specific site conditions.

There are numerous studies demonstrating that CGRs can strongly vary along altitudinal (Ponocná et al. 2016; Kharal et al. 2017) or environmental gradients (Čufar et al. 2014b; Kraus et al. 2016; Martínez del Castillo et al. 2018b). This suggests a different ability of species to cope with climate variability and change across their distribution area. De Luis et al., (2013) presented an extensive tree-ring network for Aleppo pine (*Pinus halepensis* Mill.) that was used to assess CGRs and trends in climate sensitivity across the distribution area. Climate-growth relationships can be systematically assessed for species along gradients through the distribution area of the species to systematically extend this site-specific information. It is difficult to obtain strong directional trends in climate response across the distribution range because of the diversity in environments encountered across the distribution area of a given species. As a consequence, there is a lack of information about how tree species respond to climate conditions outside of their distribution range and within the range (i.e., in areas of recent expansion, mixed stands or juvenile trees). Interestingly, De Luis et al., (2013) demonstrated that such variation in CGRs are related to prevailing climate conditions which allow for extrapolation of estimated trends across the species distribution and also into areas where the species is currently not present. Such information is useful for foresters that seek to perform assisted-migration actions, specifically into sensitive areas, i.e., at the edge of the current distribution area.

Moncayo Natural Park (MNP) is a mountain ecotone in a transitional zone between the Eurosiberian and Mediterranean biogeographical region (Longares 2004) and forms a geographical boundary for several tree species. The ecotone areas are transitional areas between two neighboring biomes that contain different vegetation types and generally are more sensitive to environmental disturbances (Risser 1995b). MNP provides a relevant sample area with a number of different sites that span different climatic types. Therefore, this area is a suitable location to apply new analysis techniques aimed to spatially test the influence of climate on forest species.

European beech (*Fagus sylvatica L.*), Scots pine (*Pinus sylvestris* L.), and Mountain pine (*Pinus uncinata* Ram.) are widespread European tree species with high economic and ecological value. The forests stands in Moncayo Natural Park represent one of the southern limits for all these species. Pyrenean oak (*Quercus pyrenaica* Willd.) distribution in Europe is limited to the Atlantic climate areas of western France and the Iberian Peninsula (Nieto Quintano et al. 2016); MNP is the northern extent of its Mediterranean range. The current distribution of these species in this Natural Park are influenced by historical land use, such as sheep and goat grazing and pine introduction via reforestation (Arrechea 2002). Graphical records (e.g., old photographs) and aerial photography indicate that the currently forested area was a meadow with isolated patches of beech and Pyrenean oak trees about one hundred years ago. The closed-canopy forest is relatively young, and the current situation does not reflect the potential spatial distribution of the species across this site. Recently, several changes in forest size and structure have been observed due to the abandonment of traditional uses triggered by protection of the region as a natural park (Martínez del Castillo et al. 2015). Specifically, beech and Pyrenean oak trees are protected by the Habitats Directive (Council Directive 92/43/EEC).

In this study, we investigated the growth response of beech, Scots pine, Mountain pine and Pyrenean oak to climate across an altitudinal-climatic gradient, and we modeled these responses over the potential distribution of each species inside the Natural Park. The following were our hypotheses: (i) the species exhibit different climate-growth relationships, which vary along the climatic gradient; (ii) variation in climate-growth relationships for each species across the altitudinal gradient is associated with the specific climatic variability; and (iii) climate-growth relationships models can be applied beyond the current distribution of each species to allocate potential migration areas (either natural or artificial via reforestation). Our final aim was to predict CGRs across the potential species distribution in MNP to investigate the use of this novel approach for the design of forest management activities geared to adapt species distributions to changing climate conditions. The obtained empirical model is based on the specific local conditions at MNP and hence may not be widely applicable. However, this new modelling approach illustrates the value of building models for specific areas that can be applied by foresters to manage the distribution of species. Assuming that tree secondary growth can be used as an appropriate indicator of tree performance related with the environmental conditions, the interpretation of this results can provide insights to design management actions geared to create stable forest communities that are able to cope with stress in changing (and more severe) climatic conditions

### *5.3.2. Methods*

#### *5.3.2.1. Climate*

The Natural Park is located in the eastern side of the Moncayo massif. Its geographical position represents an orographic barrier where the western and northwestern fronts prevent moisture from reaching the mid Ebro Valley. This situation produces a disruption of rising moist air flow that contributes to relatively frequent convective activity and results in higher amounts of precipitation at high elevations with a progressive decrease toward the lower elevations, whereas temperature follows the inverse path, with lower values at high elevations and higher values at low elevations.

With the aim to analyze the climate of the Moncayo Natural Park, three high-resolution gridded datasets of daily precipitation and maximum and minimum temperature were created using the *reddPrec* R package (Serrano-Notivoli et al. 2017c) based on the reconstructed stations of Serrano-Notivoli et al (2017a). The grids were based on a set of 2801 points regularly distributed over the study area with a spatial resolution of 200 m. Precipitation and temperature were computed daily for the period from 1950 to 2012. The annual averages for both precipitation (Figure 5.3.1.b) and temperature (Figure 5.3.1.c and 5.3.1.d) show a clear altitudinal spatial distribution. The annual amounts of precipitation reach 1,500 mm at high elevations and decrease until values drop below 400 mm at lower elevations in the eastern and southern margins (Figure 5.3.1b). The temperatures widely vary from the mean annual minimum below 0 ºC at the summit to the mean maximum over 16 ºC at the lower areas (Figure 5.3.2). Annual temperature values show a similar pattern along the altitudinal bands with a change of -0.517 and -0.523 ºC / 100 m increase in altitude for minimum and maximum temperatures, respectively, whereas annual precipitation increased by 119.89 mm / 100 m increase in altitude.

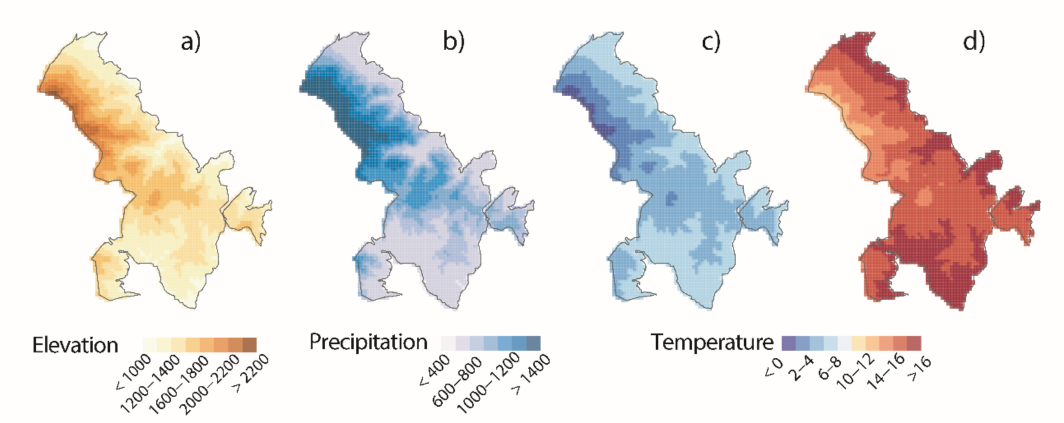


*Figura 5.3.1. Geographic and climatic gradients across study area for a) elevation, b) mean annual precipitation, c) mean annual minimum and d) mean annual maximum temperature.*

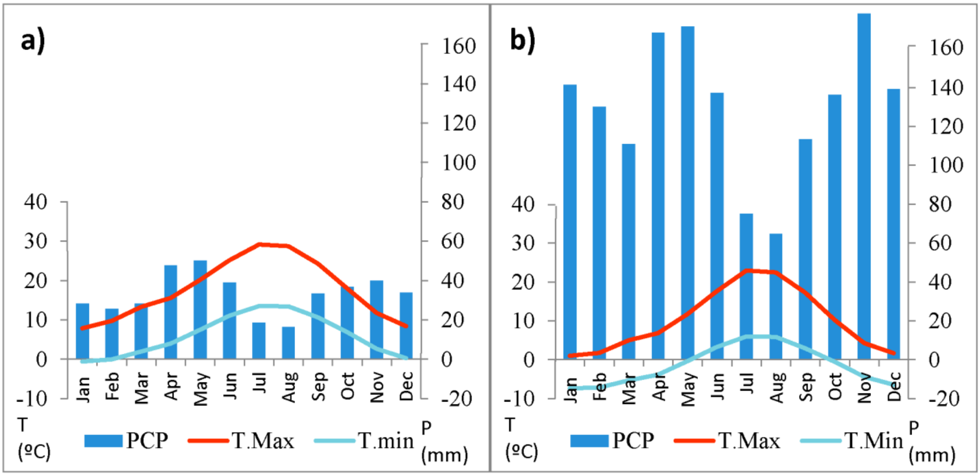


*Figura 5.3.2. Climatic diagrams at Moncayo Natural Park showing monthly precipitation (PCP), maximum temperatures (T.Max) and minimum temperatures (T.min) for a) lowest elevation 850 m.a.s.l. and b) highest elevation 2314 m.a.s.l.*

### *5.3.2.3. Tree-ring chronologies*

A total of 40 sites were selected and sampled between 2010 and 2014 along an altitudinal gradient from 950 to 1900 m.a.s.l. (Table 5.3.1 and Table S5.3.1 in Supplementary Materials). Between five and 25 healthy and dominant trees were sampled at each site with an increment borer at breast height, extracting two cores per tree. Tree cores were mounted on wooden supports, dried, sanded and scanned in the laboratory. The tree rings were measured with the TSAP-Win program and LINTAB ™ 5 measuring device (Rinntech, Heidelberg, Germany) with 0.01 mm precision. Crossdating was done using CooRecorder v8.0 software (Cybis Elektronik & Data AB. Saltsjöbaden, Sweden).

**Table 5.3.1.** Summary of study sites for each species.

| | No. sites | Altitude range | No. trees | Chronology range |
|---|---|---|---|---|
| *F. sylvatica* | 15 | 1150-1600 | 150 | 1799-2014 |
| *P. sylvestris and P. uncinata* | 11 | 1020-1900 | 147 | 1919-2014 |
| *Q. pyrenaica* | 14 | 950-1500 | 130 | 1875-2013 |

Ring-width measurements were detrended to remove biological trends using a negative exponential curve. A second detrending was then applied using a 50-year cubic smoothing spline with a 50% frequency response to filter out low frequency variation that reflects potential non-climatic disturbances. To obtain the detrended residual chronology to perform the analysis, two processes were done: an autoregressive modeling of the residuals and a bi-weight robust estimation of the mean. The detrending process and chronology computation was carried out using the dplR package (Bunn 2008).

#### 5.3.2.4. *Statistical analysis*

Correlation function coefficients (CFCs) were calculated between all 40 residual chronologies through seasonal 3-month means for respective maximum and minimum temperatures and precipitation sums from the previous summer (June, July and August) and the current summer. Correlation analysis was performed separately for each chronology with the associated climate calculated for each location.

As a second step, the variability and patterns of distribution of obtained seasonal CFCs for temperature and precipitation were explored. Generalized Additive Modelling (GAM) was used to detect relationships between the distribution patterns of obtained CFCs (dependent variable) and the mean annual values for precipitation and maximum and minimum temperature calculated for each study site (independent variables). This study is species-specific, but *P. sylvestris* and *P. uncinata* were grouped together due to similarities in climate-growth relationships found in this area between this species when compared with the other analyzed species. However, this similar behavior should not be extrapolated to other locations where both species are present.

The GAMs were constructed using the 'gam' package in R environment (Hastie and Tibshirani 1986). The quasi-binomial family was used in order to describe the error distribution (Eq 1). CFC values can theoretically vary from -1 to 1, therefore, observed values were re-scaled ($CFC_{sb}$) for model construction (Eq 2).

$$\mathrm{gam}(CFC_{sb} \sim PCP+TMAX+TMIN+c(PCP:TMEAN),\ \mathrm{family}=\text{"quasibinomial"}) \qquad \text{(Eq 1)}$$

$$CFC_{sb} = (CFCs + 1) / 2 \qquad \text{(Eq 2)}$$

The accuracy of the models was evaluated using a likelihood ratio test by comparing the obtained models (full models) with restricted models where the explanatory variables of interest were omitted and only the intercept term was included (null models). The p-values for the likelihood ratio tests that compared the full and reduced models were calculated using the Chi-square distribution.

Finally, the obtained models were applied to the current species distribution in the MNP and also for the area of the Natural Park designated by a specific altitudinal range for each species. The boundaries of this altitudinal range are limited by the highest and lowest presence of a given species inside the Natural Park (from 1100 to 1750 m for beech; from 950 to 2100 m for pines and from 900 to 1500 m for Pyrenean oak). These areas are considered as potential distribution areas for the study species as they contain the specific environmental conditions required for their survival. The climatic conditions inside the different altitudinal gradients defined for each species are gathered in the sampled zones, therefore, the application of the models to these specific climatic conditions are not an extrapolation outside the values domain on which the models are constructed. This approach is similar to the fundamental niche concept, where a combination of environmental variables defines the limits for survival without taking into account biotic competition (Reed and Clark 1978).

## *5.3.3. Results*

### *5.3.3.1. Chronologies*

In total 427 trees were sampled in the area, covering an altitudinal range from 950 m.a.s.l. to 1900 m.a.s.l. (Table S5.3.1 in supplementary material). The youngest and oldest trees sampled for each species were 71 and 215 years for beech, 41 and 95 years for pine, and 37 and 271 years for Pyrenean oak. In total 40 chronologies where constructed, 15 for beech, 11 for pines and 14 for Pyrenean oak. The statistical analysis indicated a high quality of all chronologies based on the four commonly used statistical indicators in dendrochronology: the mean correlation between ring-width series (Rbar), the expressed population signal (EPS), the signal to noise ratio (SNR) and the mean sensitivity (SENS) (Table S5.3.1). Rbar values ranged from 0.21 to 0.55, with a mean of 0.42. SNR ranged from 1.33 to 28.20, with a mean of 12.41. SENS ranged from 0.2 to 0.46, with a mean value of 0.3. All EPS values reached the threshold of 0.85, indicating that all chronologies reflect a high common environmental signal of the sampled tree populations.

### *5.3.3.2. Climate-growth analysis*

The results of the correlation analyses between the 40 chronologies and the climate variables (precipitation, maximum and minimum temperature grouped by seasons) by species are summarized in Figure 5.3.2. The boxplots represent the variability of the correlation coefficients of all sampled sites of each species, therefore, across the studied populations (Figure 5.3.2). If the box is completely beyond the dashed line (e.g. CFC for beech regarding T.max in previous summer), it implies that in all chronologies existed a significant relationship with the climate variable (in this case negative). If the box is completely inside the range described by the dashed line (e.g. CFC for beech regarding T.max in previous autumn), it implies that all chronologies do not showed a significant relationship with that climatic variable. If the box cross the dashed line (e.g. CFC for beech regarding T.max in winter), it implies that at least one chronology presented a significant relationship (in this case, one positive and another negative, but in most of the cases the significance threshold was not reached). Lastly, the dashed line indicates statistical significance ($P < 0.05$) beyond 0.25 or -0.25, threshold given by the number of years included in the analysis (i.e. 62).

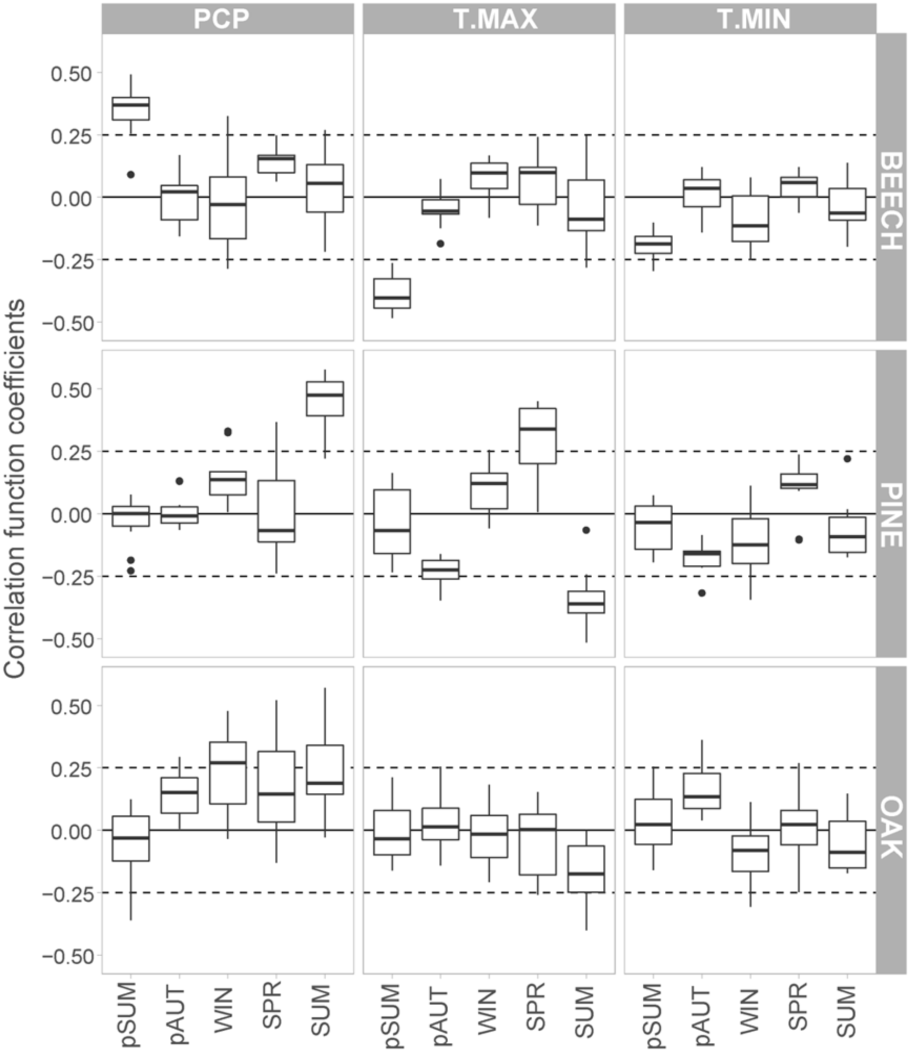


*Figura 5.3.3. Climate-growth relationships for chronologies of beech (n=15), pines (n=11) and Pyrenean oak (n=14); dashed horizontal lines indicate statistical significance (P < 0.05) for 62 years of record; PCP = seasonal precipitation, TMAX, TMIN= seasonal maximum and minimum temperature, respectively. pSUM = previous summer, pAUT = previous autumn, WIN = winter, SPR = spring, SUM = summer. The central lines of boxplots indicate the median value, vertical hinges*

*indicate first and third quartiles, error bars indicate the 95% confidence interval of the median and dots indicate outlines, values beyond the 95% confidence interval threshold.*

Beech growth was significantly related to wet and cold conditions during the summer preceding the current growing season. Precipitation had a positive and significant effect in all but one case, meanwhile the maximum temperature affected growth negatively (CFCs from -0.26 to -0.47). Large variation in correlation coefficients for current summer (precipitation and maximum temperature) and especially winter conditions (precipitation and minimum temperature) determine different responses among the 15 beech populations.

The growth of the pine populations was mainly driven by precipitation and maximum temperature during summer in the current growing season with above-average rainfall and below-average maximum temperature significantly favoring pine growth, whereas during spring, high temperatures had a significant positive influence at the majority of the pine sites. Large variation between pine populations occurred in correlations with spring precipitation and maximum temperature during the previous summer.

Pyrenean oaks were especially sensitive to precipitation. There was a positive influence of precipitation during all growing periods, even from the previous autumn. There was a general negative influence of summer maximum temperatures, significant at some sites, and a positive relationship between previous autumn minimum temperatures and Pyrenean oak growth. In all cases, minimum temperatures had less influence on growth than precipitation or maximum temperatures. Generally, the Pyrenean oak populations vary more in their climate response than those of beech and pine as indicated by the large size of the boxplots, although only the median correlation with winter precipitation was significant.

The correlation analyses indicate large differences between the average response of beech, pines and Pyrenean oak to prevailing climatic factors and, moreover, contrasting responses within species to climate conditions across the environmental gradient of the Moncayo Natural Park.

#### 5.3.3.3. *Model application*

To explore the variability of the sets of correlation coefficients yielded for the study species along the climate gradients for mean annual precipitation and the mean of the annual maximum and minimum temperatures within the study area, a total of 45 GAMs were constructed (5 seasons * 3 climate variables * 3 genera) and applied to the current species distribution in the MNP and also for the area of the Natural park designated by a specific altitudinal range for each species (considered as potential distribution areas). Predicted correlation coefficients for all analyzed seasonal climatic factors are shown in Figure 5.3.4 (beech), 5.3.5 (pines) and 5.3.6 (oak). The reliability and validity of the models were evaluated based on the deviance and the significance level (Table 5.3.2). Of the 45 models, 22 were statistically significant.

**Table 5.3.2.** Deviance and significance of GAM relating CFCs variability and mean climate conditions in the study sites. ns – not significant ($p \geq 0.05$); *($p<0.05$); **($p<0.01$); ***($p<0.001$).

| | | BEECH | | PINE | | OAK | |
|---|---|---|---|---|---|---|---|
| | | Dev. | Signif. | Dev. | Signif. | Dev. | Signif. |
| PCP | pSUM | -0.1163 | ** | -0.0546 | ns | -0.1291 | ns |
| | pAUT | -0.1147 | *** | -0.0171 | ns | -0.0730 | ns |
| | WIN | -0.4489 | *** | -0.1018 | *** | -0.2105 | ns |
| | SPR | -0.0275 | ns | -0.3091 | * | -0.3458 | ns |
| | SUM | -0.2713 | *** | -0.1349 | ** | -0.1753 | ns |
| T.MAX | pSUM | -0.0724 | *** | -0.1343 | ns | -0.1519 | * |
| | pAUT | -0.0377 | ns | -0.0231 | ns | -0.1062 | * |
| | WIN | -0.0545 | *** | -0.0723 | * | -0.1088 | ns |
| | SPR | -0.1000 | ** | -0.2223 | ** | -0.1614 | ns |
| | SUM | -0.3159 | *** | -0.1251 | ns | -0.1115 | ns |
| T.MIN | pSUM | -0.0281 | ns | -0.0813 | * | -0.1271 | ns |
| | pAUT | -0.0645 | *** | -0.0251 | ns | -0.0693 | ns |
| | WIN | -0.1347 | *** | -0.1815 | ns | -0.1386 | * |
| | SPR | -0.0221 | ns | -0.0887 | ns | -0.0381 | ns |
| | SUM | -0.1116 | *** | -0.1355 | *** | -0.1265 | *** |

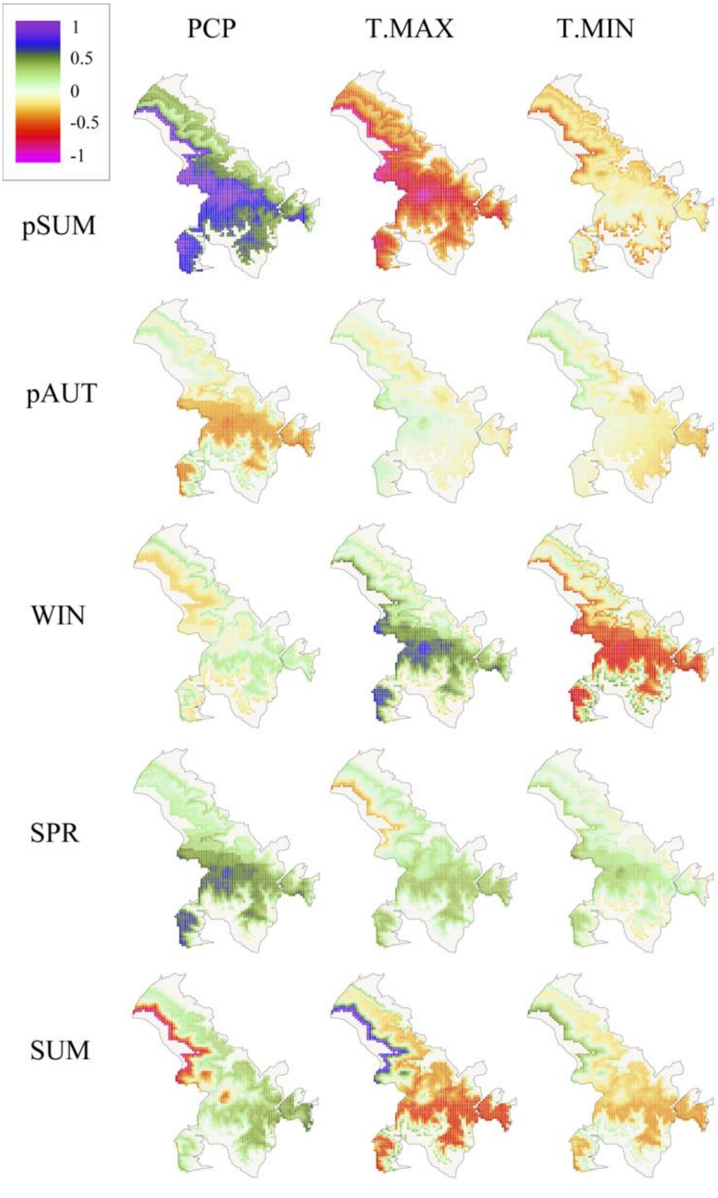


*Figura 5.3.4. Beech predicted correlation coefficients for the previous summer (pSUM) and current summer (SUM) precipitation (PCP) and maximum temperature (T.MAX) across the Moncayo Natural Park potential distribution area.*

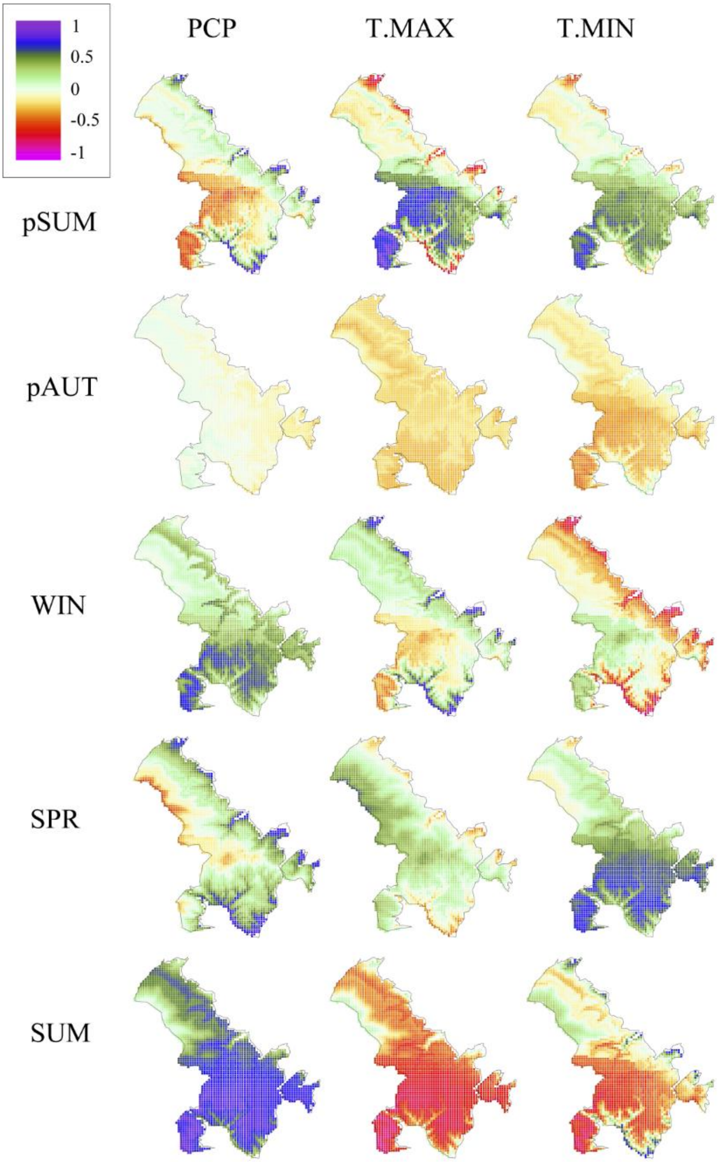


*Figura 5.4.5. Pine (P. sylvestris and P. uncinata): predicted correlation coefficients for spring (SPR) and summer (SUM) precipitation (PCP) and maximum temperature (T.MAX) across the Moncayo Natural Park potential distribution area.*

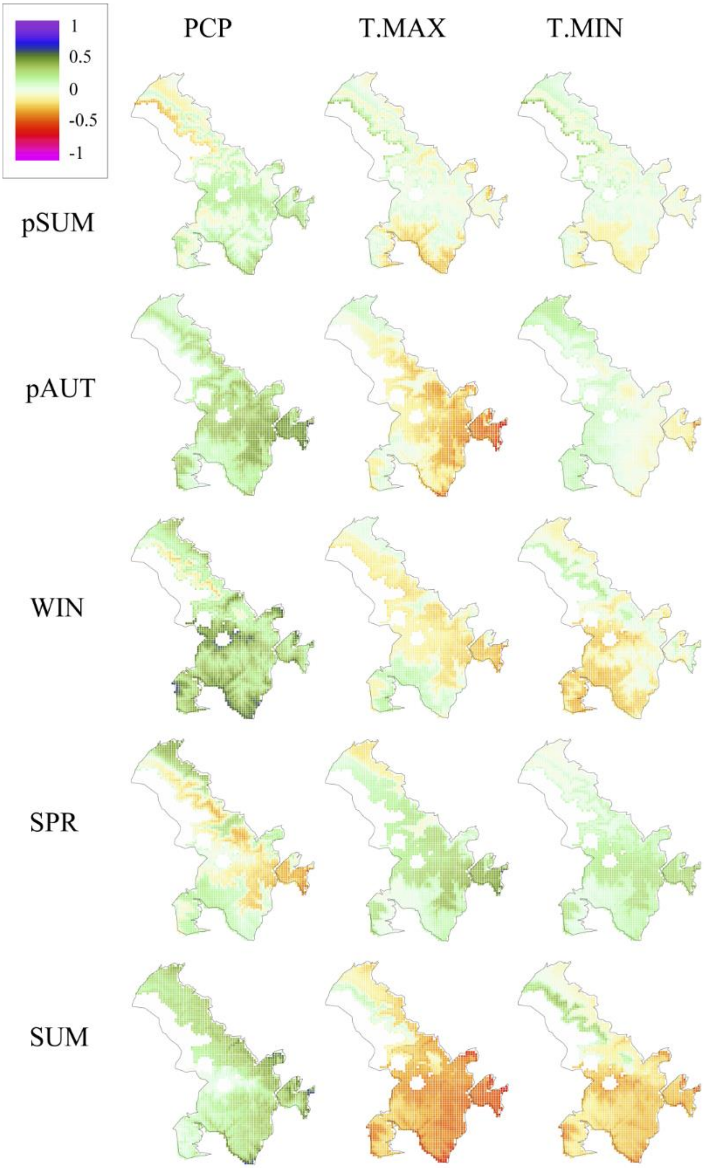


Figura 5.3.6. Oak: predicted correlation coefficients for winter (WIN), spring (SPR) and summer (SUM) precipitation (PCP) and summer maximum temperature (T.MAX) across the Moncayo Natural *Park potential distribution area*

In beech, previous summer precipitation influence was positive and the maximum temperatures played a negative role across the potential distribution area (Figure 5.3.4). The variations of CFCs associated with these climatic variables are not explained by the existing climatic gradients in the territory; therefore, the models are not significant (Figure 5.3.1). Current summer conditions had a distinct influence across the territory, shifting from positive to negative depending on altitude. The effect of precipitation for the current summer was positive in warm, dry, low-altitude areas, whereas it was negative at high altitudes where conditions were colder and wetter. High temperatures during summer affected growth positively at high altitudes and negatively at lower altitudes. Variations in CFCs during summer can be explained by climatic variability across the study areas as shown in Figure 5.3.1.

Pine growth was influenced mostly by spring and summer conditions during the current growing season (Figure 5.3.5). Precipitation in spring increased growth in low elevation zones, whereas in summer it was important all over the territory, especially in low elevation zones which are dryer. Maximum temperatures in spring increased growth in high elevation zones but in summer it became a growth-limiting factor, particularly in lower zones. In this case, CFCs significantly varied across climate gradients (Table 5.3.1).

The amount of precipitation boosted oak growth during the entire year of the growing season, although with different intensity (Figure 5.3.6). In general, the relationship between precipitation and growth was stronger in low elevation zones during spring and summer (Table 5.3.2). The occurrence of high temperatures during summer limited tree growth generally, with small variations across the study area.

### *5.3.4. Discussion*

#### 5.3.*4.1. Climatic influence on tree growth*

In Moncayo Natural Park, the studied trees (beech, pines and oaks) showed different patterns of climate sensitivity. Similar observations in climate-growth relationships at different elevations in mountain areas have also been detected in other studies (i.e., Hartl-Meier et al., 2014; Kharal et al., 2017; Ponocná et al., 2016; Wang et al., 2017). Moreover, there are some common elements for all the species, such as the general importance of summer conditions for tree growth and the variation in correlation with specific climate factors along spatial gradients.

Beech growth has proven to be sensitive to drought at numerous sites (Weemstra et al. 2013; Tegel et al. 2014; Cavin and Jump 2016; Farahat and Linderholm 2018) and also in southern marginal stands in Spain (Rozas et al. 2015; Dorado-Liñán et al. 2017). In this study we found that wet and cold conditions during the previous summer are favorable for beech growth whereas the influence of current summer conditions varied significantly along the spatial climatic gradient. At lower elevation sites, beech growth is negatively influenced by high temperatures and low precipitation during summer, which supports results of other studies (Chen et al., 2015; Zimmermann et al., 2015) and can be explained by the species' strategy of rapid stomata closure to prevent the risk of embolism and inactivation of the water transporting system (Aranda et al. 2000; Granier et al. 2007). Conversely, at higher elevations, growth is enhanced when summer conditions are warmer. Trees may benefit from higher radiation on summer, that promotes photosynthesis in higher and colder conditions, that compensates water stress and embolism on beech trees. Čufar et al., (2008) described a negative influence of August maximum temperatures on beech growth at higher elevation sites in Slovenia. This might be due to a prolonged growing season for the Slovenian beeches (until August) as reported by Prislan et al., (2013) whereas at our study site the growing period is rather short, lasting for 67 days at lower elevations and 80 days at higher elevations, starting in May or early June and ending by late-July or early-August (Martínez del Castillo et al. 2016). Therefore, beech may already be close to dormancy during the late summer. The influence of winter precipitation on beech growth differs along the altitudinal gradient; it is negative in high elevations and positive at low-elevation sites.

The growth of pines was mainly favored by wet and cold conditions during the current summer. In cold environments, high maximum temperatures during spring promoted an early start to the growing season which leads to an extended growing season that favored tree growth. Earlier cambium re-activation in pines is shown by heating experiments (Gričar et al. 2007). In summer, this relationship changed and pine growth was limited by high maximum temperature, which supports the findings of other studies (e.g., Martínez del Castillo et al., 2018b; Cailleret and Davi, 2011; Di Filippo et al., 2007) and likely related to increased drought stress caused by high evaporation rates. Pines are known to exhibit a plastic growth behavior which is indicated by their ability to anticipate favorable spring conditions and start growing early and also by re-activation of their growth after cessation from dry conditions during summer (de Luis et al. 2007b; Camarero et al. 2010; De Luis et al. 2011b; Novak et al. 2016; Martínez del Castillo et al. 2018a). Furthermore, at southern and/or low elevation sites with mild temperatures during winter, pines may not enter in a real dormancy period (Gričar et al. 2016; Prislan et al. 2016).

In the case of oak, water availability is largely determined by the amount of precipitation, which triggers tree growth in lower and dryer areas. Although oaks are known to be able to recover water potential due to a deeper and extensive root system when compared with beech (Aranda et al. 2000), a severe and prolonged water deficit leads to an irreversible cavitation of earlywood vessels with tylose formation (Pérez-de-Lis et al. 2018). Several studies identified the positive effect of spring/summer precipitation on the growth of ring-porous species (García-Suárez et al. 2009; García-González and Souto-Herrero 2017). Similarly, high maximum temperatures during summer limit oak growth across sites in Central Europe (Čufar et al., 2014; Mérian et al., 2011).

#### 5.3.4.2. *Spatial distribution of correlations between climate and growth*

As hypothesized, distribution patterns for correlations between growth of tree species and prevailing climate factors are at least partially, related to the existing climate gradients. The significance of the models proved that these influences of the seasonal climatic variables are explicable by the climate variability over the territory. This fact is most noticeable in beech, with 11 significant models out of 15, somewhat in pines, with 7 significant models out of 15 and less evident in oak, with only 4 significant models out of 15. Climate-growth relationships for the three species were tested with GAMs to create models which allow projection of the influence of climate on the growth of selected species along climate gradients within the study area.

Although the variance of some variables was largely unexplained and statistical significance was lacking (i.e., previous summer precipitation in beech), information obtained from the GAMs is still valuable. On one hand, significance models suggest the existence of a plastic climate-growth relationship for the species across the studied distribution area. Such plasticity indicates that the influence of a given climate factor is climatically determined and would probably be modified if changes in climate occur. This is key for the development of accurate predictions of species behavior across a study area under different climate change scenarios. Another fact is that the lack of significant models suggests that the influence of a given seasonal climate factor is constant across the study area (or at least not affected by prevailing climate conditions). The influence of such a seasonal climate factor is then expected to be more stable if changes in climate occur (at least if such changes do not exceed the actual climate range within the study site).

#### 5.3.4.3. *Applicability of the model approach in Moncayo Natural Park*

Over the last several decades, forest-management actions performed in MNP aimed at conserving and improving forested habitats (Martínez del Castillo et al. 2015). Specifically, the objectives for beech and Pyrenean oak forests are to improve their natural regeneration and to improve the quality and status of conservation, since these species are protected by the Habitats Directive. Conversely, pines were introduced in the park as reforestations and they are not protected by the Directive.

Or results showed that beech forest may be favored in the middle of the actual altitudinal range (1400-1500 m.a.s.l), and progressively extend to southern locations in the center of the Park where the species is currently not present. The climatic conditions of this new area are similar to the climatic conditions where beech forest is currently growing, and our models forecasted similar climate-growth relationships for the most important climatic variables influencing beech growth. However, it could not spread in the lowlands of this mountain due to higher temperatures and water scarcity.

The specific management actions in MNP for pines are aimed to naturalize the structure of the forest and reduce density by low-impact logging. The pine forest models showed that forest could be extended to high zones in the center part of the Park, which is partially unforested, given the similar climatic conditions of that area and the models results. By spreading pine forest cover to other areas, with logging actions the current pine forest at medium altitudes could be progressively replaced by protected species, in this case beech or Pyrenean oak, avoiding at the same time pine loss at MNP.

Pyrenean oak forests are affected by drought especially in low zones; therefore, logging actions to reduce tree density during dry years could compensate for growth reduction by decreasing competition. In addition, Pyrenean oak forests in Mediterranean areas largely have over-aged coppice stands where growth is reduced and trees are more sensitive to summer drought leading to oak-decline (Corcuera et al. 2006). Therefore, management actions to create uneven aged stands, as the proposed logging, may become necessary. Our results showed a positive reaction to water availability, consequently, these actions may not be necessary in rainy years, but could be very helpful during dry years.

Finally, the models suggest that the lower elevations in the southern part of the Park, in general, are not suitable for these tree species due to slightly different climate conditions.

#### 5.3.4.4. *Potential use of the model approach as a forest-management tool*

The climate-growth models, as presented in this study, provide a novel and complementary approach to forest-growth models or species-distribution models, which are important tools for forest management (Porté and Bartelink 2002; Wullschleger et al. 2014). However, those models are based on data mining or regression techniques and hence largely lack ecophysiological explanations (Walentowski et al. 2017). Although the present and future distribution of tree species is a complex combination of multiple biotic and abiotic factors, to date, models based on climate provide the best available guide for policy making (Pearson et al. 2004; Booth 2017). Moreover, our models are applied to a simple version of the fundamental niche for each species, unlike most of the species distribution models, that are based on current distribution without taking into account information on species climatic requirements beyond their potential distributions (Booth 2017).

The models are empirical and therefore the forecasted CFCs are applicable to the environmental domain from where the samples were taken. In this sense, the model interpolates the results within the environmental gradient (climatic-altitudinal gradient in this case) of the sampled area. In addition, both CFCs analysis and the modelling were carried out in a specific range of climatic variability; therefore, the results of our models are not able to be extrapolated outside this range. The extrapolation of the results outside the range (i.e., other locations of this forests species over Europe) would include unsolvable uncertainties that would produce unreliable results (National Research Council 2012). Nevertheless, the applicability of our new methodological approach is universal and may be applicable to any other environment. However, application of the approach requires a systematic sampling strategy to ensure that the application of the models do not exceed the range of values used to construct the models.

The same methodological approach can be applied to predict changes in climate-growth relationships under future climate-change scenarios. This requires input of a tree-ring network and high-resolution climate data, in addition to high-resolution future climate projections. Future climate conditions can exceed the range of the current climate variability; therefore, the models would have to extrapolate the results which might not be realistic. A methodological effort should be done in the future to address these topics, due to the importance of forest performance in future climates.

Forecasting future distribution of species is a complex task. The plastic response of species to climate variability is a key factor but it is not sufficiently incorporated into current modelling approaches. Complementary approaches, as presented here, can improve these models, but dense tree-ring networks are required.

### *5.3.5. Conclusions*

The study on the growth response of beech, Scots pine, Mountain pine and Pyrenean oak in Moncayo Natural Park yielded information on spatial changes in climate-growth relationships across the altitudinal gradient. This was mainly related to different climatic conditions; therefore, the altitude of the sampling needs to be considered in dendroclimatological studies performed in the edge distribution limit of the species or in areas with large elevation gradient.

The study presents the current relationship between tree species and climate within their realized elevation range as well as the design and application of tree-ring based models to predict performance of the species across the potential distribution areas in the Park. The model results indicate that the total forested area could be expanded with additional management actions, mainly to higher altitudes and in a central zone of the Park which is currently unforested.

Forest management policy needs better tools to manage the distribution of tree species on afforested areas according to current and expected changing climatic conditions. The newly developed modeling approach can form a key tool to support concrete forestry decisions about species selection and estimation of species performance in specific areas for which it is calibrated. Apart from their direct application, the models showed a potential for direct integration into decision-making systems in a sustainable multifunctional forest management environment. The application of the actions derived from the models would enhance sustainable forest management and could help to mitigate climate change effects.

## 5.4. Modeling tree-growth: Assessing climate suitability of temperate forests growing in Moncayo Natural Park (Spain)

### *5.4.1. Introduction*

In recent decades, forests have been altered by the effects of climate change. The effects of variation in climate conditions affect forests by changing the frequency and severity of natural hazards, such as fires, droughts, windstorms, late frost events, or insects and pathogen infestations (Dale et al. 2001). Those changes are also produced as a consequence of the interaction of numerous factors not related to natural disturbances: for instance, human activities shape forest systems, influencing their compositions, structure, and distribution (Dale et al. 2001). These activities include the intensification of forestry and agriculture, urban development, tourism, and intense recreational use, which increasingly threaten forested landscapes (Romero-Calcerrada and Perry 2004). Furthermore, the prompt abandonment of traditional activities, such as grazing, silviculture, and the demographic recession in rural areas, are causing imbalances in forest ecosystems.

Mediterranean forests are a living example of these processes, where the abandonment of agricultural land has also led to an expansion of shrubland and woodland cover (Debussche et al. 1999; Romero-Calcerrada and Perry 2004; San Roman Sanz et al. 2013). In this respect, Moncayo Natural Park, located in Spain, exhibits numerous characteristics of a typical area where once traditional local activities have progressively ceased. Traditionally, the forest was intensively used by the local population mainly for logging activities (i.e., charcoal making and firewood) and cattle exploitation (Martínez del

Castillo et al. 2015); therefore, the structure of forest was maintained as a meadow with old isolated trees or small stands mixed with open air grass zones. At the beginning of the 20th century, the involvement of the Spanish government in forest policies through reforestation led to intensive plantations (Ortigosa et al. 1990), with the aim of restoring degraded landscapes and increasing hydrological control, but the reforestations in some cases were regarded as excessive (García Pérez and Groome 2000). In the case of Moncayo, two pine species were introduced to reforest the scarce vegetation mountain slopes, occupying the natural distribution area of beech and oaks (Pellicer 2000). Later, in 1978, the area was protected as a Natural Park to preserve the special ecological values of this mountain.

All these changes in land use caused important modifications to forest cover and species distribution, which implies the need for a management strategy for forest adaptation and to ensure the preservation of the ecological values of the Natural Park, considering the different temporal scales over which ecological mechanisms and rapid environmental changes act (Vilà-Cabrera et al. 2018). This also implies that the spatial distribution of the forest species does not correspond with its potential distribution. In addition, accurately assessing the potential distribution is complex, since species distribution modeling and ecological niche modeling studies usually estimate species climate requirements by conventional analyses of only their current distributions (Booth 2017). This could be especially problematic in geographically isolated populations located at the rear edge of their distribution and adapted to local environmental conditions. These facts further highlight the need for holistic management plans based on predictions of species' performance in their natural distribution and beyond.

Tree secondary growth can be used as an indicator of tree health and general performance; this dynamic process is influenced by a complex interaction of tree physiology which, in turn, is controlled by environmental conditions (Fonti et al. 2010). Indeed, phenotypic plasticity in secondary growth allows trees to adapt to specific environmental conditions and is crucial for them to withstand environmental changes during their lifetime (Vitasse et al. 2010; Gricar et al. 2015). Therefore, knowledge of the variability of tree growth across the climatic gradients of the species distribution area may be helpful to assess forest conservation and to identify optimal zones of forest expansion.

Here, we present a novel approach to characterize the optimal zones of forest growth and potential expansion through growth suitability maps resulting from the combination of a dense tree-ring network of the main forest species of Moncayo Natural Park and a high-resolution climate dataset. Our specific objectives were defined as follows: (i) to determine the climate elements which affect tree secondary growth in *Fagus sylvatica*, *Pinus sylvestris*, *Pinus uncinata*, and *Quercus pyrenaica* at the Moncayo Natural Park; (ii) to predict the potential growth of these species all across the Natural Park area; and (iii) to establish suitability zones for each species in the park as a tool to contribute to the improvement of forest management policies

### *5.4.2. Materials and methods*

#### 5.4.2.1. Climate data

The relatively rugged orography of the Moncayo massif is a barrier to the western and northwestern fronts, resulting in frequent convective activity and consequent precipitation in high altitudes that progressively decreases with altitude.

Climate grids were generated with the *reddPrec* R package (Serrano-Notivoli et al. 2017c) based on the reconstructed stations of Serrano-Notivoli et al. (2017a). The climatic variables generated were precipitation and maximum and minimum temperature, at an annual scale for the period 1950–2012, with a spatial resolution of 200 meters (Figure 5.4.1).

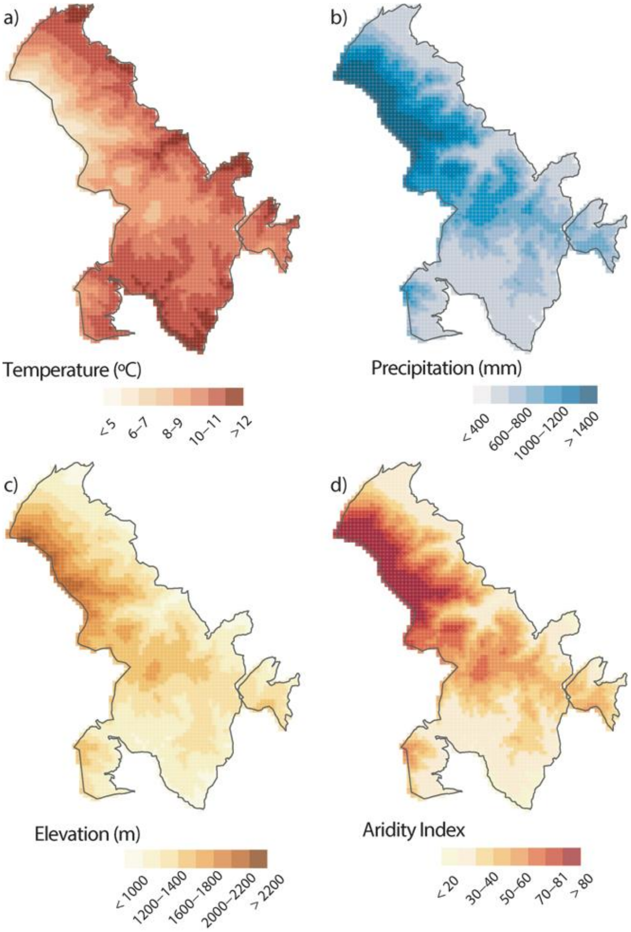


*Figura 5.4.1. Grids of climate variables. a) Mean annual temperature, b) annual precipitation, c) elevation, and d) De Martonne Aridity index.*

The climatic conditions varied widely, considering the area of the Natural Park. The monthly distribution of precipitation ranged from less than 20 mm in the summer months at low elevation to more than 170 mm in May or November at high altitudes, resulting in a range of annual precipitation from 387 to 1572 mm. The difference in maximum and minimum temperatures in the altitudinal range is from 6 ºC to 8 ºC warmer in low altitudes throughout the year.

A measure of aridity which integrates precipitation and temperature data has been calculated for each point of the climate grid. The aridity index (AI) proposed by De Martonne (1926) is given by the following relationship:

$$AI = \frac{P}{10 + T}$$

where P is the annual mean precipitation (in mm) and T (in °C) the annual mean air temperature. The climate types defined by AI vary from arid (0–10), semi-arid (10–20), Mediterranean (20–24), semi-humid (24–28), humid (28–35), very humid (35–55), to extremely humid (>55). The range of values of AI inside the Natural Park ranged from 17.96 to 109.84, with a mean value of 44 (Figure 5.4.1).

#### 5.4.2.2. Field sampling and sample processing

We sampled 40 sites, distributed across the species range and along a broad elevation range, from 950 to 1900 m.a.s.l. in the Natural Park (Table 5.4.1). The sampling covers the elevation range of the four species in the study area. A total of 427 trees were sampled from 2009 to 2014, extracting from 1 core (4.91% of the cases) to 2 cores (95%) per tree. At each site, the cores were taken at DBH from 5 to 25 healthy, dominant, and mature trees, using increment borers of 40 or 50 cm length.

**Table 5.4.1.** Summary of current species distribution and sampling points by species.

| | | Altitude range (m a.s.l.) | Mean Tº range (ºC) | Mean precipitation range (mm) | No. Sites | No. Trees | Time span (y) |
|---|---|---|---|---|---|---|---|
| Moncayo Natural Park | | 853 - 2276 | 11,8 - 4,4 | 387 - 1572 | | | |
| *F. sylvatica* | Actual distribution | 1115 - 1723 | 10,4 - 7,2 | 569 - 1413 | | | |
| | Sampled sites | 1150 - 1600 | 10,1 - 8,1 | 647 - 1274 | 15 | 150 | 1799 - 2014 |
| *P. sylvestris* | Actual distribution | 909 - 1834 | 11,4 - 6,7 | 448 - 1461 | | | |
| | Sampled sites | 1020 - 1635 | 10,5 - 7,9 | 544 - 1301 | 8 | 117 | 1919 - 2014 |
| *P. uncinata* | Actual distribution | 1296 - 2144 | 9,6 - 5,1 | 649 - 1546 | | | |
| | Sampled sites | 1765 - 1900 | 7,2 - 6,8 | 1157 - 1450 | 3 | 30 | 1935 - 2011 |
| *Q. pyrenaica* | Actual distribution | 909 - 1420 | 11,4 - 8,8 | 430 - 1110 | | | |
| | Sampled sites | 950-1550 | 10,8 - 9,2 | 464 - 929 | 14 | 130 | 1739 - 2013 |

In the laboratory, the cores were air-dried and mounted into wooden supports which were correctly oriented to show the transversal section after the samples were polished. The cores were scanned with a 2400 ppi resolution scanner and then cross-dated using CooRecorder v8.0 software (Larsson 2010). The ring widths of each core were measured using a

LINTAB™ 5 measuring device (Rinntech, Heidelberg, Germany), with a precision of 0.01 mm, and the TSAP-Win program. The quality of the dating and measuring were checked with quantitative methods with the program COFECHA, which dates the growing series against the master dating series using moving correlation analysis (Grissino-Mayer 2001). Cores including evident wood anatomical anomalies and those not successfully dated were discarded from further analysis. Finally, a total of 61,229 tree rings were dated and measured. The size of each tree (basal area) previous to each tree-ring formation was calculated for each ring, using the diameter at breast height and subtracting the tree-ring measures.

#### 5.4.2.3 Predictive growth models

Species-specific generalized linear mixed-effects models (GLMM) using a Poisson distribution of the errors were used to describe variation in tree-ring width (TRW) as a function of climate conditions.

Model <- glmer($TRW_t$~ ($AI_{mean}$ * Climate $variables_t$) + ($BA_{t-1}$ | Tree identity), family=poisson(link="log")

Total seasonal precipitation and mean seasonal maximum and minimum temperatures (from the previous summer to current autumn) were used as independent variables.

Since the importance of the different climatic elements may significantly differ across species distribution, the mean aridity index ($AI_{mean}$) was also included in the model as a site index reflecting the mean climatic characteristics of each study site. The interaction between the $AI_{mean}$ and the seasonal climate variables was also considered.

To take into account variations in the TRW of each individual tree, tree identity was used as a random effect variable. In addition, given that radial growth is well known to vary as a tree becomes larger/older (Bowman et al. 2013), the basal area of the tree in the previous year of each tree-ring formation (BA) was also included in the random term. All independent variables were standardized before model constructions to guarantee a compensated weight of each variable.

Model construction was based on information for the period of 1950 to 2013 due to the common availability of both tree-ring measurements and climatic data. The models were evaluated with a chi-squared test comparing the model (full model) with a null model (constructed including only the random effects).

In addition, the applicability domains (AD) (Norinder et al. 2016) should be considered when discussing the predictive performance of statistical model. For each species, the predictive growth models included -as independent variables- the climate conditions occurred during the year of each tree-ring formation. As a consequence, a wide range of climate conditions contained in the dendrochronological dataset of each species defines the AD of each model.

Despite the limited actual distribution of species across the Moncayo Natural Park, dendrochronological sampling, containing tree-rings from different sites and years, include a wide range of climate conditions that allows extending the domain of the obtained models to outside their actual distribution range. The climate grid included 2801 points for which seasonal climate values were estimated for the period 1951-2012 (62 years). Whether climate conditions occurred in this set of 2801*62 situations are included in the climatic domain of the dendrochronological dataset of each species has been calculated to define the AD of each model.

Finally, a suitability index was defined and calculated for each pixel as the ratio between the mean tree-ring width predicted in each pixel and the maximum tree-ring width predicted in the whole Natural Park. Thus, suitability index values for each species could vary from 0, which indicates minimum suitability, to 1, meaning maximum suitability (i.e., a value of 0.5 indicates that the growth is half of the potential maximum growth).

### *5.4.3. Results*

#### 5.4.3.1. Radial growth across species

The dendrochronological network consisted in 40 sites, where a total of 812 cores were taken, ranging from 5 to 25 trees per site (Table 5.4.1). Altogether, more than 60,000 rings were dated and measured. The tree structure of the sampled trees (DBH) and the tree-ring widths varied among the species, as shown in Figure 5.4.2. The DBH ranged from 5.74 cm, recorded in *Q. pyrenaica*, to 53.72 cm, in the case of *P. sylvestris*, with mean values of 14.54 (*Q. pyrenaica*), 21.69 (*P. uncinata*), 26.55 (*F. sylvatica*), and 29.73 (*P. sylvestris*). The tree-ring width measurements varied from 0.012 to 8.87 mm. in *Q. pyrenaica*, from 0.57 to 6.45 in *P. uncinata*, from 0.085 to 11.58 in *P. sylvestris*, and from 0.01 to 8.27 in case of *F. sylvatica*. The lower mean value was 1.057 (*F. sylvatica*), followed by 1.502 (*Q. pyrenaica*) and 2.116 (*P. sylvestris*), and the higher value was 2.296 mm (*P. uncinata*).

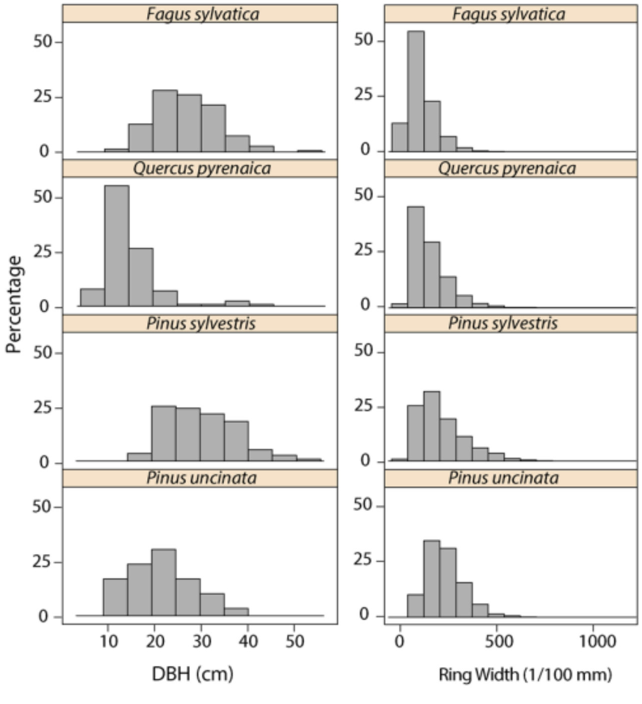


*Figura 5.4.2. Histograms of the DBHs of the sampled trees and the measured tree-ring widths.*

### 5.4.3.2. Predictive tree growth models

Predictive growth models for the analyzed species are shown in the supplementary materials (Table S5.4.1, S5.4.2, S5.4.3, and S5.4.4). Overall, most of the climatic parameters included in the models presented a significant relevance in all species. For *F. sylvatica* and *P. uncinata*, the only parameter without a significant contribution to the model was the interaction between the $AI_{mean}$ and the maximum temperature of the previous autumn; in the case of *P. sylvestris*, it was the $AI_{mean}$, meaning that the spatial variation of the aridity index did not have a significant relevance in the construction of a growth model of this species. Lastly, all parameters included were significant in the *Q. pyrenaica* growth model. The models were able to explain 66% of the total variance in the case of *P. uncinata* and 73%, 75%, and 80% in the cases of *F. sylvatica*, *Q. pyrenaica*, and *P. sylvestris*, respectively.

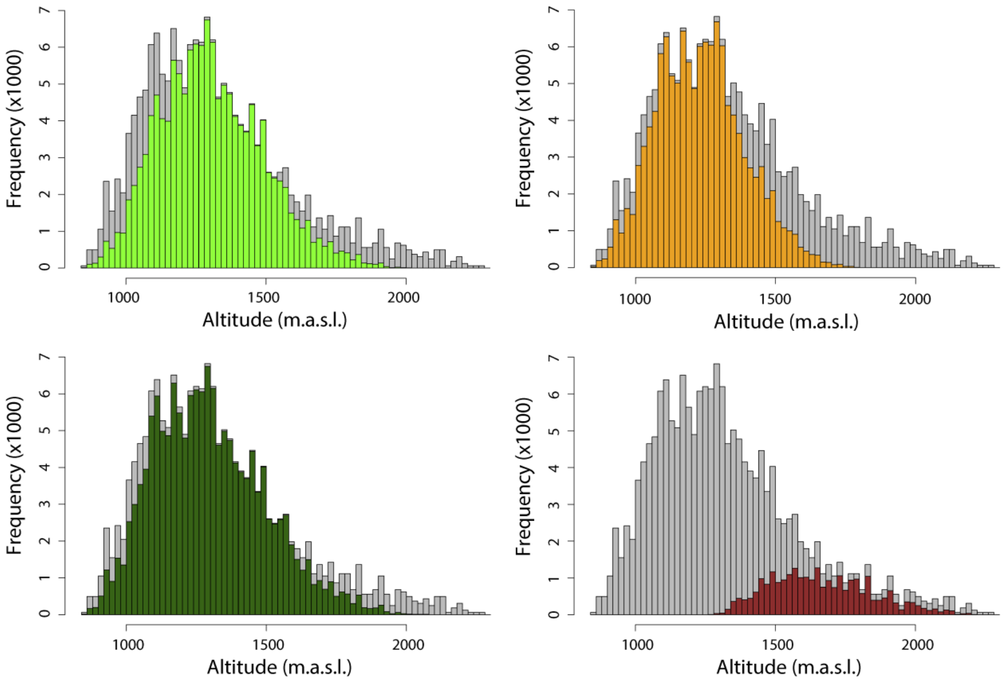


*Figura 5.4.3. Applicability domains. The altitudinal distribution of the climate range of each specie (for a) Fagus sylvatica, b) Quercus pyrenaica, c) Pinus sylvestris, and d) Pinus uncinata) F. sylvatica) overlapping the climate range across Moncayo Natural Park (grey bars).*

AD of each specie is shown in Figure 5.4.3. For *F. sylvatica*, AD includes a wide climate domain that is representative of most of the climate conditions occurred across the Natural Park from 1200 to 1600 m of altitude. At lower and higher altitudes, only certain climate conditions occurred during the period 1951-2012 are represented in the tree-ring network (Figure 5.4.3a). In case of *Q. pyrenaica*, the AD is representative of most of the conditions occurred at lower altitudes while it decrease progressively at altitudes higher than 1400 m (Figure 5.4.3b). Representativeness for *P. sylvestris* is wider including most of the climate conditions occurred from 1000 to 1800 m (Figure 5.4.3c). On the contrary, the dendrochronological network of *P, uncinata* shows a relatively good representativeness of climate conditions occurred at higher altitude being not representative of conditions occurred below 1350 m (Figure 5.4.3d).

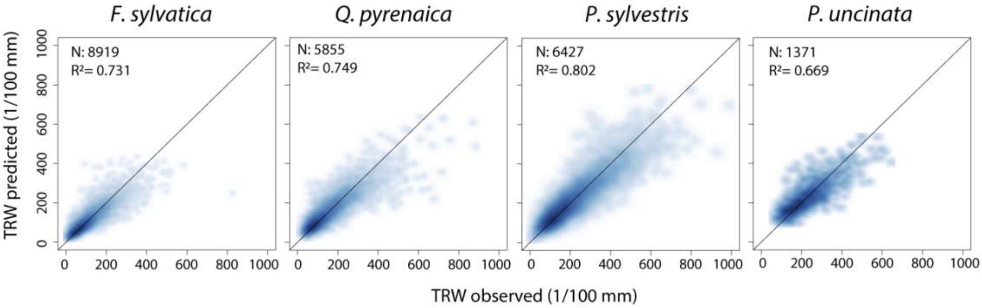


*Figura 5.4.4. Tree ring width predicted using the GLMMs versus measured tree ring width. Number of observations (N) and agreement between observations and predictions are indicated (r2).*

The growth predictions of the models (Figure 5.4.4) were computed for each species for all grid extensions (2801 points) and for all years with climate data (62 years). The spatial distribution of the mean TRW predicted at each point is shown in Figure 5.4.5 (left panel) and the distribution of the values across the altitudinal gradient of the Natural Park is shown in Figure 5.4.5 (upper-right panel).

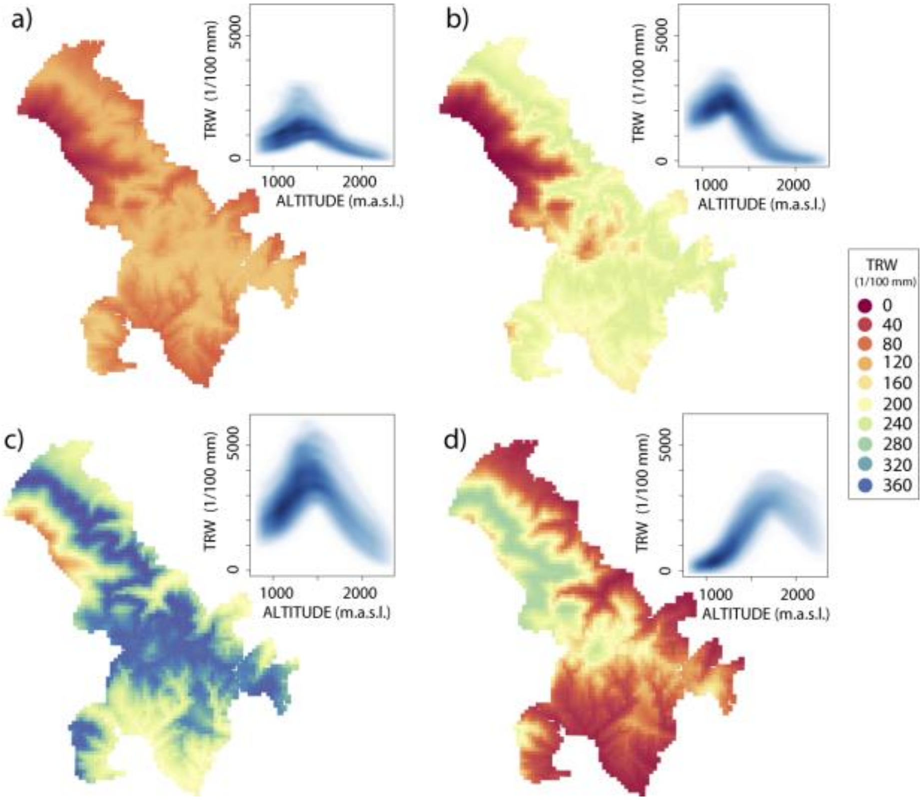


*Figura 5.4.5. Growth predictions developed by GLMM models for a) Fagus sylvatica, b) Quercus pyrenaica, c) Pinus sylvestris, and d) Pinus uncinata. Maps represent the mean annual growth predictions for the period 1951–2012 and graphs include the variability through the years across the Moncayo Natural Park.*

The maximal predicted growth of *F. sylvatica* was reached at 1337 meters. The predicted growth rapidly increased from 1000 m a.s.l. to the peak, slowly decreasing at higher altitudes. There was a higher variability in predicted growth between 1100 and 1600 m due to the different climate conditions among sites with a similar altitude across the park. Overall, the growth rates in this species were lower compared to those of the others. *Q. pyrenaica* growth reached its maximum at 1240 m a.s.l., which is higher than the mean altitude where the species is present (1118 m). At high altitudes, growth progressively decreases as the climate conditions change, reaching near-zero values of ring width over 2000 m. By contrast, *P. sylvestris* showed a high variability in their growth predictions, with this variability being rather constant along the altitudinal gradient. The maximum growth is predicted at 1430, almost 100 meters higher than the actual mean altitude of the species. Lastly, *P. uncinata* growth predictions reached minimum values at lower altitudes, which include most of the Natural Park, especially in the south and a maximum growth at 1760 m. For all the four analyzed species, the higher growth rates predicted are located within the applicability domains (AD) of predictive models which support their reliability. On the contrary, predicted growth of *P. uncinata* and *Q. pyrenaica* at lower and higher altitudes respectively, should be interpreted with special caution since represents extrapolations of the constructed models out to their AD.

Climate suitability defined by growth models was applied to the Natural Park cover for all species (Figure 5.4.6). Overall, inside the actual distribution of the species, the suitability index was high: *F. sylvatica* is present in 155 pixels, of which 81.6% scored more than 0.8 of suitability and only 4.4% less than 0.5. *Q. pyrenaica* achieved the best match between the actual distribution and the suitability index, at over 145 pixels, where 99.3% scored more than 0.8 and none less than 0.5. *P. sylvestris* was the most extended species, with a presence in

432 pixels and 78.9% with a high suitability (>0.8) and none with suitability below the average value. *P. uncinata* was present in 121 pixels, with 89.3% over 0.8 and with 5.79% under 0.5 in the suitability index.

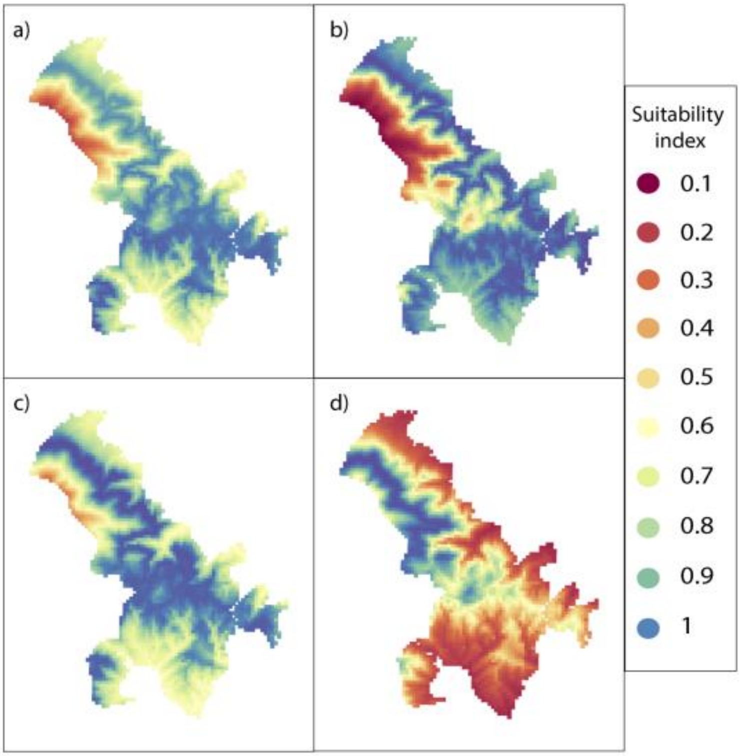


*Figura 5.4.6. Climate suitability maps ranged from 1 (maximum) to 0 (minimum) for a) Fagus sylvatica, b) Quercus pyrenaica, c) Pinus sylvestris, and d) Pinus uncinata.*

Furthermore, the suitability maps showed zones where the species are not present at this moment, but which were highly suitable for them. Considering the whole study area, consisting in 2801 pixels, the *F. sylvatica* suitability was high in large areas over the territory. Specifically, its suitability reached 0.9 in 525 pixels, and 0.8 in 1133 pixels—in other words, 40% of the territory—in contrast to the actual presence in just 5.5% of the park. *Q. pyrenaica* counted 223 pixels with more than 0.9 suitability points and without species presence, especially in low-elevation zones. *P. sylvestris* showed a high suitability index, although *F. sylvatica* and *Q. pyrenaica* were more suitable in 79 and in 108 pixels, respectively, leaving only 71 pixels where the most suitable species was *P. sylvestris*. Lastly, although *P. uncinata* is restricted to high-elevation zones occupying the majority of the suitable zone, the higher values of suitability were located at 1762 m a.s.l., higher than the mean of its actual distribution.

### *5.4.4. Discussion*

#### 5.4.4.1. Modeling climate suitability

The use of mixed-effects models applied to TRW, including climatic components and tree size as independent variables, has been proven to have the potential to predict the growth variability of species across the Natural Park. Indeed, between 65 and 80% of the variability was explained by the models, depending on the species. Other abiotic variables can interact with tree growth, such as topography, aspect, soil associations, or current management (Parresol et al. 2017; Vennetier et al. 2018), and certainly may improve the accuracy of the models, but those variables are difficult to extrapolate over the territory and would introduce uncertainties into the growth models.

The proposed models are based on easily available variables (i.e., the high resolution gridded climate dataset and tree-ring width measurements) and allow predicting a species' growth all over its distribution and in other zones where the species is not present. Like every forecasting model, these predictions are subject to uncertainties especially in areas or years where climate conditions are outside the applicability domain (AD) of species specific species. Alternative modeling approaches as classical species distribution models or ecological niche modeling are not free of such inherent limitation but fail also to integrate biological information as included in our approach (Booth 2017; Walentowski et al. 2017) that may help to obtain a more realistic approximation of species growth patterns.

Applicability domains (AC) represents the climate domains where models may exhibit sufficient predictive performance for training samples (dendrochronological network) and thus for new samples. In addition, for a different combination of seasonal climate conditions located inside the AD, their growth estimates are also expected to be as reliable as those in the training sample. However, if they are outside the AD, reliability of their estimates decrease and interpretation of predicted growth patterns should be interpreted with caution. This can be especially the case of *P. uncinata* model apply to low elevation sites and *Q. pyrenaica* model apply to high elevation areas.

Despite inherent limitations related to the applicability of obtained models all across the Natural Park, we apply them to the full climate grid. Then, for each grid pixel and for each species, the mean of the predicted TRW for all years was calculated as a general growth forecast. In addition, to guarantee the comparison between species and study sites, the tree-ring width was predicted for a theoretical tree with a common basal area of 252.91 cm2 (equivalent to 17.97 cm of diameter at breast height), which is the mean basal area of all analyzed trees before each tree ring formation.

#### 5.4.4.2. Climate-smart plastic behavior of tree species

Climatic variability is a key explanatory element of the different patterns of forest growth and its distribution around the world (Vicente-Serrano et al. 2013). The ability of forests to respond to changes in climate through genetic adaptations or phenotypic plasticity will play a decisive role in species distribution conditioning their expansion, recession, or even extinction (Matesanz et al. 2010; De Luis et al. 2013; Gentili et al. 2015).

In the case of the Moncayo Natural Park, all the studied species are in their distribution limits; therefore, their growth is likely to be constrained by the climate. *F. sylvatica* is a widespread European species, reaching at this point its southernmost forest stands. This late-successional and highly-competitive species is known to be sensitive to drought and high temperatures (Zimmermann et al. 2015; Bolte et al. 2016), both in the southernmost or xeric limits (Rozas et al. 2015) and in the core of their distribution in central Europe (Babst et al. 2013). Particularly in our study site, the growth of *F. sylvatica* is limited by an extremely short growing period: i.e., between 2 and 3 months, the shortest xylogenesis period reported in the literature (Martínez del Castillo et al. 2016). Our results confirm that growth is influenced by climate; previous and current summer conditions play an important role in this influence, and the combination of all climatic factors explains 73% of the within-tree-total growth variability. The importance of the mean value of the aridity index and its interaction with all other climatic variables in the models is indicative of the plasticity and adaptation of the species; the climatic stressors for tree growth vary across the prevailing climate.

*Q. pyrenaica* is a deciduous transitional sub-Mediterranean oak, of a character that is between Mediterranean and mesic, which finds its western edge in this region. One of the main physiological adaptations of this species is the duration of the growing season (i.e., about six months), delaying the early phenological phases to avoid late-frost events (Souto-Herrero et al. 2018). Although this species is more tolerant to both winter frost and summer drought than other *Q.* species, water stress in late spring and summer are the main constraints for xylem production (Pérez-de-Lis 2016). The combined climatic variability in the region explains 75% of the growth variability. The model shows predictions of zero growth in high elevations, constraining the possible distribution limit of the species.

The main climatic threat and stressor to *P. sylvestris,* which is one of the most widely distributed tree species over Europe in this region, is water availability, which is important throughout most of the year, as pines have a long growth period, reaching up to seven months of xylogenesis (Martínez del Castillo et al. 2016, 2018a). This species presents great variability in its growth predictions all over the Natural Park, showing its plastic behavior. On the other hand, *P. uncinata* presents less coverage over Europe and is usually limited to hilly mountains. This species has been widely used for climate reconstructions, and its growth and wood density is closely related to temperature (Büntgen et al. 2010; Konter et al. 2014) and drought (Tejedor et al. 2015), in accordance with the limited growth predictions in lower elevations and drought-prone environments with higher temperatures. Although both species showed a remarkable climate sensitivity, the explained variability of growth derived from climate varied between these two pine species, at 80% in *P. sylvestris* and 67% in *P. uncinata*.

In all studied species, the importance of the climatic variables significantly differs along the prevailing climate of each zone (e.g., a specific climatic variable can affect growth in one way in warm zones, but not in cool zones, or even affect it in the opposite way). This can be explained by the plastic behavior of tree species throughout the altitudinal gradient to specific climate conditions; overall, in higher altitudes, temperatures become more important than precipitation (Martínez del Castillo et al. 2018b). Such genetic adaptations, phenotypic plasticity, or both have been studied in other extensive analyses (Richter et al. 2012; De Luis et al. 2013) and have to be considered as an important matter in growth predictions over climate change scenarios.

#### 5.4.4.3. Climate suitability for forest management

The definition of a suitability model for forest species has been developed for management purposes since the 1980s (Tikkanen et al. 2007). Other studies dealing with the calculation of a habitat suitability index include diverse information, but they are usually incomplete, because they do not incorporate all underlying mechanisms of variation (Elith et al. 2002). Nonetheless, the climate effect is clear and present in all modeling. Therefore, assessing the climate suitability of tree species is the necessary first approach for both species modeling and management actions designed as assisted migration (Koralewski et al. 2015). In addition, the spatialization of the suitability index through the cartography of suitability—covering all of the Natural Park area—provides useful and important information for managers, such as the identification of areas where one species can be substituted by others, or favorable edges for species expansion. In this case, the potential growth is used as an integrative variable of population fitness over the territory.

Specifically, the suitability maps indicated large areas of potential expansion for all species, balanced overall by altitude. *Q. pyrenaica* showed great potential in low-elevation zones below 1100 m.a.s.l., while, for *P. uncinata*, higher performance was forecasted in high altitudes, with values even higher than its actual distribution. *F. sylvatica* and *P. sylvestris* shared their highest suitability zone in the mid-range of the altitudinal gradient of the Natural Park where the species are present, but also in the central part of the Park, which is currently under-forested. These two species are growing in the same altitudinal range, competing in their expansion. In this sense, previous research proved that *F. sylvatica* may partially substitute *P. sylvestris* areas (Martínez del Castillo et al. 2015), in accordance with recent global studies that revealed a consistent directional substitution of Pinaceae by Fagaceae worldwide (Alfaro Reyna et al. 2018) or studies showing the drought-related vulnerability of *P. sylvestris* (José Vidal-Macua et al. 2017; Sánchez-Salguero et al. 2017)

The comparison between the actual distribution of these four species in this Natural Park and the suitability maps revealed that *F. sylvatica* and *P. uncinata* are growing, in some cases, in zones with a low level of suitability, while the other two species grow in more suitable zones; therefore, the first two species may not reach their potential distribution in the Natural Park and may be favored.

### *5.4.5. Conclusions*

This study shows a novel methodology to assess the climatic suitability of forest species based on models that integrate tree growth with climate. As a case study, we addressed the climatic suitability of four tree species which are protected in

Moncayo Natural Park, in Spain. Among the investigated species, *F. sylvatica* showed a plastic behavior limited by its short growing season, but with possibilities of expansion over new zones, since it is growing in middle-suitable areas. The potential presence of *Q. pyrenaica* is limited at higher altitudes, in accordance with its climatic constraints, and it is already occupying the most suitable zones within the Moncayo Natural Park. However, potential expansion areas already exist at lower elevation zones. *P. sylvestris* share their most suitable climatic zone with *F. sylvatica*, and the promotion of one of these species may be at the expense of the other. *F. sylvatica* is an autochthone species that showed great potential to substitute the reforested *P. sylvestris* in large zones of its actual distribution. Finally, *P. uncinata* could be expanded in higher zones, where conditions are cooler and moister.

Overall, the studied species showed a certain level of climatic plasticity, and the models showed that their actual distribution is limited compared to the potential distribution given by the suitability cartography. In this sense, the proposed methodology and the application of the suitability maps may be a key element in policy-making related to adaptive management actions in forests subjected to climate change impacts.

# CAPITULO 6

# CONCLUSIONES

## 6. Conclusiones

En esta tesis se analizan tanto la distribución como el crecimiento de las principales especies forestales presentes en el Parque Natural del Moncayo, persiguiendo como fin la aplicabilidad de sus resultados a la gestión y manejo forestal, detalladas por especies.

El hayedo:

- En el periodo 1987 - 2010, ha visto su superficie incrementada en 38 has, llegando a las actuales 500 ha de extensión.
- Encuentra su óptimo de crecimiento en los 1340 m, que coincide con la altitud media a la que se encuentra esta especie en el Moncayo. Los limitantes climáticos, que son principalmente la precipitación y las temperaturas máximas del verano previo, hacen que la duración de la estación de crecimiento oscile entre los 48 y los 75 días, siendo la más corta entre las descritas en toda Europa.
- El Parque Natural del Moncayo contiene extensas zonas (hasta 2000 ha) de elevada idoneidad climática, actualmente ocupadas por otras especies o por espacios desarbolados, en las que el hayedo podría incrementar su área de distribución.

El pinar:

- En su totalidad, ha visto disminuida su extensión unas 80 ha desde 1987, siendo sustituido por otras especies y, aun así, es el género con mayor presencia en el Parque, cubriendo aproximadamente el 20% del mismo.

- La duración de la estación de crecimiento secundario en *Pinus sylvestris* varía entre los 139 y los 170 días, esto es más de cinco meses, siendo la mayor duración reportada hasta el momento en el conjunto de su área de distribución mundial. Los principales limitantes climáticos para su crecimiento son las precipitación y altas temperaturas de primavera y las precipitaciones de verano.
- El crecimiento óptimo para *Pinus sylvestris* se da a 1425 m, ligeramente más alto que la media de su distribución media actual (1347 m) y para *Pinus uncinata,* a 1762 m, resultado más cercano a su media.

El rebollar:

- Ha perdido un total de 56 has de las casi 800 ha que contaba en 1987.
- Esta especie solo se encuentra en zonas donde la idoneidad climática para la especie es alta; el 99.3% de su extensión actual se da en zonas son idoneidad mayor a 0.8 puntos. No obstante, hay más de 850 ha dentro del Parque con una idoneidad climática muy alta (>0.9) y no ocupadas por esta especie.
- Su máximo de crecimiento se encuentra a los 1240 m de altitud, mientras que la altitud media actual a la que se encuentra la especie es inferior (unos 1118 m). A mayor altitud, existe una mayor disponibilidad de agua durante

todo el año, lo que representa el principal limitante climático al crecimiento de esta especie.

En resumen, los resultados obtenidos durante el desarrollo de esta tesis pueden ser de utilidad para la gestión forestal relativa a estas especies. Los artículos publicados hacen referencia la gestión forestal y en ellos se pueden encontrar información de interés para los gestores de este espacio natural protegido, al mismo tiempo que su aplicabilidad puede ser útil en otros espacios forestales. La transferencia del conocimiento generado se hace necesaria para el desarrollo de medidas orientadas a la protección de los bosques y la adecuación a los cambios climáticos y de carácter global que acontecen actualmente y que pueden verse incrementados en el futuro.

## Conclusions

In this thesis, both distribution and growth of the main tree species in Moncayo Natural Park were analyzed to obtain applicable results by forest managers.

European beech:

- From 1987 to 2010, beech forest has increased in 38 ha., resulting in 500 ha of beech forest cover.

- The optimal altitude for this species growth is located at 1340 m in this mountain, matching the mean altitude of the current beech forest. The climatic limitations are related with the precipitation and the maximum temperatures of the previous summer. These limitations shorten the growing period, resulting in 48 – 75 days, which is the shorter growing period recorded for beech in Europe.

- There are wide zones (up to 2000 ha) of high climatic suitability for beech, currently occupied with other forest species or shrubs, hence beech forest could be expanded in Moncayo Natural Park.

Scots pine:

- The spatial distribution has decreased since 1987 in 80 ha, but in terms of occupation is still the main forest specie, occupying about 20% of the Natural Park land cover.

- Secondary growth duration varied between 139 and 170 days, which is more than five months and is the longest growth duration recorded its distribution area. The main climatic limits are the precipitation and the maximum temperatures of spring and the summer precipitations.

- The optimal altitude for Pinus sylvestris is settled at 1425 m, slightly higher than the mean of its actual distribution in the area, meanwhile the optimal altitude for Pinus uncinata is at 1762 m, closer to its mean value.

Pyrenean oak:

- The forest cover of this specie has decrease in 56 has from the 800 ha of 1987.

- The presence of this specie is confined to high climatic suitability zones; the 99.3% of its forest cover is located in zones with a climatic suitability over 0.8 points. However, there are 850 ha inside the study zone with a very high climatic suitability (>0.9) not occupied for this specie.

- Its maximum growth is located at 1240 m, which is higher than its actual mean altitude (1118 m). The higher the altitude, the higher the water availability during all year, which represents the main climatic limitation for this specie.

Overall, the results obtained during the develop of this thesis can be useful to the develop of forest management policies relatives to each species. The published scientific articles are oriented to management and each of them contain interesting information for the forest managers of the study area. In addition, the methodologies can be applicable to other forested areas. The outreach of knowledge become necessary to design management actions geared to protect forests against the current global and climatic changes and their potential arise.

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# ANEXO

# MATERIALES SUPLEMENTARIOS

**Table S5.1.1. Confusion matrix for the Landsat TM (1987) image classification.**

ACCURACY TOTALS 1987

| Class name | Reference totals | Classified totals | Number correct | Producers accuracy | Users accuracy |
|---|---|---|---|---|---|
| *Fagus sylvatica* | 50 | 44 | 44 | 88.00% | 100.00% |
| *Q. pyrenaica* | 82 | 92 | 79 | 96.34% | 85.87% |
| *Quercus ilex* | 46 | 42 | 35 | 76.09% | 83.33% |
| *Quercus petraea* | 50 | 46 | 45 | 90.00% | 97.83% |
| *Pinus sp.* | 66 | 69 | 66 | 100.00% | 95.65% |
| Bare ground | 67 | 66 | 55 | 82.09% | 83.33% |
| Mixed scrub | 99 | 101 | 86 | 86.87% | 85.15% |
| Pastures | 45 | 35 | 35 | 77.78% | 100.00% |
| Mixed shrub | 78 | 86 | 66 | 84.62% | 76.74% |
| Totals | 583 | 583 | 511 | | |

Overall Classification Accuracy = 87.65%

**Table S5.1.2**. Confusion matrix for the Landsat TM (2010) image classification.

| ACCURACY TOTALS 2010 | | | | | |
|---|---|---|---|---|---|
| Class name | Reference totals | Classified totals | Number correct | Producers accuracy | Users accuracy |
| *Fagus sylvatica* | 50 | 43 | 42 | 84.00% | 97.67% |
| *Q. pyrenaica* | 89 | 104 | 82 | 92.13% | 78.85% |
| *Quercus ilex* | 48 | 50 | 42 | 87.50% | 84.00% |
| *Quercus petraea* | 50 | 46 | 43 | 86.00% | 93.48% |
| *Pinus sp.* | 99 | 111 | 99 | 100.00% | 89.19% |
| Bare ground | 70 | 75 | 60 | 85.71% | 80.00% |
| Mixed scrub | 105 | 113 | 90 | 85.71% | 79.65% |
| Pastures | 49 | 36 | 35 | 71.43% | 97.22% |
| Mixed shrub | 81 | 60 | 49 | 60.49% | 81.67% |
| Totals | 641 | 641 | 542 | | |

Overall Classification Accuracy = 84.56%

**Table S5.3.1.** Chronologies stats of sampled sites.

| Site Code | Species | Altitude | Chrono length | No. Trees | RBar | EPS | SNR | SENS |
|---|---|---|---|---|---|---|---|---|
| M01 | *F. sylvatica* | 1200 | 1902-2014 | 21 | 0.41 | 0.95 | 19.96 | 0.33 |
| M02 | *F. sylvatica* | 1400 | 1829-2010 | 10 | 0.51 | 0.95 | 17.66 | 0.41 |
| M03 | *F. sylvatica* | 1600 | 1832-2011 | 10 | 0.51 | 0.92 | 11.30 | 0.46 |
| M04 | *F. sylvatica* | 1420 | 1835-2010 | 10 | 0.50 | 0.92 | 11.34 | 0.42 |
| M05 | *F. sylvatica* | 1500 | 1912-2010 | 15 | 0.41 | 0.94 | 15.97 | 0.38 |
| M06 | *F. sylvatica* | 1170 | 1914-2010 | 5 | 0.53 | 0.90 | 8.70 | 0.35 |
| M10 | *F. sylvatica* | 1600 | 1799-2014 | 20 | 0.48 | 0.97 | 27.27 | 0.39 |
| M11 | *F. sylvatica* | 1200 | 1904-2010 | 10 | 0.39 | 0.91 | 10.57 | 0.37 |
| M14 | *F. sylvatica* | 1440 | 1949-2010 | 5 | 0.42 | 0.85 | 5.28 | 0.34 |
| M16 | *F. sylvatica* | 1150 | 1902-2010 | 10 | 0.40 | 0.92 | 10.86 | 0.37 |
| M17 | *F. sylvatica* | 1520 | 1887-2010 | 10 | 0.44 | 0.89 | 7.89 | 0.33 |
| M26 | *F. sylvatica* | 1380 | 1825-2011 | 6 | 0.46 | 0.90 | 8.98 | 0.38 |
| M27 | *F. sylvatica* | 1320 | 1830-2011 | 6 | 0.44 | 0.88 | 7.60 | 0.32 |
| M28 | *F. sylvatica* | 1255 | 1836-2011 | 6 | 0.49 | 0.90 | 9.15 | 0.35 |
| M29 | *F. sylvatica* | 1177 | 1904-2011 | 6 | 0.47 | 0.91 | 9.48 | 0.33 |
| M01 | *P. sylvestris* | 1020 | 1919-2014 | 25 | 0.37 | 0.96 | 24.45 | 0.30 |
| M02 | *P. sylvestris* | 1510 | 1938-2014 | 25 | 0.44 | 0.96 | 23.96 | 0.23 |
| M03 | *P. sylvestris* | 1635 | 1952-2009 | 13 | 0.40 | 0.93 | 12.99 | 0.25 |
| M04 | *P. sylvestris* | 1420 | 1923-2010 | 5 | 0.39 | 0.84 | 5.25 | 0.25 |
| M07 | *P. sylvestris* | 1190 | 1933-2010 | 14 | 0.53 | 0.96 | 26.29 | 0.30 |
| M13 | *P. sylvestris* | 1400 | 1951-2010 | 15 | 0.51 | 0.97 | 28.20 | 0.28 |
| M17 | *P. sylvestris* | 1520 | 1964-2010 | 10 | 0.37 | 0.91 | 10.31 | 0.25 |
| M18 | *P. sylvestris* | 1480 | 1972-2010 | 10 | 0.53 | 0.95 | 17.89 | 0.20 |
| M19 | *P. uncinata* | 1780 | 1962-2010 | 10 | 0.35 | 0.89 | 8.03 | 0.25 |
| M20 | *P. uncinata* | 1900 | 1969-2010 | 10 | 0.26 | 0.85 | 5.52 | 0.25 |
| M40 | *P. uncinata* | 1765 | 1935-2011 | 10 | 0.38 | 0.91 | 9.62 | 0.21 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| M06 | *Q. pyrenaica* | 1190 | 1968-2010 | 5 | 0.30 | 0.88 | 3.60 | 0.23 |
| M12 | *Q. pyrenaica* | 988 | 1940-2010 | 12 | 0.50 | 0.94 | 16.52 | 0.24 |
| M13 | *Q. pyrenaica* | 1400 | 1951-2010 | 14 | 0.43 | 0.95 | 18.77 | 0.31 |
| M16 | *Q. pyrenaica* | 1150 | 1968-2010 | 10 | 0.34 | 0.90 | 8.58 | 0.24 |
| M18 | *Q. pyrenaica* | 1550 | 1895-2010 | 10 | 0.29 | 0.86 | 2.58 | 0.25 |
| M21 | *Q. pyrenaica* | 1320 | 1869-2010 | 5 | 0.27 | 0.85 | 1.33 | 0.27 |
| M23 | *Q. pyrenaica* | 950 | 1973-2011 | 10 | 0.45 | 0.92 | 12.16 | 0.25 |
| M24 | *Q. pyrenaica* | 1020 | 1974-2011 | 10 | 0.55 | 0.95 | 20.97 | 0.33 |
| M25 | *Q. pyrenaica* | 1050 | 1968-2011 | 9 | 0.37 | 0.91 | 9.97 | 0.22 |
| M30 | *Q. pyrenaica* | 1154 | 1950-2011 | 6 | 0.49 | 0.86 | 6.09 | 0.24 |
| M31 | *Q. pyrenaica* | 1036 | 1966-2012 | 9 | 0.43 | 0.92 | 11.39 | 0.30 |
| M32 | *Q. pyrenaica* | 1125 | 1963-2012 | 10 | 0.40 | 0.92 | 11.48 | 0.28 |
| M33 | *Q. pyrenaica* | 1155 | 1950-2012 | 10 | 0.38 | 0.89 | 7.93 | 0.24 |
| M34 | *Q. pyrenaica* | 1060 | 1967-2013 | 10 | 0.39 | 0.92 | 10.72 | 0.28 |

**Table S5.4.1.** Sampling locations of all chronologies ordered by species.

| Species | Site code | Altitude (m a.s.l.) | Lat. | Long. | First ring | Last ring | No. Trees | No. Samples | No. Rings |
|---|---|---|---|---|---|---|---|---|---|
| *Fagus sylvatica* | M01 | 1200 | 41.802 | -1.817 | 1902 | 2014 | 21 | 35 | 3394 |
| | M02 | 1400 | 41.805 | -1.838 | 1829 | 2010 | 10 | 19 | 3093 |
| | M03 | 1600 | 41.797 | -1.823 | 1832 | 2011 | 10 | 14 | 2010 |
| | M04 | 1420 | 41.785 | -1.806 | 1835 | 2010 | 10 | 20 | 2041 |
| | M05 | 1500 | 41.767 | -1.785 | 1912 | 2010 | 15 | 30 | 2342 |
| | M06 | 1170 | 41.770 | -1.764 | 1914 | 2010 | 5 | 10 | 771 |
| | M10 | 1600 | 41.798 | -1.824 | 1799 | 2014 | 20 | 40 | 6642 |
| | M11 | 1200 | 41.809 | -1.822 | 1904 | 2010 | 10 | 20 | 1849 |
| | M14 | 1440 | 41.760 | -1.766 | 1939 | 2010 | 5 | 10 | 577 |
| | M16 | 1150 | 41.815 | -1.837 | 1902 | 2010 | 10 | 19 | 1816 |
| | M17 | 1520 | 41.813 | -1.874 | 1887 | 2010 | 10 | 20 | 1308 |
| | M26 | 1380 | 41.805 | -1.842 | 1825 | 2011 | 6 | 12 | 2004 |
| | M27 | 1320 | 41.807 | -1.838 | 1830 | 2011 | 6 | 11 | 1792 |
| | M28 | 1255 | 41.809 | -1.831 | 1836 | 2011 | 6 | 12 | 1714 |
| | M29 | 1177 | 41.810 | -1.823 | 1904 | 2011 | 6 | 12 | 1186 |
| *Pinus sylvestris* | M01 | 1020 | 41.809 | -1.814 | 1919 | 2014 | 25 | 50 | 4145 |
| | M02 | 1510 | 41.796 | -1.823 | 1938 | 2014 | 25 | 36 | 2400 |
| | M03 | 1635 | 41.761 | -1.772 | 1952 | 2009 | 13 | 24 | 1190 |
| | M04 | 1420 | 41.785 | -1.806 | 1923 | 2010 | 5 | 10 | 752 |
| | M07 | 1190 | 41.796 | -1.805 | 1933 | 2010 | 14 | 28 | 1889 |
| | M13 | 1400 | 41.780 | -1.799 | 1951 | 2010 | 15 | 30 | 1664 |
| | M17 | 1520 | 41.813 | -1.875 | 1964 | 2010 | 10 | 20 | 840 |
| | M18 | 1480 | 41.762 | -1.845 | 1972 | 2010 | 10 | 19 | 667 |
| *Pinus uncinata* | M19 | 1780 | 41.748 | -1.795 | 1962 | 2010 | 10 | 19 | 772 |
| | M20 | 1900 | 41.748 | -1.803 | 1969 | 2010 | 10 | 20 | 692 |
| | M40 | 1765 | 41.797 | -1.831 | 1935 | 2011 | 10 | 20 | 1311 |
| *Quercus pyrenaica* | M06 | 1190 | 41.770 | -1.763 | 1938 | 2010 | 5 | 10 | 675 |
| | M12 | 988 | 41.816 | -1.791 | 1940 | 2010 | 12 | 23 | 1188 |
| | M13 | 1400 | 41.781 | -1.799 | 1951 | 2010 | 14 | 27 | 1524 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| M16 | 1150 | 41.815 | -1.838 | 1968 | 2010 | 10 | 20 | 784 |
| M18 | 1550 | 41.762 | -1.847 | 1875 | 2010 | 10 | 20 | 896 |
| M21 | 1320 | 41.759 | -1.872 | 1739 | 2010 | 5 | 9 | 1412 |
| M23 | 950 | 41.802 | -1.787 | 1973 | 2011 | 10 | 20 | 636 |
| M24 | 1020 | 41.808 | -1.805 | 1974 | 2011 | 10 | 20 | 684 |
| M25 | 1050 | 41.812 | -1.816 | 1968 | 2011 | 9 | 18 | 778 |
| M30 | 1154 | 41.665 | -1.795 | 1950 | 2011 | 6 | 11 | 420 |
| M31 | 1036 | 41.777 | -1.758 | 1966 | 2012 | 9 | 17 | 762 |
| M32 | 1125 | 41.780 | -1.765 | 1963 | 2012 | 10 | 20 | 918 |
| M33 | 1155 | 41.811 | -1.822 | 1950 | 2012 | 10 | 18 | 836 |
| M34 | 1060 | 41.774 | -1.761 | 1967 | 2013 | 10 | 19 | 855 |

**Table S5.4.2**. *Fagus sylvatica* generalized linear mixed model fit by maximum likelihood (Adaptive Gauss-Hermite Quadrature, nAGQ = 0). Family: poisson ( log )

```
Formula: TRW ~ (AI_mean) * (PCP_pSUM + PCP_pAUT +
PCP_WIN + PCP_SPR + PCP_SUM + PCP_AUT + TMAX_pSUM
+ TMAX_pAUT + TMAX_WIN + TMAX_SPR + TMAX_SUM +
TMAX_AUT + TMIN_pSUM + TMIN_pAUT + TMIN_WIN +
TMIN_SPR + TMIN_SUM + TMIN_AUT) + (BA_std |
TREE_IDENTITY)
```

| Fixed effects: | | | | | |
|---|---|---|---|---|---|
| | Estimate | Std. Error | z value | Pr(>\|z\|) | |
| (Intercept) | 7.1687977 | 0.0664238 | 107.93 | < 2e-16 | *** |
| AI_mean | -0.4625763 | 0.1006308 | -4.60 | 4.29e-06 | *** |
| PCP_pSUM | 0.1248126 | 0.0008005 | 155.91 | < 2e-16 | *** |
| PCP_pAUT | 0.0020938 | 0.0009716 | 2.16 | 0.0312 | * |
| PCP_WIN | -0.0469155 | 0.0011475 | -40.88 | < 2e-16 | *** |
| PCP_SPR | 0.0809347 | 0.0007732 | 104.67 | < 2e-16 | *** |
| PCP_SUM | 0.1604781 | 0.0009062 | 177.10 | < 2e-16 | *** |
| PCP_AUT | 0.0888910 | 0.0010174 | 87.37 | < 2e-16 | *** |
| TMAX_pSUM | -0.0534797 | 0.0015680 | -34.11 | < 2e-16 | *** |
| TMAX_pAUT | -0.0233472 | 0.0014881 | -15.69 | < 2e-16 | *** |
| TMAX_WIN | -0.0439772 | 0.0014246 | -30.87 | < 2e-16 | *** |
| TMAX_SPR | 0.1226661 | 0.0013304 | 92.20 | < 2e-16 | *** |
| TMAX_SUM | 0.1839504 | 0.0019819 | 92.81 | < 2e-16 | *** |
| TMAX_AUT | 0.0314585 | 0.0015787 | 19.93 | < 2e-16 | *** |
| TMIN_pSUM | -0.1263987 | 0.0022770 | -55.51 | < 2e-16 | *** |
| TMIN_pAUT | 0.0682432 | 0.0019766 | 34.53 | < 2e-16 | *** |
| TMIN_WIN | 0.0574982 | 0.0013420 | 42.85 | < 2e-16 | *** |
| TMIN_SPR | -0.1316095 | 0.0017896 | -73.54 | < 2e-16 | *** |
| TMIN_SUM | -0.2339282 | 0.0027301 | -85.68 | < 2e-16 | *** |
| TMIN_AUT | -0.0571837 | 0.0020477 | -27.93 | < 2e-16 | *** |
| AI_mean:PCP_pSUM | -0.0895537 | 0.0011234 | -79.72 | < 2e-16 | *** |
| AI_mean:PCP_pAUT | -0.0099474 | 0.0012877 | -7.72 | 1.12e-14 | *** |

```
AI_mean:PCP_WIN   -0.0133081  0.0015016   -8.86  < 2e-16 ***
AI_mean:PCP_SPR   -0.0694003  0.0010344  -67.09  < 2e-16 ***
AI_mean:PCP_SUM   -0.1134878  0.0012517  -90.67  < 2e-16 ***
AI_mean:PCP_AUT   -0.0620555  0.0013572  -45.72  < 2e-16 ***
AI_mean:TMAX_pSUM -0.1388445  0.0024580  -56.49  < 2e-16 ***
AI_mean:TMAX_pAUT -0.0035267  0.0023044   -1.53   0.1259
AI_mean:TMAX_WIN   0.0040967  0.0021614    1.90   0.0580 .
AI_mean:TMAX_SPR  -0.0578139  0.0021058  -27.45  < 2e-16 ***
AI_mean:TMAX_SUM   0.0421653  0.0031168   13.53  < 2e-16 ***
AI_mean:TMAX_AUT   0.0492300  0.0023847   20.64  < 2e-16 ***
AI_mean:TMIN_pSUM  0.2950002  0.0036062   81.80  < 2e-16 ***
AI_mean:TMIN_pAUT -0.0832195  0.0030377  -27.40  < 2e-16 ***
AI_mean:TMIN_WIN  -0.0217923  0.0020197  -10.79  < 2e-16 ***
AI_mean:TMIN_SPR   0.1462680  0.0028472   51.37  < 2e-16 ***
AI_mean:TMIN_SUM   0.0931231  0.0043379   21.47  < 2e-16 ***
AI_mean:TMIN_AUT  -0.1889560  0.0030624  -61.70  < 2e-16 ***
```

```
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’
0.1 ‘ ’ 1
Control: glmerControl(optimizer = "nloptwrap")
      AIC       BIC    logLik  deviance  df.resid
 1035433.3 1035724.2 -517675.6 1035351.3      8878

 Scaled residuals:
     Min      1Q  Median      3Q     Max
 -48.332  -6.543  -0.496   5.789 115.749

 Random effects:
  Groups    Name        Variance Std.Dev. Corr
  TREE_ IDENTITY (Intercept) 0.4751   0.6893
            BA_std      0.9270   0.9628   0.36
 Number of obs: 8919, groups:  TREE_IDENTITY, 150
```

**Table S5.4.3**. *Quercus pyrenaica* generalized linear mixed model fit by maximum likelihood (Adaptive Gauss-Hermite Quadrature, nAGQ = 0). Family: poisson ( log )

`Formula: TRW ~ (AI_mean) * (PCP_pSUM + PCP_pAUT + PCP_WIN + PCP_SPR + PCP_SUM + PCP_AUT + TMAX_pSUM + TMAX_pAUT + TMAX_WIN + TMAX_SPR + TMAX_SUM + TMAX_AUT + TMIN_pSUM + TMIN_pAUT + TMIN_WIN + TMIN_SPR +  TMIN_SUM + TMIN_AUT) + (BA_std | TREE_ IDENTITY)`

Fixed effects:

| | Estimate | Std. Error | z value | Pr(>\|z\|) | |
|---|---|---|---|---|---|
| (Intercept) | 7.7330580 | 0.0536331 | 144.18 | < 2e-16 | *** |
| AI_mean | -0.3367479 | 0.0794780 | -4.24 | 2.27e-05 | *** |
| PCP_pSUM | -0.0657978 | 0.0010530 | -62.49 | < 2e-16 | *** |
| PCP_pAUT | 0.0315112 | 0.0010317 | 30.54 | < 2e-16 | *** |
| PCP_WIN | 0.0456374 | 0.0012339 | 36.99 | < 2e-16 | *** |
| PCP_SPR | 0.0107408 | 0.0008611 | 12.47 | < 2e-16 | *** |
| PCP_SUM | -0.0162677 | 0.0012085 | -13.46 | < 2e-16 | *** |
| PCP_AUT | 0.0907261 | 0.0011154 | 81.34 | < 2e-16 | *** |
| TMAX_pSUM | -0.1279754 | 0.0021973 | -58.24 | < 2e-16 | *** |
| TMAX_pAUT | 0.0684061 | 0.0019555 | 34.98 | < 2e-16 | *** |
| TMAX_WIN | -0.0210808 | 0.0018606 | -11.33 | < 2e-16 | *** |
| TMAX_SPR | 0.0282060 | 0.0018861 | 14.95 | < 2e-16 | *** |
| TMAX_SUM | -0.2019854 | 0.0028856 | -70.00 | < 2e-16 | *** |
| TMAX_AUT | 0.2238243 | 0.0021720 | 103.05 | < 2e-16 | *** |
| TMIN_pSUM | 0.1466983 | 0.0031168 | 47.07 | < 2e-16 | *** |
| TMIN_pAUT | -0.0450633 | 0.0025317 | -17.80 | < 2e-16 | *** |
| TMIN_WIN | 0.0066958 | 0.0016640 | 4.02 | 5.72e-05 | *** |
| TMIN_SPR | -0.0219414 | 0.0023877 | -9.19 | < 2e-16 | *** |
| TMIN_SUM | 0.3077539 | 0.0039730 | 77.46 | < 2e-16 | *** |
| TMIN_AUT | -0.2293510 | 0.0027331 | -83.92 | < 2e-16 | *** |
| AI_mean:PCP_pSUM | -0.0650371 | 0.0017308 | -37.58 | < 2e-16 | *** |
| AI_mean:PCP_pAUT | -0.1756333 | 0.0018834 | -93.25 | < 2e-16 | *** |
| AI_mean:PCP_WIN | -0.1025106 | 0.0024469 | -41.89 | < 2e-16 | *** |
| AI_mean:PCP_SPR | -0.0976550 | 0.0016512 | -59.14 | < 2e-16 | *** |
| AI_mean:PCP_SUM | -0.1501274 | 0.0019130 | -78.48 | < 2e-16 | *** |

| | | | | | |
|---|---|---|---|---|---|
| AI_mean:PCP_AUT | 0.0180206 | 0.0020161 | 8.94 | < 2e-16 | *** |
| AI_mean:TMAX_pSUM | -0.0933450 | 0.0032278 | -28.92 | < 2e-16 | *** |
| AI_mean:TMAX_pAUT | 0.0314655 | 0.0028138 | 11.18 | < 2e-16 | *** |
| AI_mean:TMAX_WIN | 0.0337774 | 0.0028115 | 12.01 | < 2e-16 | *** |
| AI_mean:TMAX_SPR | 0.0612695 | 0.0028104 | 21.80 | < 2e-16 | *** |
| AI_mean:TMAX_SUM | -0.3415089 | 0.0041032 | -83.23 | < 2e-16 | *** |
| AI_mean:TMAX_AUT | 0.2036054 | 0.0031232 | 65.19 | < 2e-16 | *** |
| AI_mean:TMIN_pSUM | 0.1463769 | 0.0045605 | 32.10 | < 2e-16 | *** |
| AI_mean:TMIN_pAUT | -0.0301112 | 0.0036092 | -8.34 | < 2e-16 | *** |
| AI_mean:TMIN_WIN | -0.0217280 | 0.0025025 | -8.68 | < 2e-16 | *** |
| AI_mean:TMIN_SPR | -0.1226808 | 0.0034914 | -35.14 | < 2e-16 | *** |
| AI_mean:TMIN_SUM | 0.5062262 | 0.0056846 | 89.05 | < 2e-16 | *** |
| AI_mean:TMIN_AUT | -0.1698853 | 0.0039847 | -42.63 | < 2e-16 | *** |

```
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.'
0.1 ' ' 1
 Control: glmerControl(optimizer = "nloptwrap")

       AIC       BIC    logLik  deviance  df.resid
  757909.5  758183.2 -378913.7  757827.5      5814

 Scaled residuals:
     Min      1Q  Median      3Q     Max
 -43.024  -6.969  -0.751   6.118  96.461

 Random effects:
  Groups    Name        Variance Std.Dev. Corr
  TREE_ IDENTITY (Intercept) 13.30    3.647
            BA_std      12.27    3.502    0.99
 Number of obs: 5855, groups:  TREE_IDENTITY, 130
```

**Table S5.4.4.** *Pinus sylvestris* generalized linear mixed model fit by maximum likelihood (Adaptive Gauss-Hermite Quadrature, nAGQ = 0). Family: poisson ( log )

`Formula: TRW ~ (AI_mean) * (PCP_pSUM + PCP_pAUT + PCP_WIN + PCP_SPR + PCP_SUM + PCP_AUT + TMAX_pSUM + TMAX_pAUT + TMAX_WIN + TMAX_SPR + TMAX_SUM + TMAX_AUT + TMIN_pSUM + TMIN_pAUT + TMIN_WIN + TMIN_SPR + TMIN_SUM + TMIN_AUT) + (BA_std | TREE_IDENTITY)`

| Fixed effects: | | | | | |
|---|---|---|---|---|---|
| | Estimate | Std. Error | z value | Pr(>\|z\|) | |
| (Intercept) | 8.1894384 | 0.0278837 | 293.70 | < 2e-16 | *** |
| AI_mean | 0.0319044 | 0.0384744 | 0.83 | 0.406970 | |
| PCP_pSUM | 0.0573858 | 0.0006652 | 86.26 | < 2e-16 | *** |
| PCP_pAUT | 0.0236946 | 0.0007518 | 31.52 | < 2e-16 | *** |
| PCP_WIN | -0.0220649 | 0.0008816 | -25.03 | < 2e-16 | *** |
| PCP_SPR | 0.0478524 | 0.0006212 | 77.03 | < 2e-16 | *** |
| PCP_SUM | 0.1016678 | 0.0007365 | 138.04 | < 2e-16 | *** |
| PCP_AUT | 0.0789631 | 0.0007949 | 99.34 | < 2e-16 | *** |
| TMAX_pSUM | 0.0527945 | 0.0011897 | 44.38 | < 2e-16 | *** |
| TMAX_pAUT | -0.0227210 | 0.0011274 | -20.15 | < 2e-16 | *** |
| TMAX_WIN | -0.0186698 | 0.0010409 | -17.94 | < 2e-16 | *** |
| TMAX_SPR | -0.0640318 | 0.0010300 | -62.17 | < 2e-16 | *** |
| TMAX_SUM | -0.1514748 | 0.0014978 | -101.13 | < 2e-16 | *** |
| TMAX_AUT | 0.1093034 | 0.0011912 | 91.76 | < 2e-16 | *** |
| TMIN_pSUM | -0.1243827 | 0.0017386 | -71.54 | < 2e-16 | *** |
| TMIN_pAUT | -0.0856433 | 0.0014632 | -58.53 | < 2e-16 | *** |
| TMIN_WIN | 0.0748325 | 0.0009874 | 75.79 | < 2e-16 | *** |
| TMIN_SPR | 0.1518626 | 0.0013795 | 110.09 | < 2e-16 | *** |
| TMIN_SUM | 0.2193406 | 0.0020582 | 106.57 | < 2e-16 | *** |
| TMIN_AUT | -0.1534578 | 0.0015069 | -101.84 | < 2e-16 | *** |
| AI_mean:PCP_pSUM | -0.0389122 | 0.0007959 | -48.89 | < 2e-16 | *** |
| AI_mean:PCP_pAUT | -0.0487243 | 0.0008967 | -54.34 | < 2e-16 | *** |
| AI_mean:PCP_WIN | 0.0035485 | 0.0010097 | 3.51 | 0.000441 | *** |
| AI_mean:PCP_SPR | -0.0569396 | 0.0007371 | -77.25 | < 2e-16 | *** |
| AI_mean:PCP_SUM | -0.0909658 | 0.0008789 | -103.50 | < 2e-16 | *** |

```
AI_mean:PCP_AUT   -0.0634160  0.0009468  -66.98  < 2e-16 ***
AI_mean:TMAX_pSUM -0.0064010  0.0015910   -4.02 5.74e-05 ***
AI_mean:TMAX_pAUT -0.0184539  0.0015111  -12.21  < 2e-16 ***
AI_mean:TMAX_WIN   0.0322185  0.0013910   23.16  < 2e-16 ***
AI_mean:TMAX_SPR   0.0571180  0.0013847   41.25  < 2e-16 ***
AI_mean:TMAX_SUM  -0.0720809  0.0019901  -36.22  < 2e-16 ***
AI_mean:TMAX_AUT  -0.0089899  0.0015773   -5.70 1.20e-08 ***
AI_mean:TMIN_pSUM  0.0398957  0.0023573   16.92  < 2e-16 ***
AI_mean:TMIN_pAUT  0.0685291  0.0019605   34.96  < 2e-16 ***
AI_mean:TMIN_WIN  -0.0549121  0.0012715  -43.19  < 2e-16 ***
AI_mean:TMIN_SPR  -0.0572946  0.0018543  -30.90  < 2e-16 ***
AI_mean:TMIN_SUM   0.0935312  0.0028184   33.19  < 2e-16 ***
AI_mean:TMIN_AUT   0.0517507  0.0020136   25.70  < 2e-16 ***
```

```
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’
0.1 ‘ ’ 1
 Control: glmerControl(optimizer = "nloptwrap")

       AIC       BIC    logLik  deviance  df.resid
  883595.7  883873.2 -441756.8  883513.7      6386

 Scaled residuals:
     Min      1Q  Median      3Q     Max
 -43.484  -7.508  -0.780   6.798  69.639

 Random effects:
  Groups    Name        Variance Std.Dev. Corr
  TREE_ IDENTITY (Intercept) 0.6898   0.8305
            BA_std      0.7804   0.8834   0.94
 Number of obs: 6427, groups:  TREE_IDENTITY, 117
```

**Table S5.4.5.** *Pinus uncinata* generalized linear mixed model fit by maximum likelihood (Adaptive Gauss-Hermite Quadrature, nAGQ = 0). Family: poisson ( log )

Formula: TRW ~ (AI_mean) * (PCP_pSUM + PCP_pAUT + PCP_WIN + PCP_SPR + PCP_SUM +PCP_AUT + TMAX_pSUM + TMAX_pAUT + TMAX_WIN + TMAX_SPR + TMAX_SUM + TMAX_AUT + TMIN_pSUM + TMIN_pAUT + TMIN_WIN + TMIN_SPR + TMIN_SUM + TMIN_AUT) + (BA_std | TREE_IDENTITY)

| Fixed effects: | | | | | |
|---|---|---|---|---|---|
| | Estimate | Std. Error | z value | Pr(>\|z\|) | |
| (Intercept) | 7.095879 | 0.151132 | 46.95 | < 2e-16 | *** |
| AI_mean | 0.718931 | 0.124416 | 5.78 | 7.54e-09 | *** |
| PCP_pSUM | 0.010243 | 0.003212 | 3.19 | 0.001427 | ** |
| PCP_pAUT | -0.015085 | 0.003160 | -4.77 | 1.81e-06 | *** |
| PCP_WIN | 0.066862 | 0.003978 | 16.81 | < 2e-16 | *** |
| PCP_SPR | -0.102083 | 0.002571 | -39.70 | < 2e-16 | *** |
| PCP_SUM | 0.025463 | 0.003661 | 6.96 | 3.50e-12 | *** |
| PCP_AUT | 0.040953 | 0.003183 | 12.87 | < 2e-16 | *** |
| TMAX_pSUM | 0.142336 | 0.010168 | 14.00 | < 2e-16 | *** |
| TMAX_pAUT | -0.049201 | 0.008298 | -5.93 | 3.04e-09 | *** |
| TMAX_WIN | 0.128826 | 0.007719 | 16.69 | < 2e-16 | *** |
| TMAX_SPR | 0.034392 | 0.007827 | 4.39 | 1.11e-05 | *** |
| TMAX_SUM | -0.251238 | 0.011010 | -22.82 | < 2e-16 | *** |
| TMAX_AUT | 0.126226 | 0.008364 | 15.09 | < 2e-16 | *** |
| TMIN_pSUM | -0.184007 | 0.014624 | -12.58 | < 2e-16 | *** |
| TMIN_pAUT | -0.032211 | 0.009928 | -3.24 | 0.001177 | ** |
| TMIN_WIN | -0.165709 | 0.006973 | -23.76 | < 2e-16 | *** |
| TMIN_SPR | -0.187586 | 0.010276 | -18.25 | < 2e-16 | *** |
| TMIN_SUM | 0.108588 | 0.016168 | 6.72 | 1.86e-11 | *** |
| TMIN_AUT | -0.139739 | 0.010427 | -13.40 | < 2e-16 | *** |
| AI_mean:PCP_pSUM | 0.007563 | 0.002396 | 3.16 | 0.001594 | ** |
| AI_mean:PCP_pAUT | -0.007801 | 0.002321 | -3.36 | 0.000775 | *** |
| AI_mean:PCP_WIN | -0.050495 | 0.002825 | -17.87 | < 2e-16 | *** |
| AI_mean:PCP_SPR | 0.068737 | 0.001895 | 36.26 | < 2e-16 | *** |
| AI_mean:PCP_SUM | 0.008027 | 0.002696 | 2.98 | 0.002911 | ** |

| | | | | | |
|---|---|---|---|---|---|
| AI_mean:PCP_AUT | -0.039536 | 0.002334 | -16.94 | < 2e-16 | *** |
| AI_mean:TMAX_pSUM | -0.110587 | 0.007456 | -14.83 | < 2e-16 | *** |
| AI_mean:TMAX_pAUT | 0.003963 | 0.006465 | 0.61 | 0.539916 | |
| AI_mean:TMAX_WIN | -0.073239 | 0.005918 | -12.38 | < 2e-16 | *** |
| AI_mean:TMAX_SPR | 0.029425 | 0.005856 | 5.03 | 5.03e-07 | *** |
| AI_mean:TMAX_SUM | 0.121188 | 0.008451 | 14.34 | < 2e-16 | *** |
| AI_mean:TMAX_AUT | -0.063609 | 0.006411 | -9.92 | < 2e-16 | *** |
| AI_mean:TMIN_pSUM | 0.123716 | 0.011008 | 11.24 | < 2e-16 | *** |
| AI_mean:TMIN_pAUT | 0.042273 | 0.007937 | 5.33 | 1.00e-07 | *** |
| AI_mean:TMIN_WIN | 0.111066 | 0.005328 | 20.84 | < 2e-16 | *** |
| AI_mean:TMIN_SPR | 0.140428 | 0.007852 | 17.88 | < 2e-16 | *** |
| AI_mean:TMIN_SUM | 0.034269 | 0.012439 | 2.76 | 0.005869 | ** |
| AI_mean:TMIN_AUT | 0.049081 | 0.008028 | 6.11 | 9.72e-10 | *** |

```
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.'
0.1 ' ' 1

Control: glmerControl(optimizer = "nloptwrap")

     AIC       BIC   logLik deviance df.resid
175353.0 175567.2 -87635.5 175271.0     1330

Scaled residuals:
    Min      1Q  Median      3Q     Max
-36.572  -7.225  -0.630   6.991  52.234

Random effects:
 Groups    Name        Variance Std.Dev. Corr
 TREE_ IDENTITY (Intercept) 0.5454   0.7385
           BA_std      0.6069   0.7790   0.96
Number of obs: 1371, groups:  TREE_IDENTITY, 30
```