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# Impactos del cambio global en los bosques españoles en las ultimas tres decadas: efectos sobre los ciclos del agua y del carbono y la degradacion forestal

**Jesús Sánchez Dávila**

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Jesús Sánchez Dávila



CREAF



EXCELENCIA SEVERO OCHOA

# Impactos del cambio global en los bosques españoles en las ultimas tres decadas: efectos sobre los ciclos del agua y del carbono y la degradacion forestal


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# Resumen

Los bosques desempeñan un papel fundamental en el funcionamiento del sistema terrestre al regular tanto el ciclo del carbono como el del agua, además de aportar múltiples servicios ecosistémicos. En las últimas décadas, estos sistemas están siendo profundamente transformados por el cambio global, especialmente por el cambio climático y el cambio de usos del suelo. En Europa y en España, a diferencia de las regiones tropicales, la dinámica dominante ha sido la expansión forestal asociada al abandono rural, lo que ha incrementado la biomasa, la densidad de los bosques y su capacidad de almacenamiento de carbono. Sin embargo, este crecimiento también implica cambios en el balance hídrico, en la vulnerabilidad a perturbaciones como los incendios y en los procesos de degradación estructural.

En relación con el ciclo del agua (Capítulo 1 y Capítulo 2), los bosques regulan dos componentes principales: el agua verde, asociada a la evapotranspiración, y el agua azul, que incluye la escorrentía y la recarga de acuíferos. Este balance depende tanto de las condiciones climáticas como de la estructura forestal, especialmente del índice de área foliar (LAI). En España, la gran diversidad climática —desde el bioma atlántico al mediterráneo y alpino— permite analizar cómo estos factores interactúan en distintos contextos. El aumento de la cobertura arbórea y arbustiva en las últimas décadas ha incrementado la evapotranspiración, lo que tiende a reducir la disponibilidad de agua azul, un recurso clave para el uso humano. Además, el aumento de temperaturas ha intensificado la demanda evaporativa, reforzando este efecto incluso sin cambios claros en la precipitación.

Por otro lado, los incendios forestales constituyen una de las perturbaciones más importantes en los bosques españoles (Capítulo 3). Estos eventos afectan directamente al ciclo del carbono al liberar grandes cantidades de $CO_2$ almacenado en la biomasa y reducir la capacidad futura de secuestro. Aunque las políticas de supresión han reducido el número total de incendios, se ha observado un aumento en la intensidad y en los eventos extremos, lo que incrementa su impacto potencial. La respuesta de los bosques a los incendios es heterogénea y depende del tipo de vegetación, las condiciones climáticas y la historia de perturbaciones.

Finalmente, los cambios estructurales del bosque, incluyendo procesos de expansión y degradación (Capítulo 4), son clave para entender su evolución reciente. La expansión forestal en España ha sido generalizada, tanto por colonización de antiguos usos agrícolas como por el crecimiento de masas existentes. Sin embargo, este proceso coexiste con señales de degradación, como el aumento de claros en el dosel o la reducción de la densidad foliar. Estos cambios pueden estar asociados a factores como el estrés hídrico, perturbaciones locales o una creciente competencia por recursos en bosques más densos.

En cuanto a los resultados principales de la tesis, el Capítulo 1 muestra que el agua azul es más abundante en términos absolutos y relativos en las regiones más húmedas, especialmente en los biomas atlántico y alpino, y se concentra en los meses de otoño e invierno. En contraste, el agua verde domina en primavera y verano. El LAI es el principal factor explicativo del balance hídrico, con una relación no lineal: a mayor LAI, menor producción de agua azul, aunque este efecto se estabiliza en valores altos. Además, los bosques caducifolios presentan mayores niveles de agua azul que los perennes debido a la pérdida estacional de hojas, lo que reduce la interceptación y la transpiración. Estos resultados evidencian un desacoplamiento entre los componentes del ciclo del agua, controlados por factores estacionales distintos.

El Capítulo 2 revela una tendencia clara en las últimas décadas: aumento del agua verde y disminución del agua azul. Este patrón está impulsado principalmente por el incremento del LAI asociado al abandono de la gestión forestal, más que por el cambio climático. Incluso en periodos con mayor precipitación, el crecimiento de la vegetación incrementa el consumo de agua y reduce la escorrentía. Cuando la precipitación disminuye, el agua azul se ve aún más afectada, mientras que el agua verde se mantiene relativamente estable. Los escenarios de gestión muestran que la reducción del área basal puede aumentar temporalmente el agua azul, pero este efecto es de corta

duración debido a la rápida recuperación de la vegetación, lo que limita la eficacia de estas intervenciones.

En el Capítulo 3 se observa que las pérdidas de carbono debidas a incendios han disminuido en la última década en comparación con la anterior, aunque con importantes diferencias regionales. En los bosques mediterráneos las pérdidas han disminuido, mientras que en los atlánticos han aumentado, especialmente en pinares y eucaliptales del noroeste. Los hotspots de carbono no presentan en general mayores pérdidas, salvo en bosques mediterráneos esclerófilos donde están sobrerrepresentadas. Además, más de la mitad de los bosques no muestran pérdidas significativas tras incendios, lo que indica una alta resiliencia, especialmente en bosques caducifolios. No se identifican patrones consistentes en los factores climáticos o estructurales que expliquen estas pérdidas, lo que sugiere una fuerte dependencia de condiciones locales.

Por último, el Capítulo 4 muestra que, aunque los bosques españoles continúan expandiéndose, también presentan un aumento de la degradación estructural. La cobertura arbórea ha crecido en todos los tipos de bosque, pero este crecimiento se está ralentizando, probablemente debido a limitaciones de espacio y recursos. Paralelamente, aumentan indicadores de degradación como los claros en el dosel y la reducción de la densidad foliar. Este fenómeno es más acusado en bosques mediterráneos y coníferas templadas, mientras que los bosques caducifolios atlánticos permanecen relativamente estables. Las causas de esta degradación no se explican claramente por variables climáticas o estructurales a gran escala, lo que apunta a la influencia de factores locales difíciles de medir.

En conjunto, la tesis pone de manifiesto que los bosques españoles se encuentran en una fase de expansión acompañada de cambios funcionales importantes. El aumento de biomasa favorece el almacenamiento de carbono, pero también reduce la disponibilidad de agua azul y hay un aumento de la degradación.

# 1. Introducción

## 1.1 El ciclo de carbono y el agua en los bosques

Los bosques proveen de numerosos servicios ecosistémicos entre los que destacan el papel como sumideros de carbono (Whitehead, 2011), regulación hidrológica a través de la evapotranspiración y el filtrado de agua (Falkenmark & Rockström, 2006), albergando el hábitat de numerosos seres vivos (Brockerhoff et al., 2017) y usos culturales (Sutherland et al., 2016), etc.

Dentro de estos servicios, los relacionados con el ciclo del carbono son los más estudiado en ecología forestal (Acharya et al., 2019). El ciclo del carbono se ha estudiado desde a escala de árbol, a escala de rodal o regional, utilizando métodos contrastados como seguimientos ecofisiológicos, parcelas experimentales o redes de inventarios forestales (Anderson et al. 2009). En general, el stock de carbono forestal aumenta con el tiempo en ausencia de perturbaciones, tanto en el espacio al colonizar nuevos territorios como en el bosque como consecuencia del crecimiento de los árboles que lo conforman. Por otra parte, el stock de carbono del bosque disminuye con las perturbaciones, ya sean incendios, tormentas, sequias o la deforestación de origen humano (Grace et al., 2014). Estas pérdidas, especialmente la deforestación, en la actualidad se producen principalmente en los países tropicales, mientras que, en Europa, y de manera bastante generalizada, en el hemisferio norte, en las últimas décadas es más habitual una expansión del bosque por el abandono rural (Palmero-Iniesta et al., 2021).

En cambio, el ciclo del agua forestal ha sido menos estudiado que el del carbono debido a que es más complejo obtener medidas de campo. Dentro del ciclo del agua forestal se pueden distinguir dos componentes: el agua verde y el agua azul (Schlesinger & Jasechko, 2014). Una parte de la precipitación es interceptada por las copas y se evapora; el resto del agua alcanza el suelo y, a su vez, otra fracción se evapora. Del agua que llega al suelo, una fracción es absorbida por los árboles que, mediante la transpiración devuelven parte del agua absorbida en forma de vapor. La suma del agua interceptada por la copa, la evaporada desde el suelo, y la transpirada por las hojas, es el agua verde o evapotranspiración. El resto de agua, la infiltrada y no consumida, llega a los acuíferos. Otra fracción del agua se pierde por escorrentía y termina en los ríos o mares. La suma del agua que se acumula en los acuíferos y la de escorrentía es el agua azul. Esta agua azul es fundamental para la población humana, siendo consumida por la agricultura, la industria y, en menor medida como agua de boca. El agua verde, aunque no tiene un efecto directo sobre la población humana, tiene un papel importante en la regulación del ciclo del agua en la atmosfera. El agua verde suele ser es una fracción mayor que el agua azul en los bosques, siendo más alta en ecosistemas áridos (> 90%, (Ungar et al., 2013) porque los árboles tienen una transpiración mayor y llueve menos. La evapotranspiración se puede medir indirectamente mediante teledetección por imágenes satélite o datos climáticos, o modelizando con datos reales obtenidos en torres de eddy covariance (Martens et al., 2017), mientras que el agua subterránea es mucho más complicada de evaluar, pero se han hecho algunas estimaciones mediante modelización espacial de datos de campo (Estrela et al., 2012).

## 1.2. Cambio Global: cambio de usos y cambio climático en Europa

Entre el conjunto de transformaciones a gran escala en los ecosistemas de la Tierra causadas por la actividad humana, lo que conocemos como Cambio Global, dos que los que están teniendo un impacto más grande en los sistemas forestales son el cambio de usos y el cambio climático. Respecto al primero, los bosques en Europa están siendo afectados por importantes cambios estructurales y de distribución en las últimas décadas. La población europea ha aumentado en el último siglo, pero en las décadas de 1960-80 se produjo una emigración muy fuerte desde de las zonas rurales hacia las ciudades. El abandono de las zonas rurales se produjo en un contexto donde los principales sectores económicos pasaron de la agricultura-ganadería hacia el sector industrial

o de servicios. El aumento de productividad de la agricultura y ganadería con la automatización industrial redujo la mano de obra necesaria, así como de la necesidad de seguir explotando grandes extensiones. Esto produjo una bajada generalizada de la población rural europea (Hospers & Reverda, 2015). En este contexto de pérdida de población rural, que todavía se produce en la actualidad, los bosques españoles han perdido la mayoría de sus usos tradicionales, como la extracción de madera para leña (siendo sustituido por combustibles fósiles) o el ramoneo para ganadería (siendo sustituido por granjas industriales). De forma paralela, la propia extensión de los bosques a principios de siglo era reducida debido a su eliminación histórica para crear pastos para el ganado o cultivos (Valbuena-Carabaña et al., 2010). Pero en el contexto de pérdida de población por el abandono rural y los usos tradicionales, la superficie forestal arbolada ha aumentado mucho, invadiendo los pastizales o los cultivos abandonados, generalmente en las zonas menos productivas como las montañas (Améztegui et al., 2010). Esto se combina con el crecimiento de los propios árboles en las últimas décadas (Vayreda et al., 2012) y la reducción significativa de la gestión forestal y de los aprovechamientos de madera o leña. También hay un crecimiento generalizado de los arbustos tanto en el sotobosque como ocupando de forma pionera tanto los pastizales como los antiguos cultivos (Martín-Alcón et al., 2015). En conjunto, está aumentando la superficie forestal en Europa (y también en España) y además los bosques son más densos, con árboles más grandes y mayor cantidad de matorral en el sotobosque, acumulando en conjunto una mayor cantidad de biomasa forestal.

De forma paralela se ha producido un cambio climático con un aumento sostenido de la temperatura en las últimas décadas en España (Brunet et al., 2007). Por contra, la precipitación no ha seguido una tendencia lineal de cambio ya que hay contrastes tanto de años húmedos como de sequía en los últimos 100 años (Peña-Angulo et al., 2020). La precipitación tan poco ha cambiado su régimen de intensidad (mayor o menor torrencialidad) en los últimos años (Serrano-Notivoli et al., 2018). Sin embargo, sí que ha aumentado el grado de aridez de la península ibérica en las últimas décadas, no porque haya disminuido la precipitación sino porque el aumento de la temperatura ha generado una mayor demanda evaporativa (Vicente-Serrano et al., 2020).

## 1.3. Los efectos del cambio global en los bosques españoles

El ciclo del carbono forestal se está viendo afectado por el cambio global (Améztegui et al., 2010; Vayreda et al., 2012). En España la reducción de los aprovechamientos forestales de las últimas décadas ha dado lugar a una mayor acumulación de biomasa en los bosques. En contraposición con los países tropicales, donde la deforestación es una amenaza para los bosques, los bosques europeos y españoles están en una fase generalizada de crecimiento. Pero esta acumulación tiene un límite si las condiciones climáticas son adversas y las consecuencias son que los bosques también pueden sufrir un proceso de degradación. La degradación forestal es difícil de definir y se ha evaluado de diferentes formas, pero de forma general suele enfocarse en la reducción o perdida a lo largo del tiempo de: estructura, especies o comunidades, procesos biológicos (carbono, agua) o demográficos (regeneración, dispersión, etc.) (Vásquez-Grandón et al., 2018). Los cambios estructurales, como los claros (o huecos en el dosel) o la reducción de la densidad de hojas son entre los más usados como indicadores de degradación, pero estos atributos forestales para evaluar los cambios en el dosel son menos conocidos por su dificultad de medición a gran escala. Los claros son espacios abiertos dentro o entre las copas, de entre pocos a miles de metros cuadrados. Se crean de forma natural por mortalidad de los árboles, podredumbre de ramas en copas, o perturbaciones como tormentas e incendios. Un aumento de los claros en un contexto de expansión forestal sería un indicador de degradación forestal. Otro cambio estructural es la densidad de hojas (la superficie total de hojas en relación con el volumen que ocupan) que es un indicador de la productividad forestal si aumenta, pero también puede ser una medida de degradación si disminuye.

Otros eventos como las plagas o los incendios también afectan a los bosques siendo los incendios una de las perturbaciones que más efecto tienen en los bosques españoles (San-Miguel-Ayanz et al., 2018). Los incendios reducen los sumideros de carbono forestales al quemar a los árboles,

junto la perdida que supone la capacidad de secuestro de carbono que realizaban esos mismos árboles. España es junto con Portugal el país europeo con más superficie quemada por año (San-Miguel-Ayanz et al., 2018). Hay una tendencia a un menor número de incendios y superficie quemada en España por el incremento en la supresión de incendios (Urbieta et al., 2019), pero también han aumentado los incendios extremos (Rodrigues et al., 2023) y su intensidad (Alvarez et al., 2024).

La reducción de la gestión forestal, junto con el cambio climático, también está afectando el balance hídrico de los bosques. El aumento de la cubierta arbórea y arbustiva incrementa la evapotranspiración, aumentando el consumo del agua por la vegetación y reduciendo el agua azul (Mastrotheodoros et al., 2020). El incremento de la temperatura supone una mayor evapotranspiración al aumentar la demanda evaporativa de la atmósfera. Si se combina con una reducción de la precipitación, los efectos pueden ser todavía más adversos. Una ligera disminución de la precipitación puede reducir el agua azul pero no la verde, ya que los árboles seguirán extrayendo agua mientras esté disponible en detrimento del agua azul (Mastrotheodoros et al., 2020). Si la reducción de la precipitación es más elevada también tendrá consecuencias sobre el agua verde.

## 1.4. Los bosques de la España peninsular como caso de estudio

Para testar los efectos del cambio global (desarrollo del bosque y cambio climático) en los bosques, España es una zona de estudio interesante por su diversidad. España presenta tres biomas, el Atlántico en las zonas más cercanas a la costa del Atlántico; el Mediterráneo en la costa del Mediterráneo e interior del país; y el alpino en las zonas más altas de las montañas (Rivas-Martínez et al., 2017). El bioma Atlántico se caracteriza por un clima de temperatura suave todo el año, sin grandes heladas u olas de calor, y una precipitación regular a lo largo del año. El bioma Mediterráneo es más extremo siendo frio en invierno y muy cálido en verano, junto con una precipitación en general más baja que en el Atlántico y además con un patrón estación de sequía en verano. Finalmente está el bioma Alpino, caracterizado por inviernos fríos con precipitación en forma de nieve y veranos de temperaturas suaves. España también es un país muy montañoso (con altitudes que fácilmente llegan a los 2.000 metros, con un máximo a 3.400 metros) tanto en la zona Atlántica (ej. Cordillera cantábrica) como en la mediterránea (ej. Pirineos o Sierra Nevada). Estas montañas crean numerosos microclimas dentro del país, permitiendo la existencia de bosques más térmicos o templados fuera de su área de distribución dominante.

Estas variaciones climáticas y topográficas crean una gran variedad de bosques. En el Atlántico predominan los bosques de hoja caduca (ej. *Fagus sylvatica* y *Quercus robur*) con masas de pinares (*Pinus pinaster* y, en menor medida, *Pinus sylvestris*). En el clima Mediterráneo predominan los bosques esclerófilos de *Quercus ilex* y *Quercus suber*, que conviven a menudo con los pinares mediterráneos (*Pinus pinea, Pinus pinaster* y *Pinus halepensis*). Donde el clima mediterráneo es más húmedo como en las zonas montañosas o donde la topografía crea un microclima más húmedo, los bosques dominantes son robles marcescentes de *Quercus pyrenaica*, *Quercus pubescens* y *Quercus faginea*. En la montaña media predominan los pinares de pino albar (*Pinus sylvestris), hayedos (Fagus sylvatica)* y abetales (*Abies alba*) y, finalmente los bosques de pino negro (*Pinus uncinata)* que se sitúa en la alta montaña más fría y húmeda.

## 1.5. Metodologías de estudio: inventarios y remote sensing

Los inventarios forestales nacionales suelen cubrir toda la extensión forestal de un país con muestreos de inventario con parcelas permanentes. Las variables medidas dentro de las parcelas varían en cada país o entre inventarios, pero de forma general suelen medir el diámetro a la altura del pecho de los árboles, su altura, si el árbol está vivo o muerto y la especie. De forma recurrente también se suele medir la cobertura de dosel en la parcela, la presencia o cobertura de arbustos, la topografía, la presencia de plántulas o regenerado, etc. Los inventarios forestales nacionales

suelen hacerse en mallas regulares cada cierto número de km en un muestreo sistemático y repetirse de forma periódica (normalmente cada 10 o 15 años). El inventario forestal nacional de España tiene, hasta la fecha, tres inventarios disponibles: entre 1986-1996, 1997-2008 y 2009-25. Al abarcar todo el país mediante un muestreo sistemático, identificando las especies de árboles y sus características, así como al tener un muestreo repetido a lo largo de más de tres décadas, el inventario forestal nacional español es una fuente de información muy adecuada para testar los efectos del cambio global en los bosques ibéricos.

Sin embargo, hay mediciones de campo difíciles de obtener a escala de país inclusive en los inventarios forestales nacionales, como la cobertura o características del dosel. Para ello hay otras metodologías que permiten hacerlo: así, las tecnologías de la teledetección permiten obtener medidas de campo a una escala muy detallada. En concreto, la tecnología LiDAR (Light Detection and Ranging) permite, mediante un sensor, emitir pulsos de luz y capturar sus retornos (Wulder et al., 2012). Los pulsos de luz chocan con objetos y, midiendo el tiempo que tarda en regresar ese pulso de luz, se puede calcular la distancia recorrida y, de esa forma, obtener la información tridimensional de los objetos. Dependiendo de la cantidad de pulsos emitidos los "objetos" pueden identificar desde edificios (LiDAR con una baja densidad de puntos por metro cuadrado) hasta gotas de agua (una alta densidad de puntos por metro cuadrado). El sensor LiDAR puede colocarse en diferentes plataformas, desde coches hasta aviones. El LiDAR aéreo permite cubrir extensiones de terrenos muy amplias. En España se dispone de un LiDAR aéreo en abierto dependiente del gobierno que cubre el país entero a lo largo del tiempo a través de vuelos (actualmente hay tres vuelos disponibles: 2008-2015, 2015-2021, 2021-2025), permitiendo evaluar cambios estructurales forestales a lo largo del tiempo y el espacio. La densidad de puntos del LiDAR no es muy alta (entre 0,5-5 puntos por metro cuadrado) pero suficiente para obtener métricas forestales a una escala espacial muy precisa (1 metro cuadrado). Si el LiDAR es multitemporal permite medir cambios estructurales a lo largo del tiempo como la cobertura de dosel forestal (Ucar et al., 2018) o atributos más detallados como la densidad de hojas (Milodowski et al., 2021) difícilmente medibles en campo a escalas grandes. Los datos obtenidos a través de LiDAR pueden combinarse con los de inventarios forestales nacionales para obtener una evaluación de cambios estructurales de muy pequeña escala para distintos tipos de bosque que permiten describir procesos de degradación imperceptibles o muy difíciles de medir con otras técnicas.

## 1.6. Objetivos y capítulos de la tesis

En esta tesis doctoral se van a estudiar los efectos del cambio global (cambios estructurales y climáticos, junto con las perturbaciones como los incendios) en el ciclo del carbono y el agua. En particular: los patrones espaciales del ciclo del agua verde y azul de los bosques (Capitulo 1) y sus cambios en el tiempo (Capitulo 2); el efecto de los incendios en la pérdida de carbono forestal (Capitulo 3); y los patrones recientes de expansión y degradación del dosel arbóreo en el tiempo (Capitulo 4).

Específicamente, en el Capítulo 1 se analiza el patrón espacial del agua azul y verde en los bosques de la España peninsular en relación con los diferentes tipos funcionales de bosques (fagáceas perennes y caducas, coníferas) y bioclimas (atlántico, mediterráneo y alpino), y como las variables forestales estructurales (leaf area index: LAI, área basal) y climáticas (temperatura, precipitación y derivados) afectan al ciclo del agua forestal. El ciclo del agua forestal debido a su dificultad para obtener medidas de campo es poco conocido a escala de país en España, siendo la mayoría de los trabajos a escala experimental de parcela (del Campo et al., 2018, 2019). Las diferencias en el ciclo del agua forestal en los diferentes tipos de bosques, climas y sus drivers ambientales pueden ser conocidos a través de la modelización ecohidrológica (De Cáceres et al., 2023), que puede permitir conocer el ciclo del agua a una escala espacial mucho más amplia difícilmente evaluable con datos de campo. Además, se puede analizar la variación del ciclo del agua a lo largo

del tiempo y como las diferencias estructurales y climáticas han afectado a esos cambios. El balance hídrico en España ha podido tener un aumento del agua verde debido al crecimiento del bosque y, en contraprestación, una disminución del agua azul, pero si hay una reducción de la precipitación ambos flujos de agua pueden haber disminuido.

En el Capítulo 2 se analiza el patrón temporal del agua azul y verde en las últimas tres décadas en los distintos bosques de España en un contexto de cambio en la estructura (árboles de mayor tamaño y mayor cobertura arbórea y arbustiva consecuencia de la reducción de la gestión forestal) y cambio climático (mayor temperatura y subidas/bajadas de precipitación). También se analiza un escenario de gestión (reducción del área basal) para evaluar el efecto de la gestión en la producción de agua azul. La hipótesis es que el agua verde ha aumentado (y el agua azul disminuido) debido al crecimiento del bosque, pero la reducción de la precipitación puede haber afectado más al agua azul que la verde. En cuanto a la gestión, la hipótesis es que la reducción de área basal puede aumentar el agua azul, pero solamente a corto plazo, ya que la recuperación de superficie de hojas es alta.

En el capítulo 3 se analiza el efecto de los incendios en las pérdidas de carbono almacenado en los bosques españoles en las últimas tres décadas. El balance de carbono forestal ha sido estudiado ampliamente en España mediante inventarios forestales. Sin embargo, el efecto de los incendios, que es una de las mayores perturbaciones ambientales en España, en las emisiones de $CO_2$ no ha sido evaluado en los bosques españoles. Los incendios pueden suponer perdidas de carbono en los bosques, pero su cuantificación, distribución, y los drivers ambientales que determinan esas pérdidas se conocen poco. A su vez la variación temporal del efecto de los incendios en el carbono forestal también ha sido poco evaluada. En el capitulo se cuantifica la perdida de carbono aereo en dos periodos consecutivos mediante inventarios forestales por tipos de bosques, diferenciando ademas si los bosques eran hotspot o no y si las perdidas de carbono estan sobre o infrarepresentadas en los hotspot.

En el capítulo 4 se analiza, como la estructura forestal ha cambiado en las últimas décadas en los bosques españoles mediante LiDAR multitemporal. Esta metodología permite medir cambios estructurales como la extensión o atributos más detallados como la densidad de hojas difícilmente medibles en campo a escala de país. Los inventarios forestales nos indican que los bosques españoles siguen creciendo pero también se ha señalado un aumento de la defoliación y de la mortalidad. La información del LiDAR aplicados sobre las parcelas de los inventarios forestales permite conocer ambos procesos (crecimiento y degradación) a lo largo del tiempo y el espacio. En particular, se ha medido el cambio de cubierta arbórea, la cobertura de claros en las copas, y la densidad de hojas. Estas medidas indican tanto si hay expansión (cubierta arbórea) como degradación (claros y reducción de la densidad de hojas), y se analiza también si hay variables estructurales o climáticas detrás de estos cambios.

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# Capítulo 1

## Regional patterns and drivers of modelled water flows along environmental, functional, and stand structure gradients in Spanish forests

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**Regional patterns and drivers of modelled water flows along environmental, functional and stand structure gradients in Spanish forests.**

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## Abstract

The study of the water cycle in the forest at large scales, such as countries, is challenging due to the difficulty of correctly estimating forest water flows. Hydrological models can be coupled to extensive forest data sources, such as national forest inventories, to estimate the water flow of forests over large extents, but so far the studies conducted have not analysed in detail the role of stand structure variables or the functional traits of the forest on predicted blue/green water flows. In this study, we modelled the water balance of Spanish forests using stand structure and species data from forest inventories to understand the effects of climate, stand structure, and functional groups on blue water flows. We calculated blue water and green water flows and expressed them relative to received precipitation. Relative blue water flow was mainly concentrated in the wetter regions (Atlantic and Alpine biomes) of Spain (around 25 %) in comparison with the Mediterranean biomes (10-20%) and during the autumn-winter season. Leaf Area Index (LAI) of the forest stand is the most important predictor of relative blue water, exhibiting a negative effect until it reaches a plateau at higher levels (around 2.5-3). Deciduous forests showed a greater relative blue water flow than evergreen functional groups (25-35 % and 10-25% respectively), primarily due to leaf fall during the autumn-winter season. This study highlights how green water is decoupled from blue water, namely, blue water depends on winter and autumn precipitation, while green water depends on the spring and summer water demand and how the species functional traits (deciduous vs evergreen) can influence the blue water production.

## 1. Introduction

Forests are one of the most important ecosystems on the planet and constitute a supplier of carbon and water for humanity (MEA, 2005). Even though water is the main determinant of vegetation worldwide (Wang-Erlandsson et al., 2022), the water cycle is particularly challenging to study because of the difficult to measure its components. The water cycle in forests depends on the precipitation that falls in the forest, which can be partitioned into the green water and the blue water (Caldwell et al., 2016; Schlesinger and Jasechko, 2014). The green water is the evapotranspiration flow from the forest to the atmosphere, formed by the water transpired by plants, together with the evaporation of intercepted precipitation by vegetation and the evaporation from the soil surface (Llorens et al., 2011). Climate, specific traits, stand forest structure, and their interactions determine the partitioning of precipitation between green water and blue water. Forest evapotranspiration is determined by local climate conditions, such as air temperature, radiation, vapour pressure deficit or soil water availability (Granier et al., 2000). Moreover, plant transpiration is different among species depending on their specific traits, as leaf area, xylem traits determining the efficiency of water transport or leaf phenology (evergreen and deciduous) (Ford et al., 2011). Stand forest structure is also key in rainfall partitioning through its relationship with stand LAI (total area of leaves of the canopy per unit horizontal ground area) which is a key variable determining transpiration (Granier et al., 2000) and/or the interception of vegetation. On the other hand, blue water can be split into two flows: the surface runoff and the surplus of groundwater by the system and available downstream.

Green water reduces the amount of blue water produced at local scale but recycles the water through evapotranspiration at global scale (Ellison et al., 2012). Green water flow is usually greater than blue water's in forests and grasslands in comparison with croplands or wetlands due to the greater transpiration of the former (Oki and Kanae, 2006). Green water represents around 40-70 % of water flow in temperate and boreal forests (Schlesinger and Jasechko, 2014), and even 90-100 % in dryer environments or years, including Mediterranean forests (Ungar et al., 2013; Campos et al., 2016; Qubaja et al., 2020). The combination of different rainfall dynamics, transpiration, stand structure, and specific life traits can modify the partitioning between green and blue water. For instance, water yield can be affected by the temporal distribution of rainfall events (seasonality and torrentiality). Relative water interception by trees decreases when rainfall increases, being greater in arid environments compared to humid forests (Levia and Frost, 2003). In Mediterranean forests the interception is greater than in temperate forests due to the smaller rainfall amount and intensity and the higher evaporation caused by the higher temperature (Limousin et al., 2008). However, evaporation of intercepted water is lower during late-summer intense convective storms since the rainfall intensity is very high and of short time (torrentiality) (Llorens and Domingo, 2007). Physiological and phenological differences among species also modulate water flows. Evergreen Mediterranean trees can reduce their transpiration in summer (water saver) but deciduous trees increase it due to higher water demand (water spender) (Baquedano and Castillo, 2006; Klein, 2014; Link et al., 2014; McDowell et al., 2008). Therefore, Mediterranean forests show transpiration seasonality, with a reduction in stomatal conductance during the summer drought, while the transpiration in temperate forests follows leaf phenology more closely (Llorens et al., 2011).

Water balance in forests has been studied mainly at local and landscape scales, like in watersheds (Caldwell et al., 2016; Guzha et al., 2018; Schwärzel et al., 2020) or forest stands (Benyon et al., 2017; Simonin et al., 2007). Analyses at regional scales have also been carried out (Hoek van Dijke et al., 2022; Mastrotheodoros et al., 2020; Sun et al., 2005), analysing the water flow variation by topoclimate or landscape vegetation cover with hydrological models. The study of water fluxes in forest ecosystems is an important challenge to forest management. Ecohydrological simulations have been shown as a valuable tool to understand water fluxes at different spatial scales, complementing the limited field data available (Hoek van Dijke et al., 2022; Mastrotheodoros et al., 2020). The effect of stand structure variables on water flow have been studied at local scale with field data (Benyon et al., 2017; Simonin et al., 2007). Nevertheless, landscape-level ecohydrological simulations have been most often carried out without incorporating the role of the stand structure variables or the differences in species and functional composition (Hoek van Dijke et al., 2022; Mastrotheodoros et al., 2020).

In our study, we analysed the spatial pattern and partitioning of blue and green water in Spain using ecohydrological simulations with the MEDFATE water balance model (De Cáceres et al., 2023, 2015) using detailed field stand structure and species composition derived from forest inventory data. We simulated water flows and their green and blue water components at daily resolution, and we studied the spatial distribution of relative blue water and its seasonality. Spain is an adequate region to study the partitioning between blue and green water, because it shows contrasting climate gradients, in terms of temperature, rainfall amount and seasonal distribution. Importantly, it includes a contrasted climate between the Mediterranean area —with hot temperature, low precipitation and seasonal drought— and the temperate area —with warm temperature, higher rainfall amount and without seasonal drought (Rivas-Martínez et al., 2011). In addition, peninsular Spain harbours both temperate and Mediterranean forests that span a broad gradient of forest types and stand structures that can modify the partitioning between blue and green water. The questions addressed by the study are: 1) Which are the spatio-temporal patterns of blue and green water along the Spanish Peninsula and among climate subregions? 2) How this partitionin between blue and green water varies among contrasting forest functional groups? 3) Which are the main climatic and forest structural drivers of this partitioning between blue and green water?

## 2. Material and Methods

### 2.1 Study area

The studied area spans the forested areas of Spain, including the Iberian Peninsula and the Balearic Islands, but excluding the Canary Islands. This encompasses two climatic domains: the temperate climate with Atlantic Sea influence, in the north and west parts of the Iberian Peninsula, and the Mediterranean climate, in the rest of the territory. The temperate climate is wetter and colder, while the Mediterranean climate is hotter and drier. We have classified the Iberian territory into six biomes (see map in Figure S1) according to the Iberian climate classification of (Allué Andrade et al., 1990): (i) Arid (9.0 % of the Spanish surface), with warm winters and summers and very low precipitation (< 400 mm); (ii) Temperate Mediterranean (34.8 %), hot in winter and summer with low precipitation (400-600 mm); (iii) Continental Mediterranean (30.9 %), cold in winter and hot in summer with low precipitation (400-600 mm); (iv) Submediterranean (11.0 %); cold in winter and hot in summer with wetter precipitation (about 800 mm); (v) Atlantic (10.5 %), characterized by a mild winter and summer and high precipitation (> 1000 mm); and (vi) Alpine (3.8 %), very cold in winter and cool in summer and high precipitation (> 1000 mm).

### 2.2. Forest inventory data

We used the permanent fields plots from the Spanish national forest inventories to characterize the predominant species and stand structure variables across the study area. The Spanish national forest inventories (SFI) are distributed with a systematic survey along the forested areas with a density of ~1 plot/sq km. Specifically, we used the third inventory (SFI3) carried out in 1997-2008, which is the most recent and complete survey available to date. Spanish permanent field plots have four concentric circular sub-plots with radii of 5, 10, 15 and 25 m. Trees were identified and measured within variable circular size plots (5 m radius for trees with dbh $\geq$ 7.5 cm, and trees with 2.5 $\leq$ dbh $\leq$ 7.5 cm are counted; 10 m radius for trees with dbh $\geq$ 12.5 cm; 15 m radius for trees with dbh $\geq$ 22.5 cm; and 25 m radius for trees with dbh $\geq$ 42.5 cm). Moreover, the shrub species or genus within the 10-m-radius subplot were measured with their corresponding percent cover values and average height.

We focused on the field plots with > 70 % of plot basal area of the most predominant tree native species (Table S1) and an overall basal area of > 3 sq m/ha (to ensure that very sparse woodlands, which can hardly be considered a forest, were excluded), resulting in a total number of plots of 32,514. Plots were classified according to the dominant species in terms of basal area, into five functional groups: temperate (e.g., *Fagus sylvatica*) and Mediterranean deciduous (e.g., *Quercus pyrenaica*), temperate (e.g., *Pinus sylvestris*) and Mediterranean coniferous (e.g., *Pinus pinea*) and sclerophylls (e.g., *Quercus ilex*) (see Figure S3 for SFI3 map of the plots selected and Table S1 for the classification of the tree species in these five groups).

### 2.3. Environmental variables

We downloaded the daily data of total precipitation and maximum, mean and minimum temperature for the 5 years before and after the date of survey for every plot (that is, 10 years per plot) from E-OBS data at 1 km horizontal resolution (Moreno and Hasenauer, 2016); ftp://palantir.boku.ac.at/Public/ClimateData). Topographic variables of slope, aspect and altitude were derived from a digital elevation model (DEM) at 25 sq m of the PNOA Spanish project through the IGN website (downloaded on 14/02/2022; https://centrodedescargas.cnig.es/CentroDescargas/index.jsp#). We used these topographic variables to obtain daily values of the relative humidity, solar radiation and potential evapotranspiration (PET) per plot through the *meteoland* R package (De Cáceres et al., 2018). We characterized plot-level climatic conditions using three climatic indexes; climatic moisture (mean annual precipitation/mean annual PET), continentality (mean temperature of the hottest month -

mean temperature of the coldest month) and precipitation seasonality ((standard deviation of monthly precipitation/mean of monthly precipitation) * 100).

A summary of the main stand structure and climate characteristic of the different functional groups and biomes is shown in Table S2.

### 2.4. MEDFATE model

MEDFATE model (version 2.9.3) has been designed to simulate plant water balances and soil in structurally- and compositionally-heterogeneous forest stands (De Cáceres et al. 2015; De Cáceres et al., 2023). MEDFATE uses daily weather as input and most processes are simulated at daily time steps. Aboveground stand structure is represented in terms of total crown ratio (CR), height (H) and leaf area index (LAI) of a set of woody plant cohorts. The soil is represented by vertical layers having different hydraulic properties and each cohort may have a different root distribution, specified using the depth corresponding to cumulative 50 % and 95 % of fine roots (Z50 and Z95, respectively).

Each day, the model updates the leaf area for (semi-) deciduous vegetation based on a simple phenological model that dictates leaf budburst and leaf drop. This model relies on the SGDD parameter, representing the degree days needed for budburst (assuming evergreen plants maintain a consistent leaf area throughout the simulation). Subsequently, the model revises the light attenuation within the canopy, adhering to the Beer-Lambert model, as well as the canopy's water storage capacity, which signifies the minimum water quantity required to saturate the canopy. Following the canopy status update, the model addresses the input of water from precipitation. Prior to augmenting the soil layers' water content, the model initially deducts the water loss from rainfall due to interception and surface runoff. Rainfall interception loss is estimated using the simplified version of the Gash model (Gash et al., 1995), while runoff is calculated according to USDA SCS curve number method (Boughton, 1989). Processes related to lateral water transfer are omitted from consideration. Soil water storage capacity and water potential are derived from soil texture through pedotransfer functions (Saxton et al., 1986). When replenishing a specific soil layer, a portion of the water is assumed to directly infiltrate the layer below, as determined by microporosity (Granier et al., 1999). The water percolating from the deepest layer is presumed to be lost through deep drainage.

To assess plant transpiration, the model initially calculates a distinct estimation of the maximum transpiration for the entire plant community (including trees and shrubs) —that is, without considering the soil water deficiency. This calculation is done for each taxon and takes into account the atmospheric evaporative demand. It involves two taxon-specific parameters: aTmax and bTmax. parameters. The estimation of maximum transpiration for the entire stand (Emax,stand), excluding considerations for soil water deficit, relies on the daily Penman's potential evapotranspiration (PET) and an empirical relationship established by Granier et al. (1999). But MEDFATE modified the Granier equation with aTmax and bTmax:

$$\frac{E_{\text{max,stand}(i)}}{\text{PET}} = a_{\text{Tmax}} \cdot \text{LAI} + b_{\text{Tmax}} \cdot \text{LAI}^2,$$

where aTmax and bTmax represent species-specific parameters (De Cáceres et al., 2023). Assuming reliable species-specific estimates are accessible for aTmax and bTmax, the equation can be applied to calculate Emax,stand(i). Once Emax,stand(i) is determined for each species in the stand, the portion of shortwave radiation absorbed is employed to estimate its maximum transpiration (Emax(i)) from Emax,stand(i) (Korol et al., 1995).

Moreover, the cohort's transpiration is influenced by the vertical distribution of fine roots, the soil moisture profile, and two parameters specific to the taxon: Ψ extract and c extract. These parameters represent the soil water potential at which 50 % of the maximum transpiration occurs, and the slope of a Weibull function that regulates the rate of transpiration decline, respectively.

The plant's water status is expressed as a plant water potential, denoted as Ψ plant, which is defined as an "average" of the soil water potential in the rhizosphere. The model monitors the effects of drought by assessing the proportion of hydraulic conductance lost due to stem cavitation, referred to as PLC. Increases in PLC occur whenever Ψ plant decreases, following a xylem vulnerability curve characterized by the parameters VC_stemc and VC_stemd. PLC sets limits on actual transpiration rates and does not decrease even when Ψ plant increases. It is worth noting that the effects of cavitation can only be reversed, i.e., PLC can be reduced, through the formation of new sapwood, as outlined by Choat et al., 2018.

### 2.5. Parameter estimation

Data from forest inventory plots included tree height (*H*) and tree diameter at breast height, which was used to obtain estimates of foliar biomass (hence leaf area after multiplying by *SLA*) and crown ratio (*CR*) via species-specific allometries (see Table S1-3 of De Cáceres et al., 2023 for more details). In shrubs, foliar biomass is calculated from shrub height via species-specific allometries. In the model, *SLA* (Specific Leaf Area (sq *mm/mg*)), *the ratio of leaf area to leaf dry mass*, is constant for every specie (De Cáceres et al., 2023). Leaf area index (LAI in $m^2 \cdot m^{-2}$) was calculated from the foliar biomass (in $kg \cdot m^{-2}$) by using a *specific leaf area* coefficient (SLA, in $m^2 \cdot kg^{-1}$) that is species-specific (LAI = foliar biomass * SLA). Taxon-specific parameter details are shown in supplemental material of De Cáceres et al., 2023. Soil data of each forest inventory plot was extracted from the SoilGrids database (Hengl et al., 2017). For all plots four soil layers down to a total depth of 4 m were initially considered, but the deepest layers were merged into a rocky layer (95 % of rocks) following the depth of the R horizon. A monotonous increase in rock fragment content across soil layers from the surface to the rocky layer was defined based on surface stoniness classes determined in SFI3 plot surveys.

### 2.6. MEDFATE simulations

MEDFATE was run on each selected SFI3 plot using daily weather data (temperature and precipitation, PET, radiation and relative humidity) corresponding to a 10-yr period centered on the year of the SFI3 sampling (1997-2008). We calculated the blue water as the sum of the runoff and deep water and the green water as the evapotranspiration (that included the sum of the transpiration, interception and soil evaporation).

### 2.7 Model evaluation

MEDFATE predictions have already been evaluated at the forest stand scale in terms of soil moisture dynamics, plant transpiration and water status in Mediterranean forest (De Cáceres et al., 2021, 2015). Given the focus of the present work, we evaluated regional-scale patterns of green and blue water predicted by MEDFATE against those produced by alternative methods. First, we did a comparison between the results for average blue water of MEDFATE with the average blue water from the Precipitation Runoff Integrated Model (SIMPAL acronym in Spanish) of the Spanish government. SIMPAL model is calibrated with stations that measure stream flows across Spain and it is interpolate a 1 $km^2$ resolution for the whole country (Estrela et al., 2012). Second, we compared green water patterns predicted by MEDFATE against those of GLEAM, which is derived from satellite data and covers the world with a resolution of 0.25 degrees (Martens et al., 2017). We used the GLEAM v3.8a that defines the evapotranspiration as the sum of transpiration (from short and tall vegetation), interception (from tall vegetation), soil and open water evaporation and snow sublimation.

### 2.8. Statistical analysis

Our analyses focused on relative blue water, the ratio between simulated annual mean blue water and the total precipitation as response variable. The variation of relative blue water across biomes and functional groups was analysed using beta regression models (Ferrari and Cribari-Neto, 2004). We used beta regressions because the response variable was a proportion. A post-hoc Tukey's test was applied for pairwise comparisons between groups (i.e., biomes and functional groups).

The effect and importance of climate, topographic and stand structure variables in the partitioning of blue/green water of every functional group were analysed with XGBoost regression. XGBoost is a machine learning system that builds a sequential series of shallow regression trees with a gradient boosting technique (Chen and Guestrin, 2016). XGBoost regression was used because it allows to analyse lineal and non-lineal responses and correlated variables. A regression tree is trained by splitting the input dataset into increasingly homogeneous subsets at each decision nodes and choosing the split that maximizes the distance between different terminal nodes. 14 different climatic variables calculated as the mean annual values of the 10 years of climate data for every plot (mean, maximum and minimum temperature, solar radiation, moisture and continentality indexes) and the mean of seasonal variables (precipitation of spring, winter, summer, and autumn; precipitation seasonality index) were used as predictors. A topographic variable (slope) and two stand structure variables (basal area and LAI of the plot) were also included. Basal area serves as an indicator of canopy cover, as it is calculated by summing the trunk cross-sectional area at breast height of all trees per hectare, and higher basal area values can result in increased interception. LAI determine the transpiration of the trees and shrubs through of the leaf surface. LAI of the plot was calculated from the sum of the LAI of trees and shrubs. One model for each of the five functional groups was computed. The models were tuned for finding the best hyperparameters and they were evaluated using a k-fold cross-validation procedure (Ten-fold with five repetitions), following a stratified random sample into k subsamples of the dataset. A forward feature selection method for selecting the predictor variables with a spatial cross-validation (Meyer et al., 2018)was used. The models were built for each predictor pair combination and the best was selected. The remaining predictors were tested by adding them to the best combination pair. This procedure continued until neither of the remaining predictors resulted in an improvement of the model. Variable importance in the retained variables was evaluated by computing the fractional contribution of each feature to the model based on the total gain of these variables splits (*Gain*), the relative number of times a feature is used in trees (*Frequency*) and the relative value of the feature observation (*Cover*). We estimated the $R^2$ to test the accuracy of the final models with: 1-(Sres/Stot), being Sres the sum of the squared differences between the observed values and the predicted values, and Stot is the total sum of squares, which is the sum of the squared differences between the observed values and the mean of the observed values. All statistical analyses were conducted with R v. 4.1.1., with the packages *xgboost* (Chen et al., 2015) and *caret* (Kuhn, 2008).

## 3. Results

### 3.1. Model evaluation

The comparative indicated that the blue water of the SIMPAL model and the green water of GLEAM followed the same regional patterns that MEDFATE (Figure 1). SIMPAL reaches higher values of blue water in the Atlantic biome and lower values in west Temperate Mediterranean than MEDFATE. In opposition GLEAM evapotranspiration is higher in the west Temperate Mediterranean and lower in the Atlantic forest than MEDFATE. MEDFATE models at stand scale whereas SIMPAL and GLEAM models are at regional scale. At stand scale the evapotranspiration is high in the Atlantic forest and then the blue water is lower. West Temperate Mediterranean is characterized by forest of low basal area and LAI (Table S2, Figure S4). Therefore, the evapotranspiration is lower and blue water higher than surrounding forest. In other words, the differences observed seem to arise from the fact that MEDFATE takes into account the stand structural characteristics, which are difficult to represent in models based on interpolation (SIMPAL) or remote sensing (GLEAM).

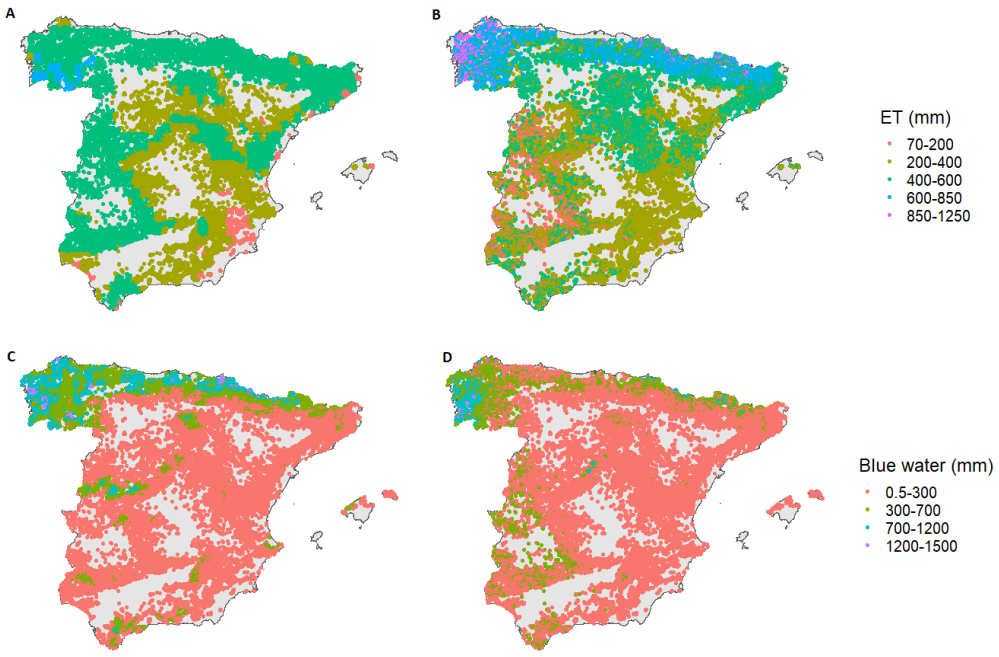



Figure 1. Average evapotranspiration (ET) maps for SFI3 plots according to GLEAM (A) and MEDFATE (B) (Spearman correlation=0.62, $R^2$=0.218) and average blue water maps for SFI3 plots according to SIMPAL (C) and MEDFATE (D) (Spearman correlation=0.70, $R^2$=0.354).

### 3.2. Spatial patterns of blue water in the Spanish biomes

Forests with the highest absolute amount of blue water (> 500 mm) were mostly concentrated in the coast of the Atlantic Sea and in the Pyrenees (Figure 2A). The south of the Spanish Peninsula in the Temperate Mediterranean biome and some areas inside the Continental Mediterranean biome had values between 300-500 mm. The rest of the country had lower blue water values (< 300 mm), manly in the eastern and Mediterranean regions. Relative blue water showed a very similar spatial pattern, with the highest values located in the coast of the Atlantic Sea and the Pyrenees (Figure 2B). In the southwest of Spain and in the Mediterranean mountain regions the relative blue water was also high (> 50 %). Forests in the eastern Mediterranean region had the lowest values. The Arid and Continental Mediterranean biomes showed a very large percentage of plots (> 70 %) with low relative blue water (< 15 %), whereas the Atlantic and Alpine biomes showed higher plots (> 50 %) with high blue water (> 30 %) (Table S3). Temperate Mediterranean and Submediterranean biomes showed more intermediate values, although the Temperate had the percentage of plots with highest blue water (> 60 %) among all biomes. The results of the beta regression model and post-hoc Tukey´s test indicated that there were differences among biomes in the percentage of blue water (Table 1, Figure 3, see Figure S5-S6 for interception and soil evaporation differences): relative blue water was higher in the Atlantic and Alpine biomes (mean over 25 %) followed by the Temperate Mediterranean and Submediterranean biomes, with the Arid and Continental Mediterranean biomes showing the lowest values (mean of 10-15 %). The absolute values showed a similar pattern that the relative blue (see Figure S7).

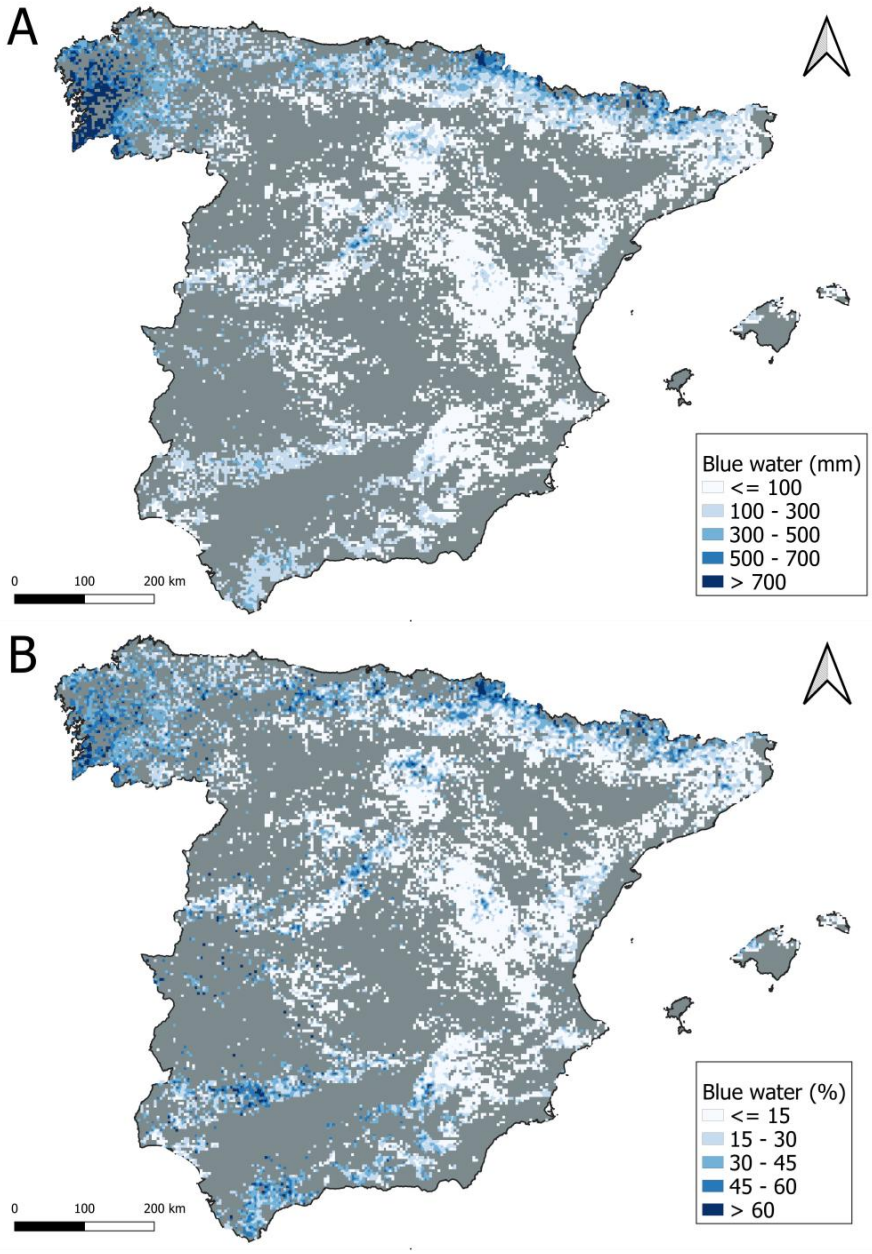



Figure 2. Total (A) and relative (B) blue water in the Spanish Peninsula and Balearic Islands. In grey, no forest covers. Maps were realized with a rasterization of the SFI3 plots results at 1 km$^2$.

Table 1. Results of the beta regression models on relative blue water (%): for the different biomes, indicating the estimate, standard deviation (SE), statistic and p-value of each of them. A positive value indicates that an increment occurred in the biome with respect to the observed values in the intercept.

| **Variable** | **Estimate** | **SE** | **Statistic** | **p-value** |
|---|---|---|---|---|
| Intercept (Arid) | -1.90 | 0.02 | -71.1 | < 0.001 |
| Temperate Mediterranean | 0.49 | 0.02 | 17.6 | < 0.001 |
| Continental Mediterranean | -0.28 | 0.02 | -10.1 | < 0.001 |

| | | | |
|---|---|---|---|
| Submediterranean | 0.22 | 0.027.8 | < 0.001 |
| Atlantic | 1.21 | 0.0241.8 | < 0.001 |
| Alpine | 1.06 | 0.0333.0 | < 0.001 |

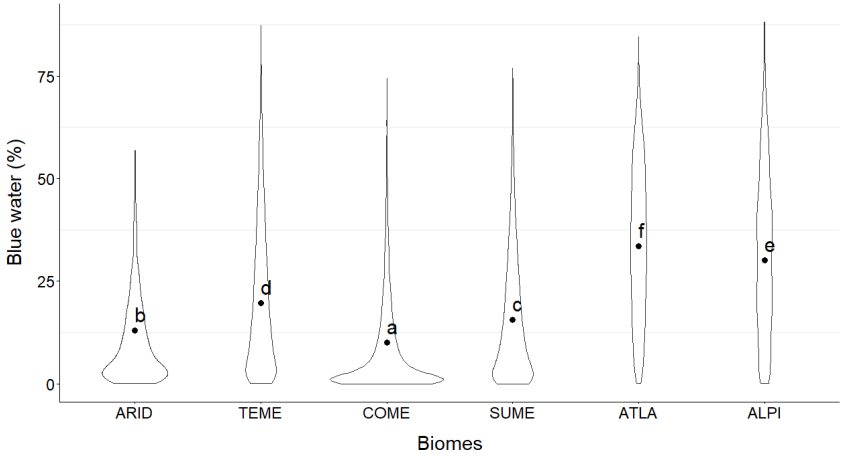



Figure 3. Percentage of blue water in the different biomes. Different letters denote significant differences among biomes ($p$<0.01) after Tukey's test. Abbreviations of the biomes: ARID, Arid; TEME, Temperate Mediterranean; COME, Continental Mediterranean; SUME, Submediterranean; ATLA, Atlantic; ALPI, Alpine.

### 3.3. Patterns of blue water among forest functional groups

Beta regressions models and post-hoc Tukey´s test indicated that there were also differences among functional groups in the percentage of blue water (Table 2, Figure 4, see Figure S8-9 for interception and soil evaporation differences). Relative blue water was high in temperate deciduous (35 %) followed by temperate coniferous, Mediterranean deciduous and sclerophylls (20-25 %). Mediterranean coniferous had the lowest value (close to 10 %). The absolute values showed a similar pattern that the relative blue with the temperate deciduous with the highest values (see Figure S10).

Table 2. Results of the beta regression models on relative blue water (%) for the different forest functional groups, indicating the estimate, standard deviation (SE), statistic and p-value of each of them. A positive value indicates that an increment occurred in the functional group with respect to the observed values in the intercept.

| **Variable** | **Estimate** | **SE** | **Statistic** | **p-Value** |
|---|---|---|---|---|
| Intercept (Temperate deciduous) | -0.47 | 0.01 | -33.2 | < 0.001 |
| Mediterranean deciduous | -0.76 | 0.02 | -33.7 | < 0.001 |
| Temperate coniferous | -0.93 | 0.02 | -42.4 | < 0.001 |
| Mediterranean coniferous | -1.42 | 0.01 | -85.7 | < 0.001 |
| Sclerophylls | -1.02 | 0.01 | -53.8 | < 0.001 |

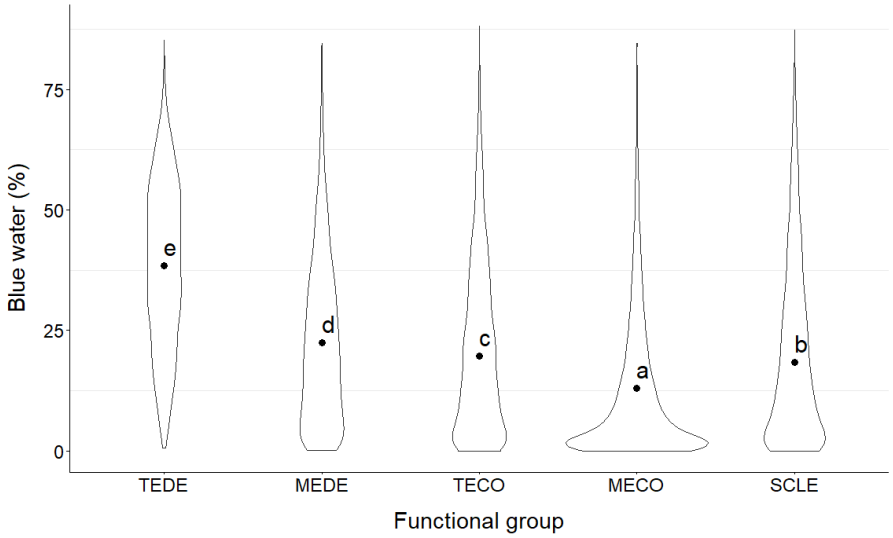



Figure 4. Percentage of blue water of the different functional groups of species. Different letters denote significant differences among forest types ($p$<0.01) after Tukey's test. Abbreviations of the functional groups: TEDE, Temperate deciduous; MEDE, Mediterranean deciduous; TECO, Temperate coniferous; MECO, Mediterranean coniferous; SCLE, sclerophylls.

The analysis of seasonality using monthly-aggregated data showed that the amount of blue water in forests of the different functional groups strongly varied throughout the year. In the Temperate deciduous forests, total blue water was higher than total evapotranspiration in autumn and winter (Figure 5A), whereas in other functional groups, the values of the two flows were similar along the year, except in spring-summer, when the green water was higher. In the Mediterranean coniferous forests, evapotranspiration was higher than blue water all year long. Relative flows showed that blue water was minimum in the summer season in all groups and higher than evapotranspiration only in autumn-winter in temperate deciduous forests (Figure 5B).

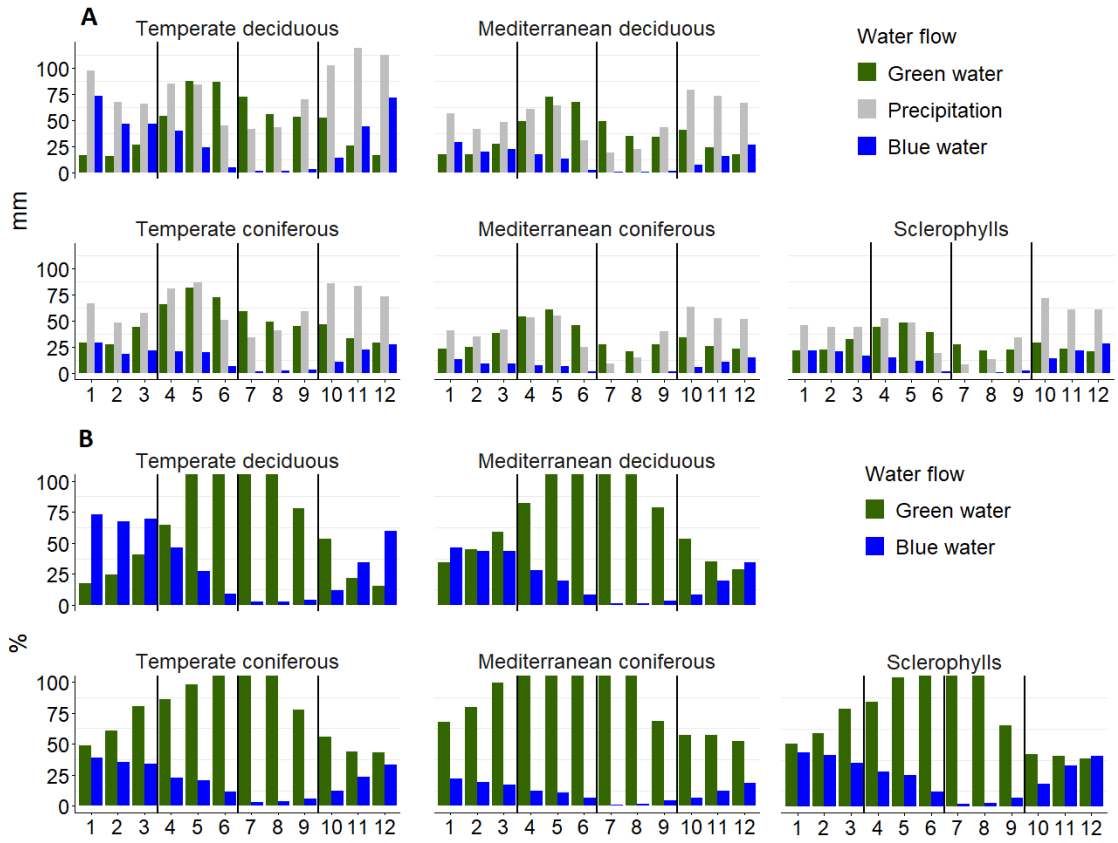



Figure 5. Total (A) and relative (B) green water and blue water, and total precipitation by different functional groups throughout the year. Note that evapotranspiration can be higher than precipitation during summer months, due to plant transpiration and bare soil evaporation of water available in the soil. Relative evapotranspiration has been truncated to 100 % of precipitation with the aim to improve the visualization of water export. A line marks the seasons in the months.

### 3.4. Main drivers of the partitioning between blue and green water

XGBoost models showed high accuracy, with $R^2 > 75$ % in most functional groups (Table S4). These analyses revealed that LAI was the most important predictor of relative blue water in all functional groups (Figure 6). The second and third most important variables were climatic moisture index and winter precipitation, except for Mediterranean deciduous, which was autumn precipitation (see Figure S11-12 for spatial variation of climatic moisture and winter precipitation). The other variables retained in the models had low significance.

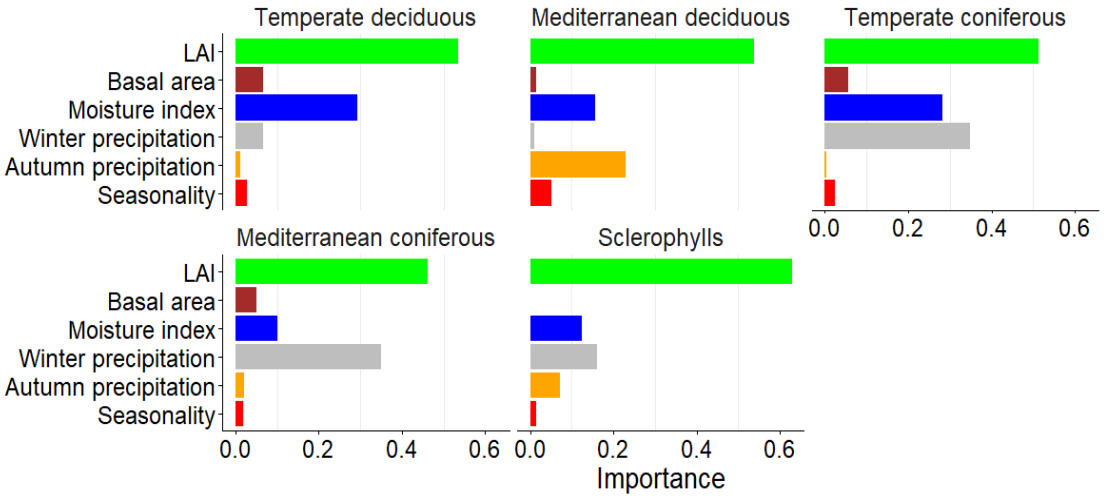



Figure 6. Average importance from Gain, Cover and Frequency values for every predictor variable retained in the XGBoost models for the five functional groups.

Partial dependence plots showed that LAI had a strong and negative effect on relative blue water (Figure 7). Nevertheless, this effect was different depending on the functional group. The temperate deciduous forest showed the highest percentage of blue water for the whole LAI gradient, being always with a value over 20 %. The other forest types showed similar patterns among them, with a larger drop until LAI < 3 and values around 10 % afterwards. The only exception was the group of Mediterranean conifers, which showed lower % of blue water than the other groups throughout the LAI gradient. Climatic moisture index showed a positive effect in all groups. The three angiosperm groups had similar slope and showed higher values than the two gymnosperm groups (Figure 7B). Winter precipitation had a positive effect in all functional groups except in the Mediterranean deciduous (Figure 7C). Temperate deciduous forests showed higher values through the whole winter precipitation gradient.

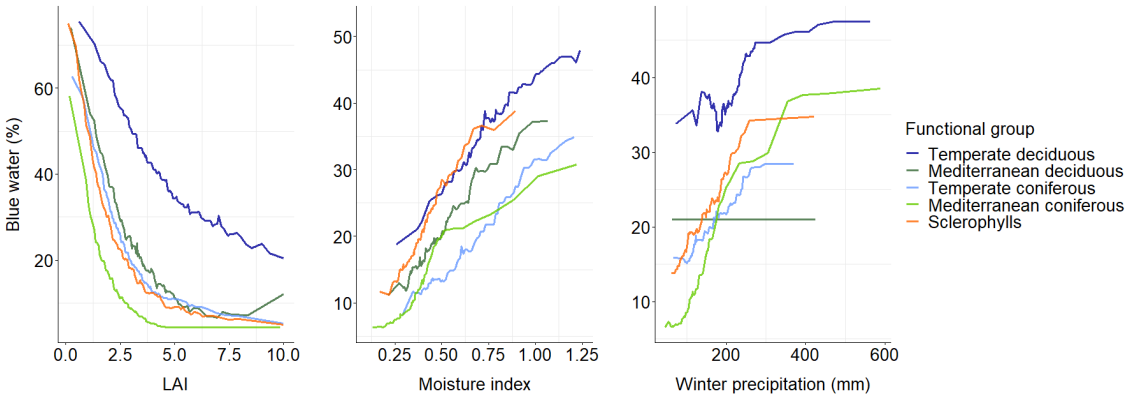



Figure 7. Partial dependence plots for the three main predictor variables (A, LAI; B, Climatic moisture index; C, Winter precipitation) and their effect on blue water percentage for the different functional groups.

## 4. Discussion

### 4.1. Spatio-temporal patterns

Blue water spatial patterns showed that most Spanish forests have a proportion of the precipitation below 15 % as blue water (Figure 3). This pattern was expected, since most of the Spanish forests

are in Mediterranean climate, and in these dry environments the evaporative demand is high and the majority of water evapotranspired or intercepted by the canopy (Ungar et al., 2013). In contrast, in the Atlantic and alpine biomes, the proportion of rainfall as blue water can be higher than 25 %, because these biomes are wetter and colder than the Mediterranean and, thus, the evapotranspiration is lower and precipitation is higher (Kosugi and Katsuyama, 2007; Mastrotheodoros et al., 2020). Moreover, in some mountain areas in the continental Mediterranean biomes (e.g., Sierra Nevada, Sierra de la Demanda), the amount and proportion of blue water is also high (Figure 2A, 2B). These regions are wetter than the rest of Mediterranean biomes and an increase of precipitation determines an increase in blue water (Helman et al., 2017). Interestingly, in other areas of southern Spain, in the temperate Mediterranean biome, the proportion of blue water can also be higher than 20 % (e.g., Sierra Morena; Table S3), not because they have a higher rainfall but because this biome has very open forests, with LAI values lower than the rest of biomes (Table S1). Transpiration is the main component of the green water in arid environments and decrease in wetter regions where the interception increases their importance (see Figure S13). This result is concordant with the global patterns of green water flux where the transpiration is bigger in arid environments (Good et al., 2017).

The analysis of seasonal dynamics by forest type showed that, in forests of all functional groups, there is more blue water during autumn and winter months. In contrast, the evapotranspiration was higher in spring-summer. In Mediterranean climates there is a decoupling between rainfall and temperature (Baldocchi and Xu, 2007), with higher rainfall in spring and autumn and higher temperatures in summer. For this reason, plants have more photosynthetic activity and growth in spring (when rainfall is high) and more transpiration in summer (when temperature is highest) (Baquedano and Castillo, 2006; Link et al., 2014), when trees use the groundwater stored in the soil (Jost et al., 2005). Water loss by run off or deep drainage is higher in autumn-winter because water is not fully exploited by the forest in this lower-photosynthetic period and, thus, green water is lower than would be possible by falling rain (Helman et al., 2017; Williams et al., 2012). According to our results (Figure 5) blue water is concentrated in this period of lower or dormant vegetation activity (i.e., late autumn and winter).

### 4.2. Differences of blue water between forest functional groups

The analysis of the percentage of blue water of the different functional groups of species showed that temperate deciduous forests had the highest value, followed by Mediterranean deciduous forests (Figure 4). The rest of forest types had lower values (Figure 4), mainly the Mediterranean coniferous, which have shown a high green water of almost 90 %, as also observed in studies at the plot level (Ungar et al., 2013). The seasonal dynamics of these flows in the different forest types show that deciduous forests have more blue water in autumn and winter months than evergreen forests (Figure 5). This indicates that the main factor that explains the differences in relative blue water between forest types is the shedding of leaves (or its lack of shedding) during the cold part of the year. Although deciduous trees are mainly water-spender since their transpiration is higher than that of evergreens (Baldocchi et al., 2020), they shed their leaves in autumn and their interception and evapotranspiration are lower than those of evergreens in autumn/winter (Figure 5). Moreover, due to their shape coniferous needles intercept more the rainfall than the deciduous ones for the same area of leaves (Carlyle-Moses, 2004). Although green water is higher in deciduous than in evergreen forests in summer (Figure 5), total annual blue water seems to be more determined by leaf phenology, which conditions the destination of the autumn-winter precipitation and determines the differences between deciduous and evergreen forests. Also, climate partial plots showed that at the same level of climatic moisture index and winter precipitation, deciduous forests have greater relative blue water than coniferous and sclerophylls (Figure 7B-C).

But once the differences between deciduous and evergreen forests are highlighted, the next aspect that stands out when comparing the different types of forests is that, for each category of leaf phenology, the proportion of blue water depends mainly on climate. Thus, temperate deciduous

forests have more relative blue water than Mediterranean deciduous ones (Figure 4). Temperate deciduous forests, which are the ones exporting most blue water in relation to their precipitation, are mainly concentrated in the Atlantic and alpine biomes, where precipitation is higher and transpiration is lower, while Mediterranean deciduous forests are concentrated in Mediterranean biomes, where precipitation is lower and transpiration is higher (Table S2). The same pattern happens in evergreen forests: temperate coniferous forests have percentage of blue water higher than Mediterranean coniferous forests because precipitation in the biomes where they are more abundant is also higher than in the Mediterranean. The lowest value of blue water in Mediterranean coniferous forests is particularly relevant, because this is the most abundant forest type in Spain, and it is predominant in the Mediterranean biomes (Table S1). Finally, sclerophyll forests produce more blue water than Mediterranean coniferous forests, although both are situated in Mediterranean biomes and are evergreen. Sclerophyll forests have higher transpiration than Mediterranean coniferous ones (del Campo et al., 2019; Sánchez-Costa et al., 2015)but the total LAI of their stands is lower (Table S2), which determines the different pattern obtained (as explained in the next section).

### 4.3. Differences in stand structure determining blue water

The analysis of the drivers affecting relative blue water showed that LAI is the most important predictor of blue water (Figure 6). In our simulations, relative blue water was often very high (> 60 %) when LAI was < 1. Transpiration and interception are higher when the LAI of the stand is higher and, therefore, the water is transpired and intercepted by leaves. But the temperate deciduous forests showed higher blue water for the same LAI values. Deciduous trees present higher evapotranspiration than evergreens at the same level of LAI (Baldocchi et al., 2010)but, as described previously, LAI effect is modulated by leaf phenology, since blue water in these forests is concentrated in winter. When LAI is very low, evergreen forests can show a higher relative blue water. For instance, the temperate Mediterranean biome showed more % of plots with a higher relative blue water than Atlantic or alpine biomes (Table S3) because the mean LAI of their forests is lower than the rest of biomes (see Table S1). This points out the importance of stand structure and composition, since in a drier environment, LAI values higher than 2-3 sq m/sq m can strongly reduce the relative blue water. This effect is higher if the forest is evergreen, which is the predominant type in the Mediterranean. Relative blue water of Mediterranean deciduous forests is higher than that of evergreens, because a decrease of LAI in evergreen forests decreases tree transpiration but increases evaporation from the soil surface, which is high in the Mediterranean climate even in winter (Raz-Yaseef et al., 2010). Management of blue water in forests has been focused in modifying the basal area of the stand (del Campo et al., 2014). Nevertheless, in this study basal area was a limited predictor of the blue water in comparison with LAI. LAI of the stand increases with basal area until a threshold and then it remains stable (Figure S14). Although the increase of basal area through time reduces blue water (Caldwell et al., 2016), a plateau is expected in the long term, since LAI will not increase more after a maximum is reached. For this reason, blue water did not reduce excessively when LAI was higher than 3 (Figure 7A). The reduction of basal area in the forest through thinning is a recurrent way of increasing blue water (Ameztegui et al., 2017; del Campo et al., 2018; Simon and Ameztegui, 2023), but this non-linear relationship between basal area and LAI implies that only a heavy management for reducing basal area would be effective for reducing the LAI of the stand and, thus, increasing blue water.

### 4.4. Limitations

Model simulations to estimate water flows is not the same as observing them and can led to artifactual results. In this sense, it is necessary to continue improving the ecohydrological model design parametrization to improve their accuracy, including the completion of traits of many species for the parameterization, a better soil database, or the inclusion of lateral water flows (in the case of MEDFATE model). Model evaluation is another key aspect to increase realism and

usefulness of predictions. The model MEDFATE has been validated in Mediterranean forests at local scale with field ground data, but it has not been validated at country scale with field data like eddy flux or sap flow data, and it might have lower accuracy in the Atlantic or alpine biome or with some tree species. Nevertheless, the comparison between MEDFATE results and another land surface products showed a similar regional patterns. Despite accepting these limitations, the lack of field data at bigger scales encourages the use of models to study water flows at country or continental scale.

## 5. Conclusion

Ecohydrological models like MEDFATE allow to model different species and stand structures, improving our insights about the role of forests in water flows. Thus, we can split the fluxes of water at stand level and understand the role of species, climate and stand structure variables in the different water flows: transpiration, interception, runoff, etc. Moreover, the incorporation of forest inventories to these models allows to do analyses at large spatial scales across multiple climates, forest typologies and species composition. In the current context of global change, the knowledge of water fluxes in forests is essential to be able to define strategies to improve the water budget, and especially in dry environments like the Mediterranean, where water is scarce and the previsions are in the line of increasing drought periods. Thus, in the context of global change we are suffering (Hoerling et al., 2012; Lionello et al., 2014), the low amount and proportion of blue water in great part of Spain is an important problem in the water supply for the agriculture or human consumption in the region (Ellison et al., 2012). The consequences that this lack of blue water might have on the entire silvoagropastoral system in the whole region, aggravated by the harsher conditions expected in the future, should make us reflect on what kind of forest management could be more effective in the next decades.

**Code availability.** The model code of MEDFATE is available at https://github.com/emf-creaf/medfate. The MEDFATE model code is explained in De Cáceres et al. (2023).

**Data availability.** Spanish forest inventory data are available at https://www.miteco.gob.es/es/biodiversidad/temas/inventarios-nacionales/inventario-forestal-nacional/.

**Author contributions:**

JSD, MC, JV and JR contributed to the study conception and design. JSD conducted the modelling with the support of MC. JSD wrote the manuscript with the assistance of the rest of the authors. All authors discussed the results and edited the manuscript.

**Competing interests:**

The authors declare that they have no conflict of interest.

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## Supplemental Material

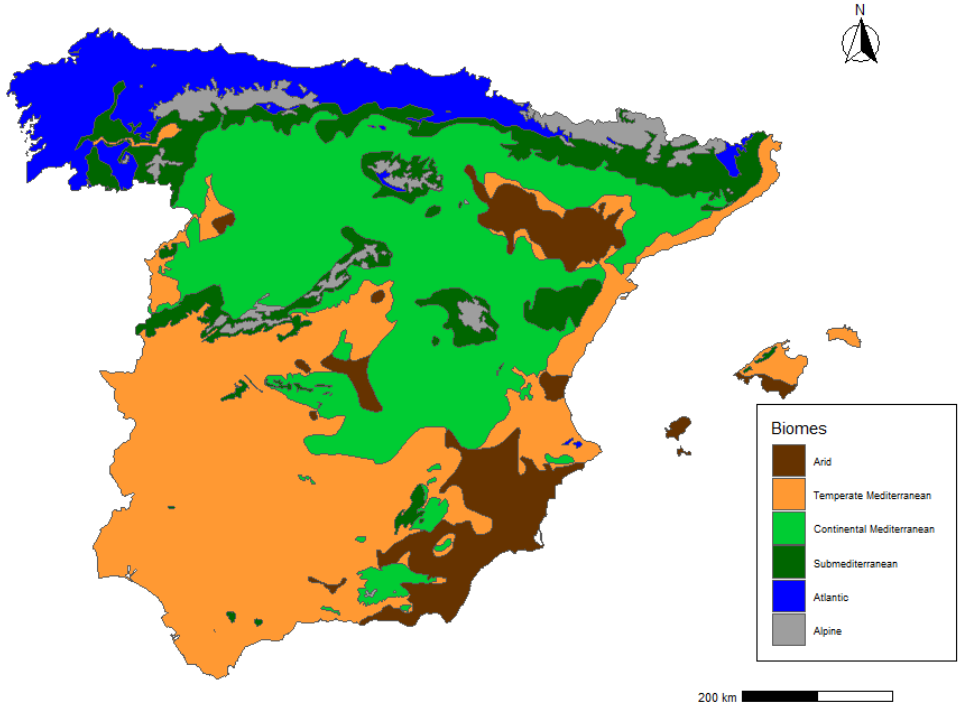



**Figure S1.** Climatic biomes in the Spanish Peninsula and Balearic Islands.

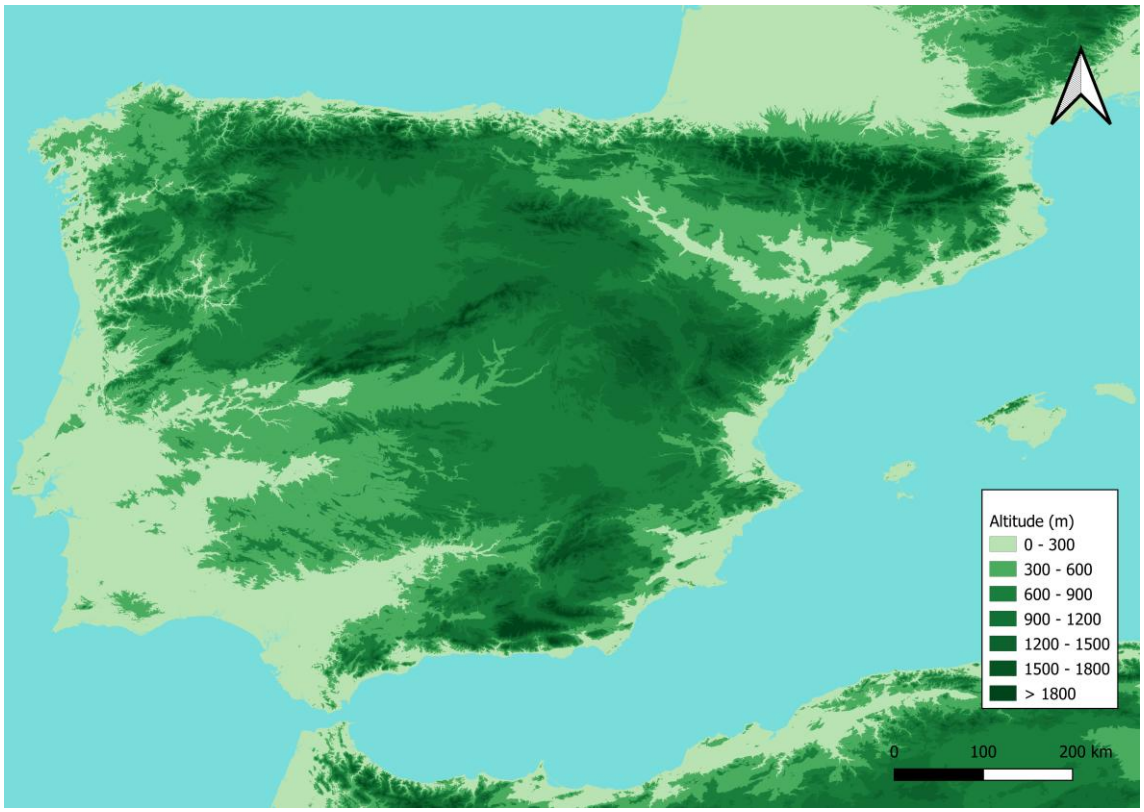



**Figure S2.** Altitude in the Iberian Peninsula and Balearic Islands.

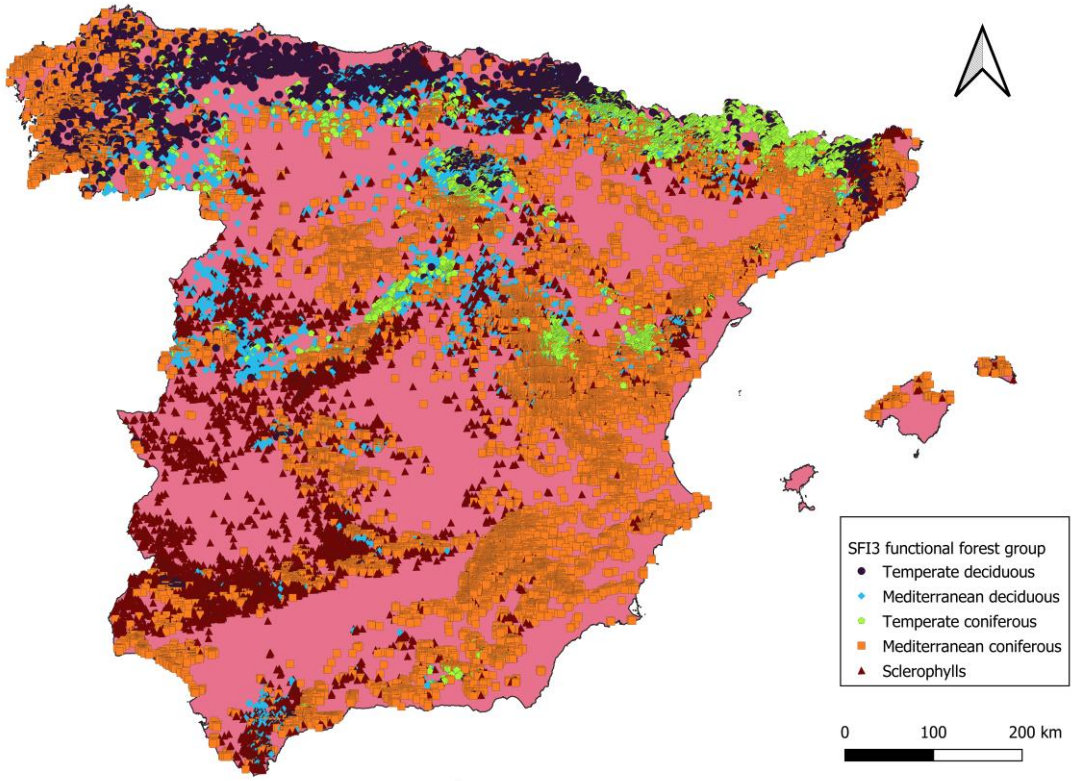



**Figure S3.** SFI3 plots by functional forest group

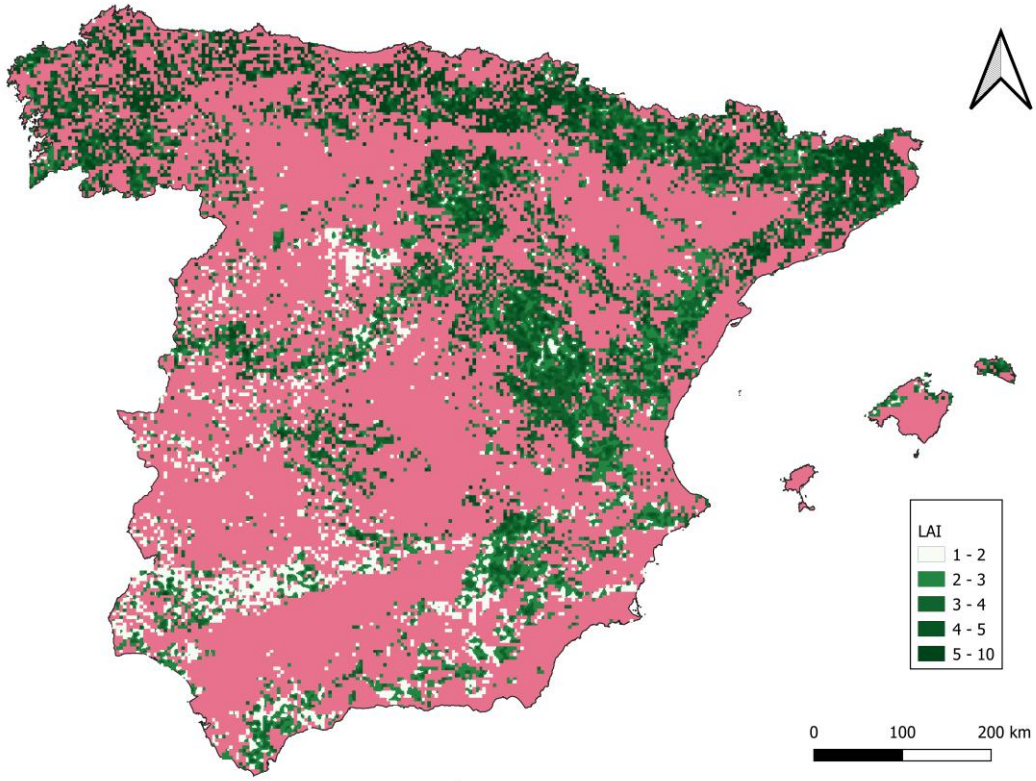



**Figure S4.** LAI of the Spanish Peninsula and Balearic Islands forest.

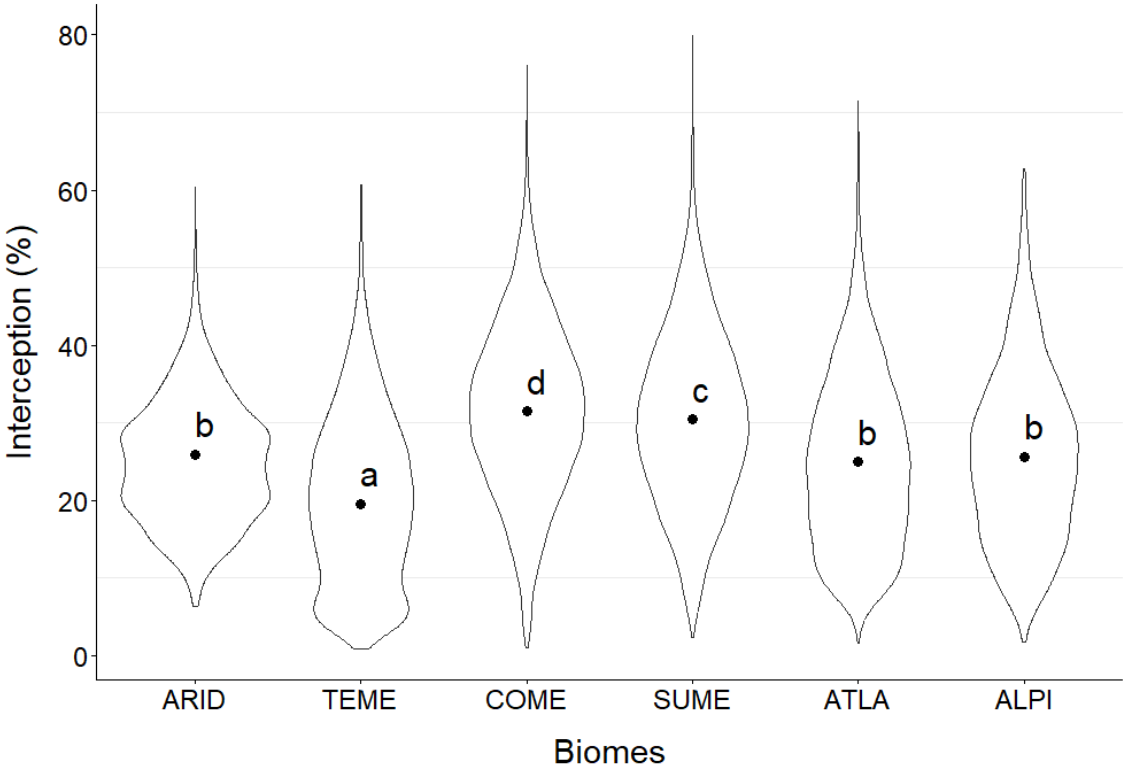



**Figure S5.** Percentage of interception in the different biomes. Different letters denote significant differences among biomes ($p < 0.01$) after Tukey's test. Abbreviations of the biomes: ARID, Arid; TEME, Temperate Mediterranean; COME, Continental Mediterranean; SUME, Submediterranean; ATLA, Atlantic; ALPI, Alpine.

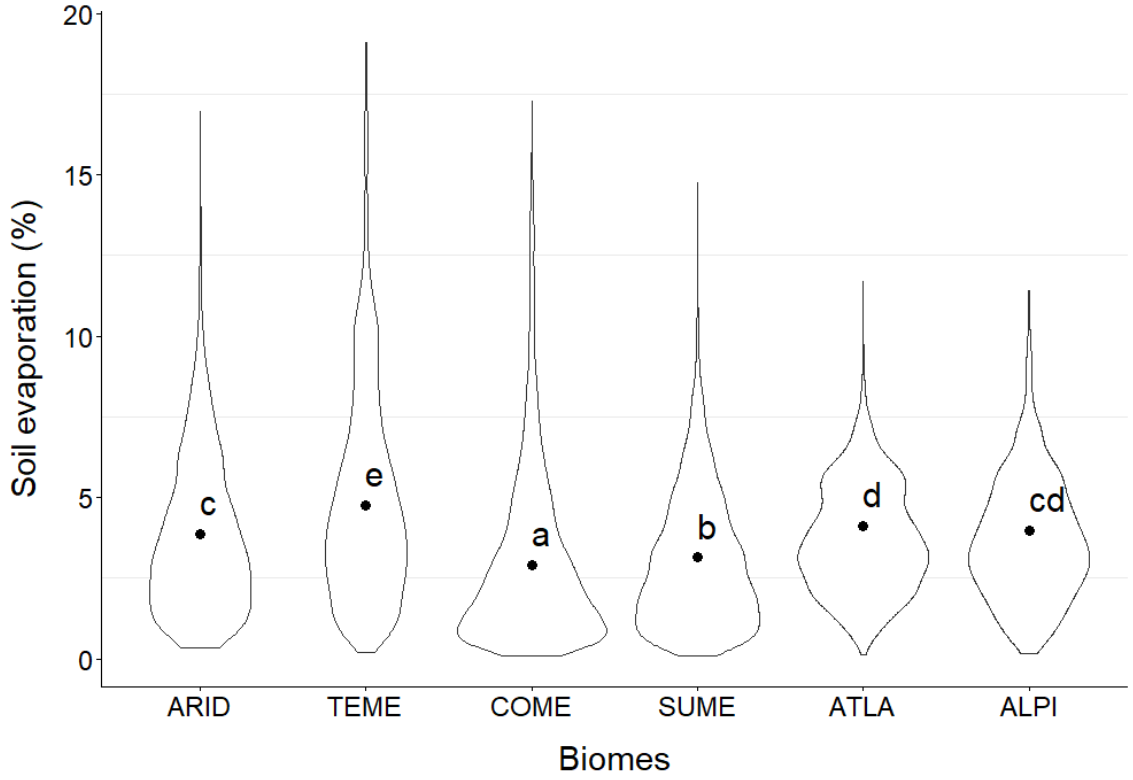



**Figure S6.** Percentage of soil evaporation in the different biomes. Different letters denote significant differences among biomes ($p < 0.01$) after Tukey's test. Abbreviations of the biomes: ARID, Arid; TEME, Temperate Mediterranean; COME, Continental Mediterranean; SUME, Submediterranean; ATLA, Atlantic; ALPI, Alpine.

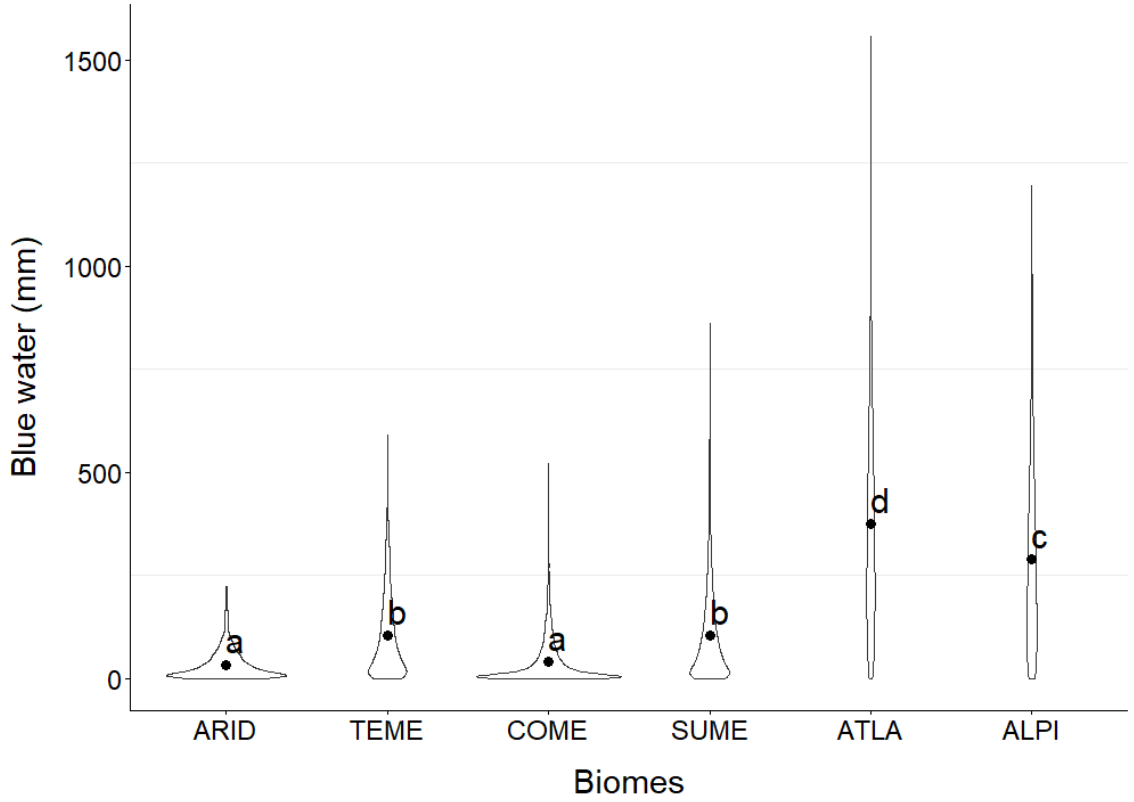



**Figure S7.** Blue water amount in the different biomes. Different letters denote significant differences among biomes ($p < 0.01$) after Tukey's test. Abbreviations of the biomes: ARID, Arid; TEME, Temperate Mediterranean; COME, Continental Mediterranean; SUME, Submediterranean; ATLA, Atlantic; ALPI, Alpine.

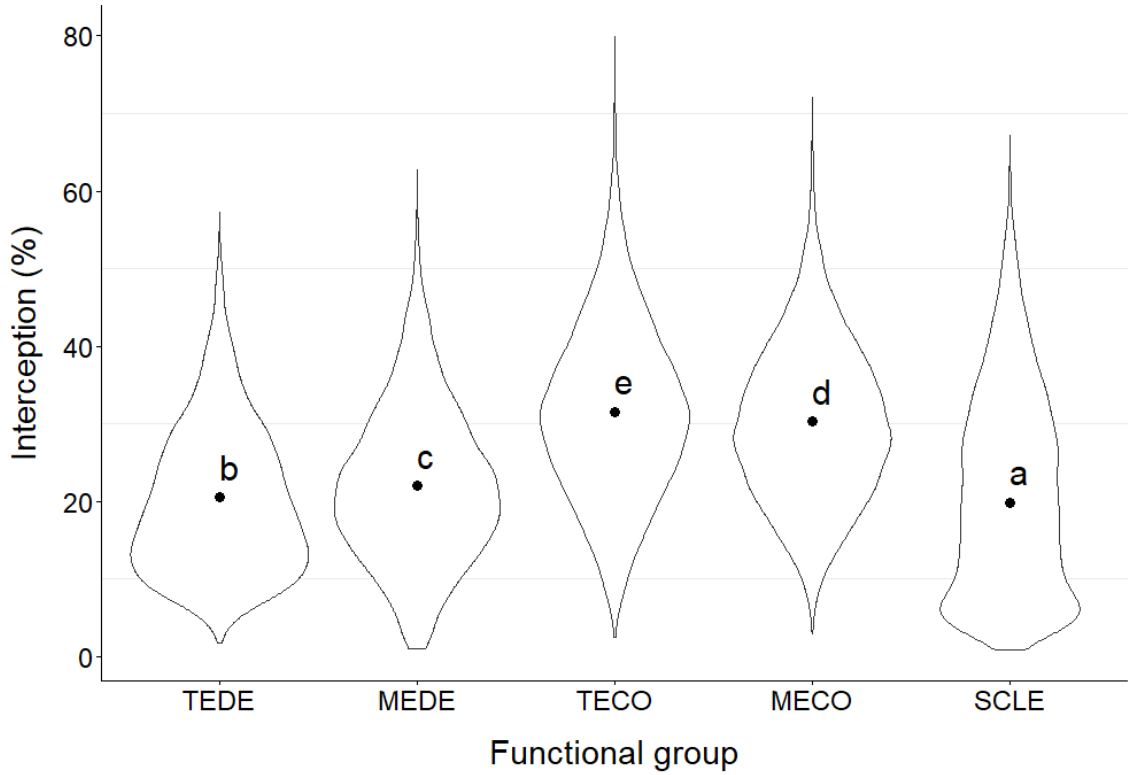



**Figure S8.** Percentage of interception of the different functional groups of species. Different letters denote significant differences among forest types ($p < 0.01$) after Tukey's

test. Abbreviations of the functional groups: TEDE, Temperate deciduous; MEDE, Mediterranean deciduous; TECO, Temperate coniferous; MECO, Mediterranean coniferous; SCLE, sclerophylls.

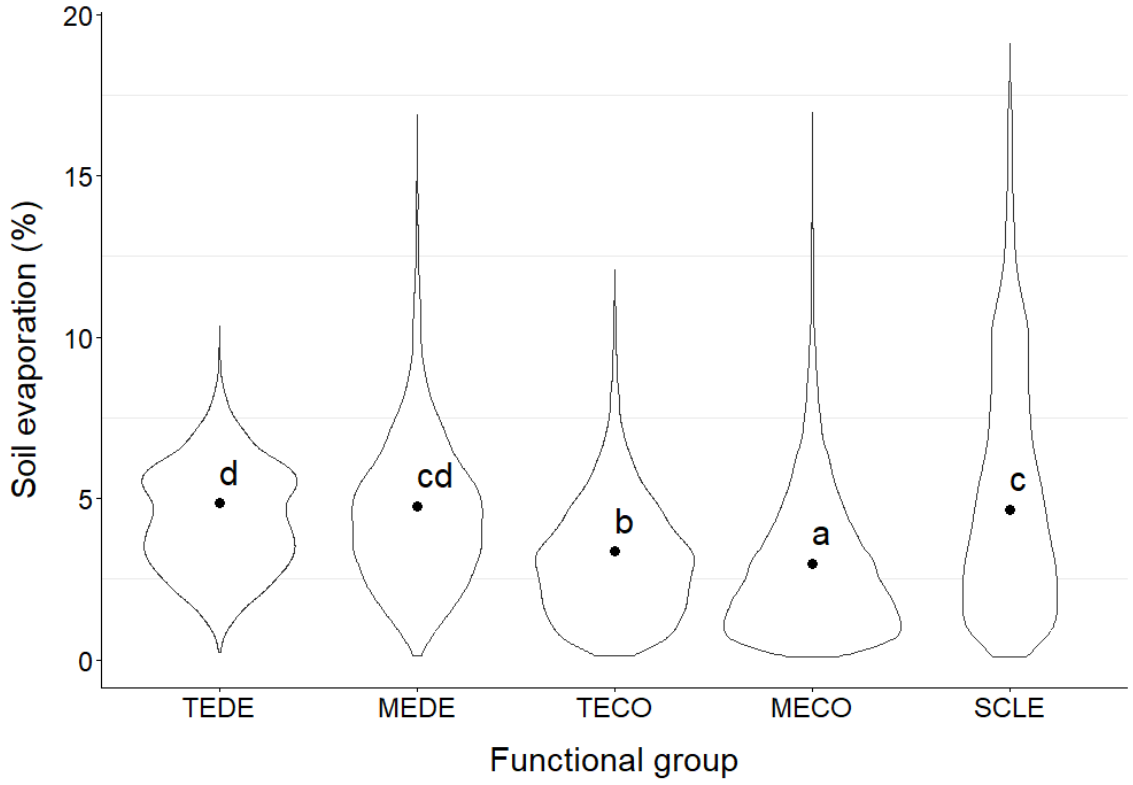



**Figure S9.** Percentage of soil evaporation of the different functional groups of species. Different letters denote significant differences among forest types ($p < 0.01$) after Tukey's test. Abbreviations of the functional groups: TEDE, Temperate deciduous; MEDE, Mediterranean deciduous; TECO, Temperate coniferous; MECO, Mediterranean coniferous; SCLE, sclerophylls.

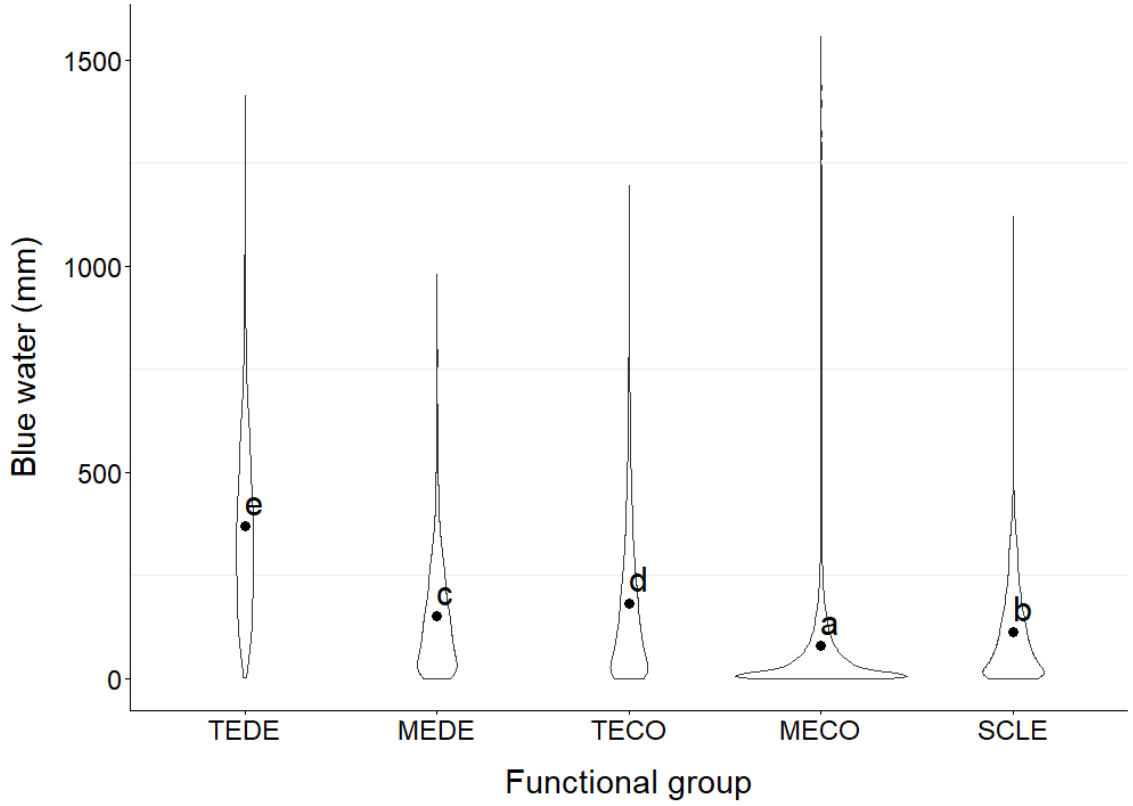



**Figure S10.** Blue water amount of the different functional groups of species. Different letters denote significant differences among forest types ($p < 0.01$) after Tukey's test. Abbreviations of the functional groups: TEDE, Temperate deciduous; MEDE, Mediterranean deciduous; TECO, Temperate coniferous; MECO, Mediterranean coniferous; SCLE, sclerophylls.

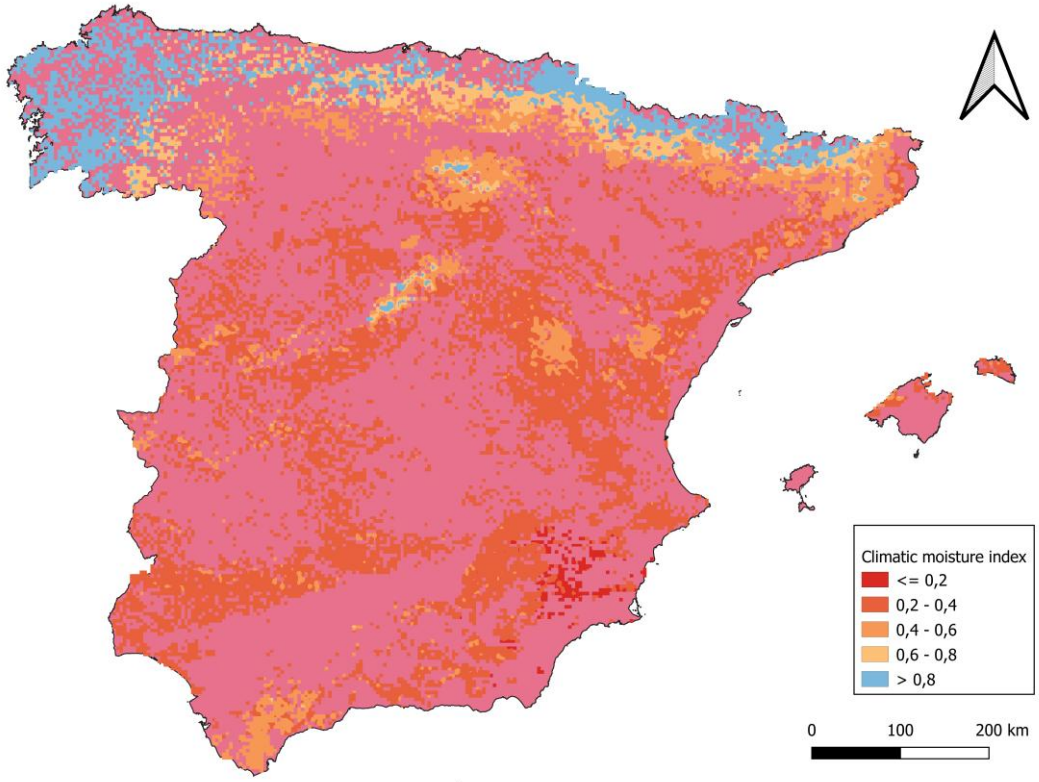



**Figure S11.** Climatic moisture index in Spanish Peninsula and Balearic Islands.

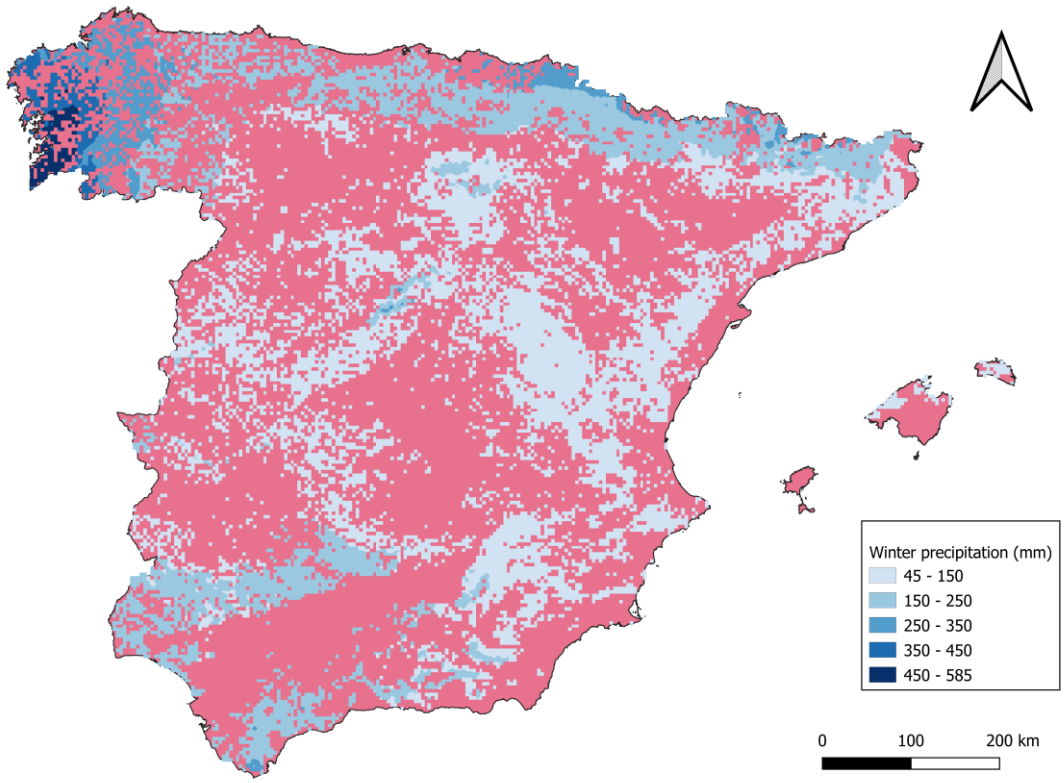



**Figure S12.** Winter precipitation in Spanish Peninsula and Balearic Islands.

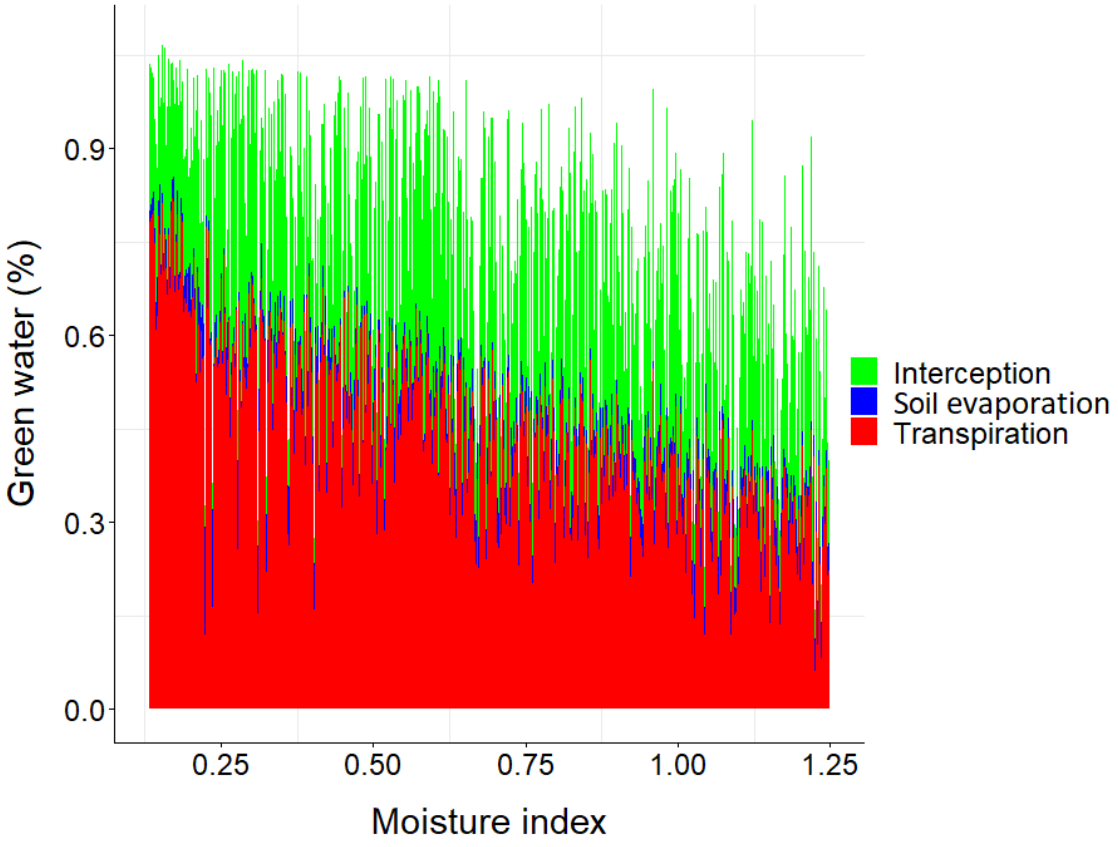



**Figure S13.** Green water partitioning (interception, soil evaporation and transpiration) along the moisture index gradient.

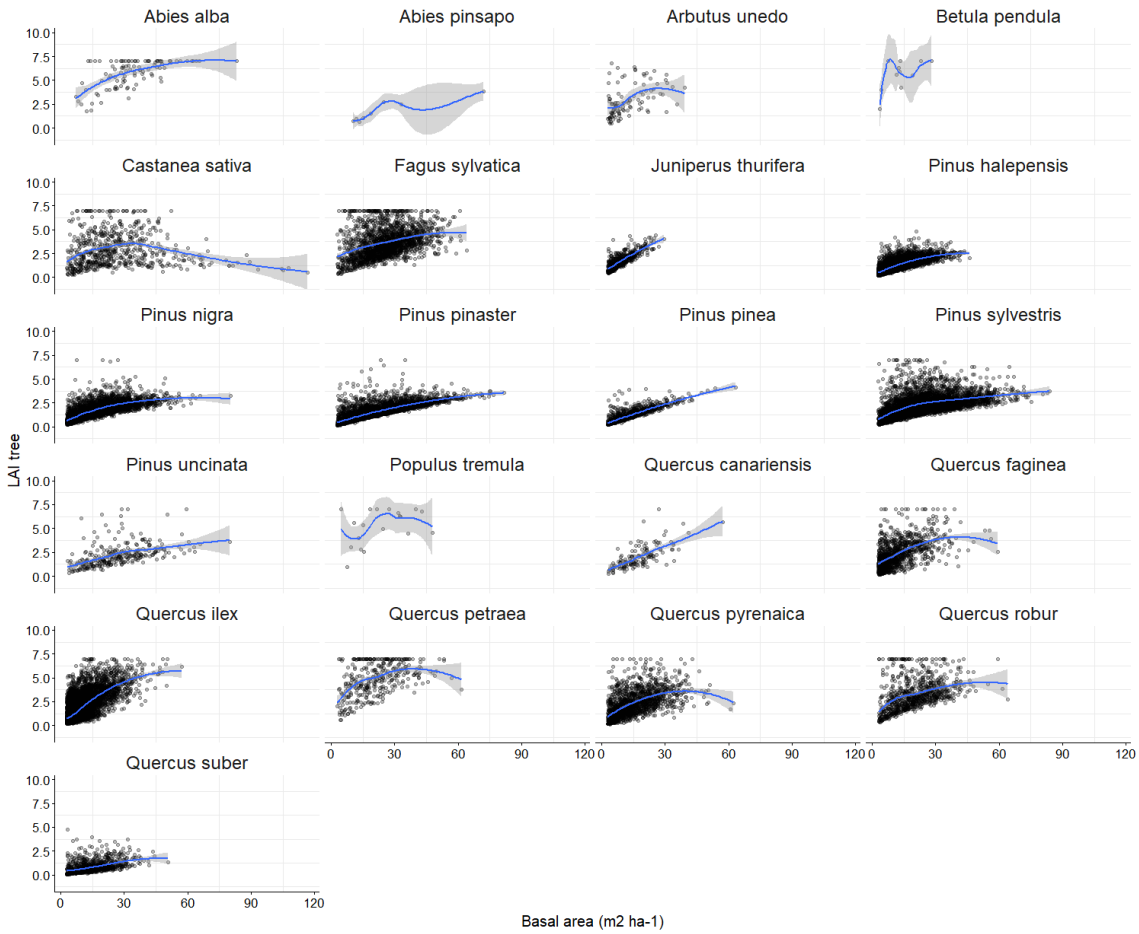



**Figure S14.** Relationship between the simulated LAI of the trees and basal area from the SFI3 by species.

**Table S1.** Classification into functional groups of the predominant tree species in the study area and the number of plots of each of them.

| **Functional group** | **Predominant species** | **Number of plots** |
|---|---|---|
| Temperate deciduous | *Betula pendula* | 11 |
| Temperate deciduous | *Castanea sativa* | 611 |
| Temperate deciduous | *Fagus sylvatica* | 1864 |
| Temperate deciduous | *Populus tremula* | 19 |
| Temperate deciduous | *Quercus petraea* | 336 |
| Temperate deciduous | *Quercus robur* | 807 |
| Mediterranean deciduous | *Quercus canariensis* | 134 |
| Mediterranean deciduous | *Quercus faginea* | 1077 |
| Mediterranean deciduous | *Quercus pyrenaica* | 1413 |
| Temperate coniferous | *Abies alba* | 98 |
| Temperate coniferous | *Abies pinsapo* | 8 |
| Temperate coniferous | *Pinus sylvestris* | 4312 |
| Temperate coniferous | *Pinus uncinata* | 275 |
| Mediterranean coniferous | *Juniperus thurifera* | 603 |
| Mediterranean coniferous | *Pinus halepensis* | 5746 |
| Mediterranean coniferous | *Pinus nigra* | 3439 |
| Mediterranean coniferous | *Pinus pinaster* | 4682 |
| Mediterranean coniferous | *Pinus pinea* | 1489 |
| Sclerophyll | *Arbutus unedo* | 101 |
| Sclerophyll | *Quercus ilex* | 4542 |
| Sclerophyll | *Quercus suber* | 947 |

**Table S2.** Characteristics Mean and standard deviation of stand structure variables and climate variables grouped in the different forest functional forest types groups by biome. Basal area ($m^2$ $ha^{-1}$); LAI T = Tree LAI; LAI S = Shrub LAI; MeanT = Mean annual temperature (ºC); TPre = Mean Total annual precipitation (mm). Mean and standard deviation are showed for all the values.

| **Functional group** | **Biome** | **Nº plots** | **Basal area** | **LAI of Trees** | **LAI of Shrubs** | **MeanT** | **TPre** | **Precipitation seasonality** | **Climatic moisture** | **Continentality** |
|---|---|---|---|---|---|---|---|---|---|---|

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Temperate coniferous | Alpine | 1506 | 26.9±14.7 | 2.3±1.3 | 0.9±0.9 | 8.3±1.5 | 872±237 | 35.3±12.4 | 0.9±0.4 | 16.0±1.5 |
| | Atlantic | 828 | 26.3±14.3 | 2.7±1.3 | 1.3±1.0 | 10.5±1.2 | 910±147 | 31.0±8.2 | 0.8±0.2 | 15.1±0.9 |
| | Continental Mediterranean | 451 | 20.8±12.1 | 1.9±0.9 | 1.3±1.0 | 10.7±1.0 | 534±77 | 45.6±9.4 | 0.4±0.1 | 17.4±1.6 |
| | Submediterranean | 1908 | 21.8±12.5 | 2.2±1.1 | 1.3±1.0 | 10.2±1.3 | 685±152 | 36.5±10.7 | 0.6±0.2 | 16.3±1.3 |
| | Alpine | 370 | 25.1±12.2 | 4.4±1.6 | 0.7±0.9 | 8.7±0.9 | 866±158 | 32.8±7.6 | 0.9±0.3 | 14.8±1.0 |
| | Atlantic | 2597 | 24.2±12.1 | 3.5±1.6 | 1.4±1.1 | 11.5±1.4 | 995±218 | 34.5±8.9 | 0.9±0.2 | 13.4±1.5 |
| | Continental Mediterranean | 56 | 22.9±10.0 | 4.0±1.7 | 0.8±0.9 | 10.5±0.7 | 640±92 | 33.9±6.0 | 0.6±0.2 | 15.7±1.0 |
| | Temperate Mediterranean | 105 | 19.8±10.3 | 1.9±1.2 | 1.0±0.9 | 15.1±1.1 | 616±143 | 63.9±8.9 | 0.5±0.2 | 16.4±1.1 |
| | Submediterranean | 541 | 24.3±14.6 | 3.6±1.8 | 1.3±1.1 | 11.2±1.5 | 762±189 | 39.2±11.8 | 0.7±0.2 | 15.3±1.2 |
| Mediterranean coniferous | Alpine | 103 | 20.0±13.1 | 1.8±1 | 1.5±1.0 | 10.3±1.3 | 643±152 | 40.4±11.3 | 0.5±0.2 | 16.9±1.5 |
| | Arid | 1244 | 8.6±5.2 | 0.9±0.5 | 1.5±0.8 | 15.3±1.3 | 311±47 | 52.5±4.2 | 0.2±0 | 17.8±1.2 |
| | Atlantic | 910 | 22.8±12.1 | 1.8±0.9 | 2.0±1.0 | 13.3±1.2 | 1365±322 | 47.7±8.0 | 1.2±0.3 | 11.5±2.0 |
| | Continental Mediterranean | 5969 | 15.1±10.1 | 1.4±0.7 | 1.7±1.0 | 12.6±1.4 | 435±66 | 47.6±7.3 | 0.3±0.1 | 17.9±1.1 |
| | Temperate Mediterranean | 4770 | 13.5±8.7 | 1.2±0.6 | 1.5±0.8 | 15.2±1.5 | 418±90 | 57.5±8.4 | 0.3±0.1 | 18.0±1.8 |
| | Submediterranean | 2971 | 18.5±12.0 | 1.7±0.8 | 1.6±0.9 | 12±1.6 | 546±147 | 44.5±10.5 | 0.4±0.1 | 17.3±1.5 |
| Mediterranean deciduous | Alpine | 126 | 16.7±9.7 | 2.5±1.4 | 1.4±1.0 | 9.8±0.9 | 679±131 | 42.8±10.0 | 0.6±0.2 | 16.5±1.3 |
| | Atlantic | 421 | 17.7±10.3 | 2.6±1.5 | 1.8±1.0 | 11.4±1.1 | 864±160 | 37.6±9.6 | 0.7±0.2 | 14.1±1.2 |
| | Continental Mediterranean | 682 | 10.0±7.0 | 2.0±1.3 | 1.6±0.9 | 11.7±1.1 | 501±87 | 44.1±9.0 | 0.4±0.1 | 17.3±1.2 |
| | Temperate Mediterranean | 337 | 12.6±8.3 | 1.5±1.1 | 1.3±0.9 | 15.6±1.5 | 532±98 | 65.7±7.5 | 0.4±0.1 | 16.5±2.4 |
| | Submediterranean | 1176 | 15.1±9.6 | 2.4±1.3 | 1.6±1.0 | 11.4±1.2 | 610±140 | 43.2±11.7 | 0.5±0.1 | 16.6±1.3 |
| Sclerophyll | Alpine | 45 | 14.1±8.3 | 3.0±1.3 | 1.2±0.7 | 10.4±0.8 | 811±124 | 25.4±6.8 | 0.7±0.2 | 14.9±0.9 |
| | Arid | 46 | 6.9±4.0 | 1.5±0.9 | 1.1±0.7 | 13.5±1.1 | 368±44 | 56.4±4.4 | 0.3±0.1 | 18.3±0.7 |
| | Atlantic | 206 | 18.5±10.5 | 3.6±1.7 | 1.9±1.0 | 12.7±1.1 | 843±181 | 32.3±8.1 | 0.7±0.2 | 14.0±1.5 |
| | Continental Mediterranean | 1754 | 9.2±5.8 | 2.1±1.3 | 1.5±1.0 | 12.4±1.2 | 456±67 | 46.7±8.6 | 0.4±0.1 | 17.8±1.2 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Temperate Mediterranean | 4229 | 8.6±5.9 | 0.9±0.7 | 1.0±1.0 | 16.3±1.2 | 493±86 | 64.2±7.2 | 0.3±0.1 | 17.7±2.0 |
| | Submediterranean | 1295 | 13.6±8.1 | 2.7±1.4 | 1.6±0.9 | 12.6±1.5 | 591±126 | 39.0±11.3 | 0.5±0.1 | 16.4±1.3 |

**Table S3.** Proportion of plots in the different categories of relative blue water in the different biomes. n, number of plots.

| **Biome** | **Distribution of values of Relative blue water (%)** | | | | | |
|---|---|---|---|---|---|---|
| | **n** | **0-15** | **15-30** | **30-45** | **45-60** | **>60** |
| Arid | 1,290 | 74.6 | 19.7 | 4.9 | 0.8 | 0.0 |
| Temperate Mediterranean | 9,444 | 39.7 | 22.0 | 14.9 | 11.5 | 11.9 |
| Continental Mediterranean | 8,912 | 78.0 | 13.4 | 5.3 | 2.0 | 1.3 |
| Submediterranean | 7,891 | 58.1 | 24.3 | 12.0 | 4.4 | 1.2 |
| Atlantic | 4,962 | 18.0 | 24.7 | 27.1 | 21.8 | 8.4 |
| Alpine | 2,150 | 23.1 | 25.6 | 25.8 | 16.8 | 8.7 |

**Table S4.** Importance of the variables retained in the XGBoost models and their $R^2$ by functional group.

**Temperate coniferous ($R^2$=90,04)**

| **Variable** | **Gain** | **Cover** | **Frequency** |
|---|---|---|---|
| LAI | 0,592 | 0,467 | 0,482 |
| Climatic moisture index | 0,286 | 0,291 | 0,269 |
| Winter precipitation | 0,094 | 0,136 | 0,135 |
| Basal area | 0,019 | 0,067 | 0,079 |
| Precipitation seasonality index | 0,006 | 0,033 | 0,031 |
| Autumn precipitation | 0,002 | 0,007 | 0,004 |

**Mediterranean coniferous ($R^2$=79,85)**

| Variable | Gain | Cover | Frequency |
|---|---|---|---|
| LAI | 0,398 | 0,476 | 0,509 |
| Winter precipitation | 0,48 | 0,357 | 0,211 |
| Climatic moisture index | 0,071 | 0,075 | 0,158 |
| Precipitation seasonality index | 0,019 | 0,011 | 0,025 |
| Basal area | 0,018 | 0,07 | 0,062 |
| Autumn precipitation | 0,014 | 0,012 | 0,035 |

**Sclerophylls ($R^2$=89,97)**

| Variable | Gain | Cover | Frequency |
|---|---|---|---|
| LAI | 0,772 | 0,563 | 0,55 |
| Winter precipitation | 0,089 | 0,221 | 0,174 |
| Autumn precipitation | 0,065 | 0,079 | 0,071 |
| Climatic moisture index | 0,058 | 0,119 | 0,195 |
| Precipitation seasonality index | 0,017 | 0,018 | 0,011 |

**Temperate deciduous ($R^2$=75,49)**

| Variable | Gain | Cover | Frequency |
|---|---|---|---|
| LAI | 0,64 | 0,507 | 0,458 |
| Climatic oisture index | 0,267 | 0,304 | 0,307 |
| Winter precipitation | 0,049 | 0,075 | 0,077 |
| Basal area | 0,031 | 0,078 | 0,09 |
| Precipitation seasonality index | 0,01 | 0,025 | 0,046 |
| Autumn precipitation | 0,003 | 0,011 | 0,022 |

**Mediterranean deciduous ($R^2$=77,61)**

| Variable | Gain | Cover | Frequency |
|---|---|---|---|
| LAI | 0,601 | 0,519 | 0,491 |
| Autumn precipitation | 0,262 | 0,235 | 0,191 |
| Climatic moisture index | 0,102 | 0,17 | 0,194 |
| Precipitation seasonality index | 0,026 | 0,046 | 0,082 |
| Winter precipitation | 0,005 | 0,007 | 0,021 |
| Basal area | 0,004 | 0,022 | 0,02 |

# Capítulo 2

## Recent water cycle changes in Spanish forests are driven by stand structure more than climatic changes

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**Recent water cycle changes in Spanish forests are driven by stand structure more than climatic changes**

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## Abstract

The water cycle in forests of many regions is being impacted by climatic changes, often including a decrease in precipitation and an increase in temperature, leading to an increase in green water (evapotranspiration) and a decrease in blue water (runoff + drainage). Additionally, forest expansion and development are prevailing processes in many rural areas due to the abandonment of traditional land uses**.** Stand leaf area growth further amplifies green water and reduces blue water availability. However, the interaction between climate change and stand structure changes is not well understood at large scales. We modeled Spanish forest water cycle using national inventories (1990–2020), analyzing climate and forest structure trends at plot level. Using three inventory surveys, we assessed green and blue water changes across forest types and compared managed vs. unmanaged forests. Results show green water increased and blue water decreased over time. Leaf area index (LAI) growth (trees and shrubs) had a stronger effect on green water than climate change. These factors, along with recent precipitation declines (2010–2020), also significantly reduced blue water. Basal area reduction improved blue water yield, but only in the short-mid-term, as stand LAI tended to recover over time. This study demonstrates that changes in stand structure can be as important, if not more so, than climatic changes in influencing the water cycle at the regional level. Moreover, our results support the idea that basal area reduction, i.e. through management or disturbances, can enhance blue water production, especially if these reductions are large and maintained.

**Keyword:** blue water, evapotranspiration, green water, forests, climate change, management

## 1. Introduction

Forests provide humanity with numerous ecosystem services, one of the most important is water provisioning (MEA, 2005). Precipitation reaching forests is partitioned into different components. First, forests retain water through canopy interception. The remaining water reaching the soil evaporates from its surface, infiltrates into the soil, or leaves as surface runoff. In turn, infiltrated water can be absorbed by plant roots and return to the atmosphere via transpiration, or it can percolate beyond the reach of roots, contributing to groundwater levels. The water returned to the atmosphere is the evapotranspiration (ET) or *green water* (interception + transpiration + soil evaporation) and the water exported to the watershed is the *blue water* (surface runoff + deep drainage) (Falkenmark and Rockström, 2006). At the forest stand scale, there is usually a trade-off between the green and blue water since when the first increases, the second often

decreases. In forest ecosystems, green water is around 40-70% of the water balance in wetter biomes and in the range of 80-100% in drier biomes (Qubaja et al., 2020; Schlesinger and Jasechko, 2014).

Recent decades have witnessed a synergistic effect of temperature increases and changes in precipitation patterns in many areas of the world (Masih et al., 2014; Spinoni et al., 2015; Sun et al., 2021). Meteorological droughts decrease soil water inputs, while rising temperatures increase the potential evapotranspiration (PET), resulting in edaphic drought and plant water stress. However, the different components of the forest water cycle are not equally affected. Thus, trees transpire more with higher temperatures or PET, even during meteorologically dry periods, as long as soil water is available, and, consequently, green water may increase during meteorological droughts when coupled with higher evaporative demand. On the other hand, under these conditions blue water decreases due to both reduced rainfall and increased evapotranspiration (Mastrotheodoros et al., 2020).

Changes in forest distribution and structure can have a strong impact on the water cycle. During the last decades, forests in many of Northern-hemisphere countries are in expansion due to the abandonment of traditional practices like livestock grazing and wood extraction as fuel (Garbarino et al., 2020; Navarro and Pereira, 2012; Palmero-Iniesta et al., 2021). The abandonment of traditional practices have also led to a general increase in forest tree size and density in the last decades (Mönkkönen et al., 2022; Spiecker et al., 2012; Vayreda et al., 2012). This context of forest expansion and stand development can lead to increased green water due to the larger canopy leaf area, resulting in greater interception and transpiration fluxes (Jaramillo et al., 2018). Comparisons between different stand densities and thinning treatments at local scale have been conducted to understand the effects of stand structure variables on the water cycle (Kurzweil et al., 2021; Molina et al., 2021). These works have showed that an intense basal area reduction (>30%) is needed for increasing the blue water (Kurzweil et al., 2021). However, a very intense thinning (>50%) promotes the growth of understory plants competing for water and, as a consequence, a reduction of the water yield (Molina et al., 2021).

Climate change and changes in forest stand structure and species composition interact in complex ways. An increase in evaporative demand often increases ET, but a combined increase in basal area, or a change in composition towards water spender species, can increase ET more than expected (Caldwell et al., 2016). The reduction of the forest basal area due to forest management or natural disturbances decreases leaf area and hence rainfall interception and stand transpiration (Ameztegui et al., 2017). Nevertheless, a decline in precipitation can decrease the total blue water yield regardless of stand basal area (Kurzweil et al., 2021). Moreover, the reduction of tree basal area often leads to an increase in the transpiration of the remaining trees and/or the increase of the shrub understory cover, hence counterbalancing the effect of thinning on the water balance (Molina et al., 2021). Therefore, understanding the role of climate and stand structure change and their combined effect on the forest water cycle remains a challenging task.

In the Mediterranean basin there has been an increase in climatic aridity during recent decades, due to the increase in PET and the decrease in precipitation (García-Herrera et al., 2019; Hanel et al., 2018). Moreover, in this region, human pressure in forests has been reduced, which has led to an increase in the forest surface at the landscape level (Vadell et al., 2016), an increase in tree density and tree size at the stand level (Vayreda et al., 2012) and an increase in the understory shrub cover in a generalized way (Martín-Alcón et al., 2015)**.** All these structural changes can increase forest evapotranspiration through

the increase of the canopy leaf surface area (De Cáceres et al., 2015). In this work we take an eco-hydrological modelling approach to analyse changes in the forest water cycle in Spanish forests over the three past decades, using repeated forest inventory data (~ 1990 – ~ 2020). We ask the following questions: 1) How have the components of the water cycle in Spanish forests changed in recent decades? 2) What are the effects of climate and stand structure on changes in the green and blue water cycle? 3) Can basal area reduction improve the blue water supply in the short-, mid-term? Specifically, we want to know the role of changes in climate and stand structure as drivers of changes of blue and green water components of the water cycle. Moreover, to evaluate the role of basal area reduction, we compare the effect of an increase or a decrease of forest basal area in the inventory plots on the green and blue water components.

## 2. Material and Methods

### 2.1. Forest inventory data

We carried out our study in the forested areas of Spain, excluding the Balearic and Canary Islands. We used the repeated permanent field plot data from the Spanish national forest inventory (SFI) to characterize tree species composition and stand structure variables across the study area and through time. The SFI covers the forested areas of Spain with a density of ~1 plot/km$^2$. SFI field plots have four concentric circular subplots with radii of 5, 10, 15 and 25 m. Trees were identified and measured within variable circular size plots (5 m radius for trees with diameter at breast height (DBH) ≥ 7.5 cm; 10 m radius for trees with DBH ≥ 12.5 cm; 15 m radius for trees with DBH ≥ 22.5 cm; and 25 m radius for trees with DBH ≥ 42.5 cm). Shrub species within the 10-m-radius subplot were measured with a percent cover value and mean height. We used the second inventory (SFI2) carried out in 1986-1996, the third inventory (SFI3) carried out in 1997-2008, and the fourth inventory (SFI4) carried out in 2009-2024. We only used permanent plots included in all three forest inventory surveys. We calculated the basal area (BA, as indicator of canopy cover) for each SFI plot at each inventory (SFI2, SFI3, and SFI4) and selected pure forests (more of 70% of basal area of one species): 94.17% of the plots were classified as pure. We excluded non native species, such as those from the *Eucalyptus* genus. We also excluded riparian trees, like *Populus alba* or *Fraxinus angustifolia*, because they are affected by the local conditions of the rivers and we do not have information from these environments. We also removed field plots with a total BA < 3 m$^2$/ha in SFI2, as we did not consider them as forest. We classified the plots according to the dominant tree species into five functional groups: temperate deciduous (e.g., *Quercus robur*), Mediterranean deciduous (e.g., *Quercus pyrenaica*), temperate coniferous (e.g., *Pinus sylvestris*), Mediterranean coniferous (e.g., *Pinus halepensis*) and sclerophylls (e.g., *Quercus ilex*) (see Table S1 for the classification of the tree species in these five groups). Overall, we selected 11,456 forest plots.

We evaluated the reduction of basal area in the SFI plots between inventory surveys. Specifically, we classified the SFI2 plots with a decrease of ≥ 15% of previous basal area between SFI2 and SF3 (1,381 plots) as *disturbed* plots, while the remaining plots (those with a basal area increase or a decrease ≤ 15% between SFI2 and SFI3; 10,075 plots) as *undisturbed* plots. The decrease in basal area through inventories can be due to thinning but also to natural disturbances (e.g. fires, windstorms, etc.). Although we cannot know the exact origin of the basal area decrease we assumed that the natural disturbances may

be equivalent to thinning, in terms of their effect on hydrological fluxes, since they have the effect of basal area decrease.

### 2.2. Meteorological variables

Iberian Spain has mainly two climatic domains, the temperate climate around the Atlantic sea in the north and west part of the country, and the Mediterranean climate in the rest of the country (Rivas-Martínez et al., 2017). We downloaded the daily total precipitation and maximum, mean and minimum temperature for the 5 years before and after the date of survey for every plot in each SFI inventory (that is, 10 years per plot per SFI inventory) from E-OBS data at 1 km horizontal resolution (Moreno and Hasenauer, 2016); https://doi.org/10.1002/joc.4436 ). Topographic variables of slope, aspect and altitude were derived from a digital elevation model (DEM) at 25 m2 of the PNOA Spanish project through the IGN website (downloaded on 09/02/2024; https://centrodedescargas.cnig.es/CentroDescargas/index.jsp#). We used these topographic variables, and daily temperature/precipitation from E-OBS, to estimate daily values of relative humidity, solar radiation and potential evapotranspiration (PET) per plot through the meteoland R package (De Cáceres et al., 2018). We summarized climatic conditions in forest plots using the climatic moisture index (i.e., mean annual precipitation/mean annual PET) and precipitation seasonality (defined as the standard deviation of monthly precipitation divided by the mean of monthly precipitation, and expressed in percent), since theses indices have been shown to be drivers of spatial variation in the components of forest water cycle in Spain (Sánchez-Dávila et al., 2024).

### 2.3. MEDFATE model

The MEDFATE model (version 2.9.3) is designed to evaluate soil and plant water balances in heterogeneous forest stands (De Cáceres et al., 2015, 2023). It has been previously validated with measurements from instrumentalized forests stand data for soil moisture dynamics, plant transpiration and plant water status in Mediterranean forests plots at local scale of Spain and Italy (De Cáceres et al., 2015, 2021; Saponaro et al., 2025); at multiple country scale (mainly in Europe, see De Cáceres et al., 2023) with experimental forest plots of sap flow (SAPFLUXNET; (Poyatos et al., 2021)) and flux eddy covariance (FLUXNET; (Pastorello et al., 2020)); and it was compared with another modelling products for evapotranspiration and run-off at the country level in Spain (Sánchez-Dávila et al., 2024). We included model evaluation results from previous works in Table S2 for the transpiration, soil water content, and evapotranspiration (ET) per tree species and site. When data were not available for Spain, we included evaluation results from nearby countries (France, Italy and Portugal). The field data (derived from sap flow or eddy covariance for transpiration and ET, respectively, or soil moisture sensors for soil water content) cover the majority of the main tree species in Spanish forests. We also included in Table S2 watershed-level runoff evaluation results for two different Spanish watersheds at daily and monthly scale. The evaluation results showed a good performance of MEDFATE modelling with an $R^2 > 0.6$ and $R > 0.7$.

We used landscape hydrological simulations from modelling due to the lack of water flux field data at country scale and across decades. Hydrological modelling has been shown as a valuable tool to understand water fluxes at different spatial scales (Mastrotheodoros et al., 2020; Sánchez-Dávila et al., 2024). Using daily weather inputs, the model simulates forest hydrology processes at daily time steps. Aboveground stand structure is represented by leaf area index (LAI), crown ratio and height of woody plant

cohorts. Soil is represented by a set of vertical layers with different hydraulic properties, and each cohort may have a different root distribution, specified using parameters Z50 and Z95, representing the depths at which 50% and 95% of fine roots are located.

The model updates leaf area daily for semi-deciduous vegetation, based on a simple phenological model that dictates leaf budburst and leaf fall. Evergreen plants maintain a consistent leaf area throughout the simulation. The model estimates light attenuation in the canopy using the Beer-Lambert model and calculates the canopy's water storage capacity, representing the minimum water needed to saturate the canopy. Water input from precipitation is adjusted for interception and surface runoff before augmenting soil layers' water content. Rainfall interception loss is estimated using the Gash model (Gash et al., 1995) and surface runoff using the USDA SCS curve number method (Boughton, 1989). Processes related to lateral water transfer are omitted. Soil water storage capacity and potential are derived from soil texture using pedotransfer functions (Saxton et al., 1986). Vertical water flows are modelled using a multiple bucket-model approach but allowing a fraction of water to percolate to deeper layers before filling the current one. Water percolating from the deepest layer is presumed lost through deep drainage.

Plant transpiration is calculated by PET, via an empirical relationship between maximum transpiration and LAI (Granier et al., 1999), root distribution, soil moisture, and two taxon-specific parameters that describe the transpiration decline following soil water depletion. Plant water potential (Ψplant) represents the plant-averaged water status, and is estimated as the average soil water potential in the plant rhizosphere. Drought effects are monitored by assessing hydraulic conductance lost due to stem cavitation (PLC), which sets limits on actual transpiration rates. The model simulates drought legacy effects, because PLC does not automatically decrease even when Ψplant increases and can only be progressively reduced through the formation of new sapwood (Choat et al., 2018).

Parameter estimation

Data from forest inventory plots include tree height and DBH, used to estimate foliar biomass and crown ratio via species-specific allometries (see Tables S1-3 of De Cáceres et al. 2023 for details). Shrub foliar biomass is calculated from shrub cover and mean height. The model uses a constant Specific Leaf Area (SLA) in each specie. Leaf area index (LAI) is calculated from foliar biomass by using species-specific SLA (LAI = foliar biomass * SLA). Soil data for each plot is extracted from the SoilGrids database (at 250 m cell size) (Hengl et al., 2017), considering four soil layers down to 2 m depth. Deeper layers merge into a rocky layer, with rock fragment content increasing monotonously from surface to depth based on surface stoniness classes determined in SFI plot surveys.

MEDFATE simulations

MEDFATE was run on each selected SFI plot using daily weather data (temperature and precipitation, PET, radiation and relative humidity) corresponding to a 10-yr period of climatic data around the survey date of each SFI inventory. We calculated the blue water as the sum of surface runoff and deep drainage, and the green water as total evapotranspiration (that included the sum of transpiration, interception and soil evaporation).

## 2.5. Statistical analyses

We averaged the blue and green water for each SFI plot as the mean annual values (mm/yr) of the 10 years around the survey dates of the three SFI inventories. We applied the same process to the moisture and precipitation seasonality indices and the mean of the cumulative precipitation by season. The variation of blue and green water amount and the blue water ratio (blue water amount/total precipitation or runoff coefficient) was analysed using a post-hoc Bonferroni test for pairwise comparisons between SFI surveys by functional groups.

We calculated the difference between the SFI3 and SFI2 (hereafter SFI2-3) and between SFI4 and SFI3 (hereafter SFI3-4) for the blue and green water as response variables for the different functional groups. The importance of the change in climate (annual precipitation, precipitation of each season, mean annual temperature, mean annual moisture and seasonality index) and stand structure variables (basal area, tree and shrub LAI) on the blue and green water change were analysed with XGBoost regression. XGBoost is a machine learning system that builds a sequential series of shallow regression trees with a gradient boosting technique (Chen and Guestrin, 2016). XGBoost regression was used because it permits the analysis of linear and non-linear responses and correlated variables. A regression tree is trained by splitting the input dataset into increasingly homogeneous subsets at each decision nodes and choosing the split that maximizes the distance between different terminal nodes. One model for each of the five functional groups in each SFI change (SFI2-3 and SFI3-4) was computed (sample size, 11,456 SFI plots). The models were optimized for the best hyperparameters and evaluated using a ten-fold cross-validation procedure with five repetitions, based on a stratified random sample. A forward feature selection method with spatial cross-validation (Meyer et al., 2018) was applied to choose predictor variables. Models were built for each predictor pair combination, and the best pair was identified. Additional predictors were tested by adding them to the best pair until no further improvement was seen. The importance of retained variables was evaluated by calculating the average contribution of each feature using Gain (Measures the improvement in predictive accuracy contributed by a feature at its split points), Frequency (Counts how often a feature is used across all trees as a simplified proxy for importance), and Cover (Quantifies the proportion of observations affected by a feature's splits). The $R^2$ was estimated to assess the final model accuracy.

The effect of basal area reduction between SFI2 and SFI3 on the amount of green and blue water between SFI surveys per forest functional forest group was analyzed using a two-way repeated measures ANOVA, with management as fixed factor and the SFI2, SFI3 and SF4 inventories as repeated measures.

All statistical analyses were conducted with R v. 4.1.1., with the packages *xgboost* (Chen et al., 2015) and *caret* (Kuhn, 2008) for XGBoost regression.

## 3. Results

### 3.1. Changes in the components of the water cycle in the last decades

Green water showed a significant increase (according to the post-hoc Bonferroni test) during the SFI2-4 period in all functional groups (Figure 1). This increase was greater in the SFI2-3 period (from 365 to 425 mm, on average) than in the SFI3-4 period (from 425 to 440 mm), where the Temperate deciduous and Mediterranean deciduous forests did not show a significant difference. Similarly, a generalized decrease in blue water amount and percentage in the last decades was observed for all functional groups (Figure 1). The

decrease was also bigger in the SFI2-3 period (226 to 188 mm) than the SFI3-4 period (188 to 163 mm). The decomposition of the green water into water fluxes showed that both interception and transpiration increased across the forest groups in the first decade (Figure S2). Nevertheless, in the second decade the interception was similar or even smaller across forest groups whereas the transpiration was bigger in all forest groups.

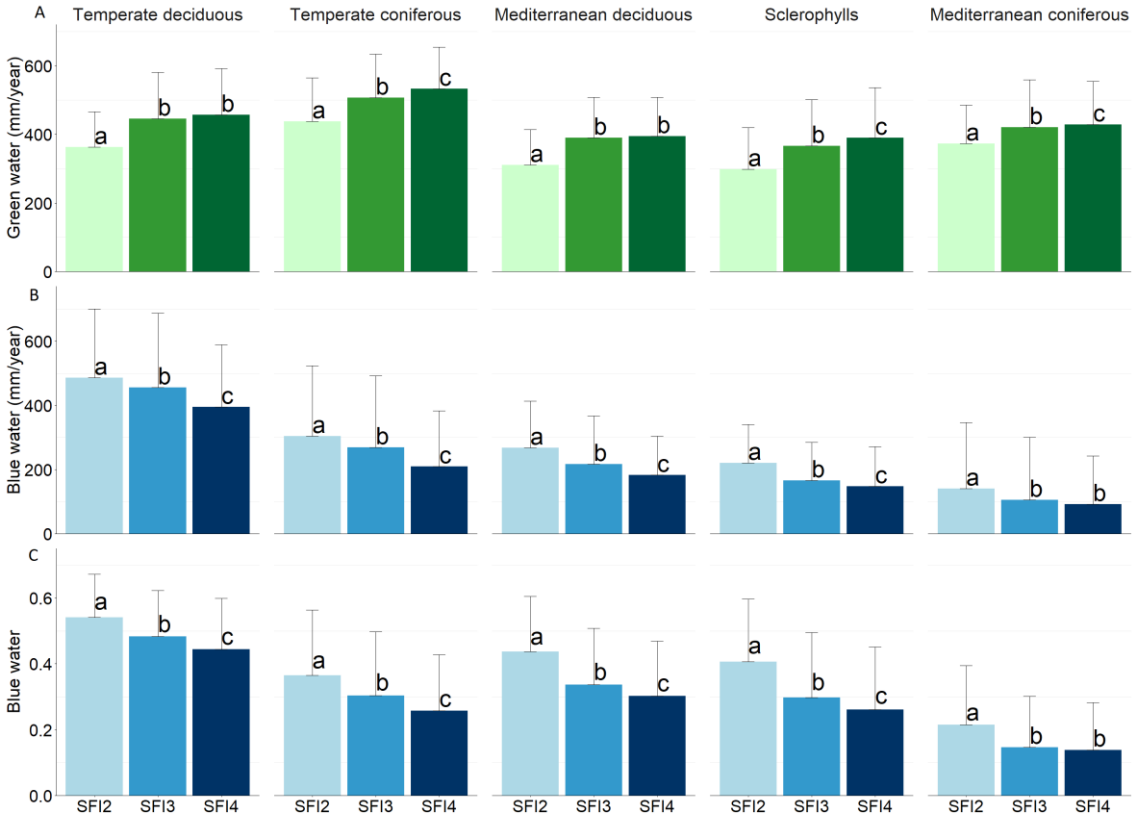



Figure 1. Mean (± standard error) of green water, blue water and relative blue water per functional forest types in the three SFI surveys. Different letters denote significant differences ($p < 0.05$) among SFI surveys after the Bonferroni post hoc test.

In the SFI2-3 period, green water change increased more in the north than in the south of Spain (Figure 2A). In the SFI3-4 period, this increase was lower and decreased in the northwest (Figure 2B). The blue water changes indicated that some forest areas in the north part of Spain increased in blue water between SFI2-3 (Figure 2C) and SFI3-4 (Figure 3D). Excluding these areas, the decrease in blue water was generalized across the Spanish forests in both the Atlantic and Mediterranean regions.

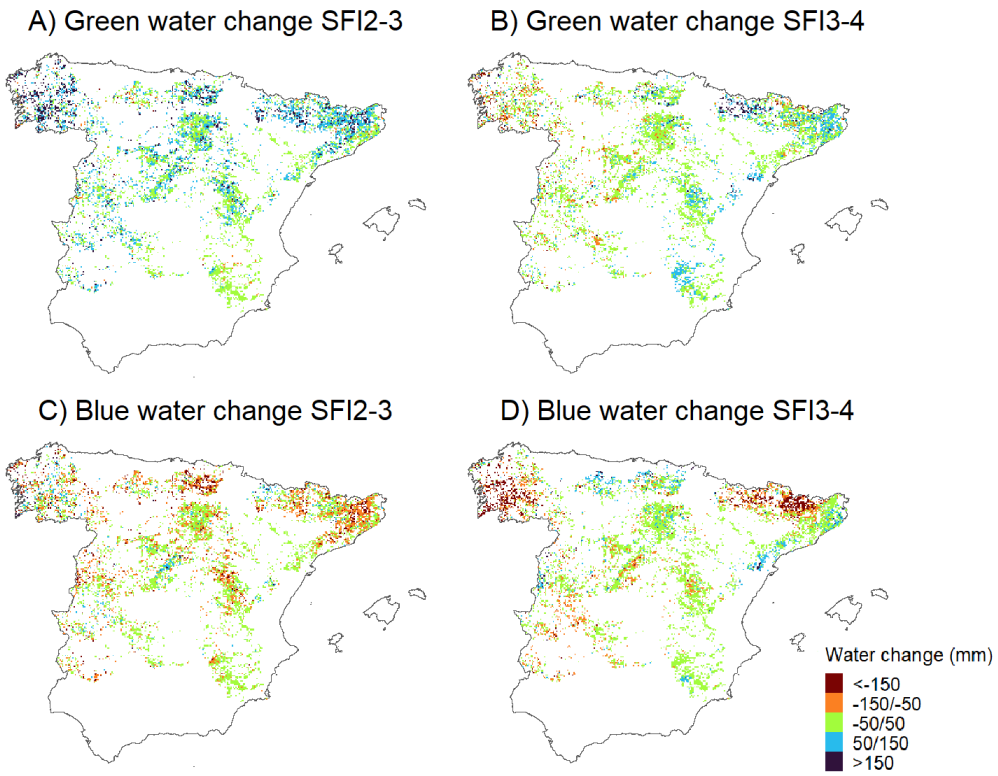



Figure 2. Change in green (A and B) and blue (C and D) water (in the periods SFI2-SFI3 and SFI3-SFI4, respectively) across Spanish forests.

### 3.2. Effects of climate and stand structure on changes in the water cycle

The climate and stand structure variables differed between inventory periods. Thus, the moisture index showed a significant increase in the period between SFI2 and SFI3 and a decrease between SFI3 and SFI4 and this result was consistent for all functional forest types (Figure S1). Precipitation showed the same pattern, with a significant increase between SFI2 and SFI3 and a decrease between SFI3 and SFI4 for all functional forest types (except in the Mediterranean coniferous plots). Temperature showed a significant increase from SFI2 to SFI3 and SFI4 in all functional types except in the Temperate deciduous (Figure S1).

Concerning the structural variables, both basal area and tree LAI showed a significant increase from SFI2 to SFI3 and SFI4 for all functional forest types (Figure S1). Finally, shrub LAI showed the same pattern except in sclerophyll and Mediterranean coniferous plots, where it did not increase during the second period (SFI3-SFI4).

The models obtained by the machine learning system applied (Figure 3, see Table S3 for $R^2$ and the complete list of the retained predictors and their importance in the models) indicated that the changes of tree and shrub LAI were the most important drivers of the changes in green water in the periods SFI2-SFI3 and SFI3-SFI4. Changes in shrub LAI were more important than changes in tree LAI in all forest types in the period SFI2-SFI3. In the SFI3-SFI4 period shrub LAI changes were more important or equal than tree LAI changes in all forest functional groups. These changes in LAI were not related to climate change (see Table S5 for results of XGBoost regression between stand LAI change and climatic change variables). Precipitation and basal area changes were also included as predictors in the models but had a low importance.

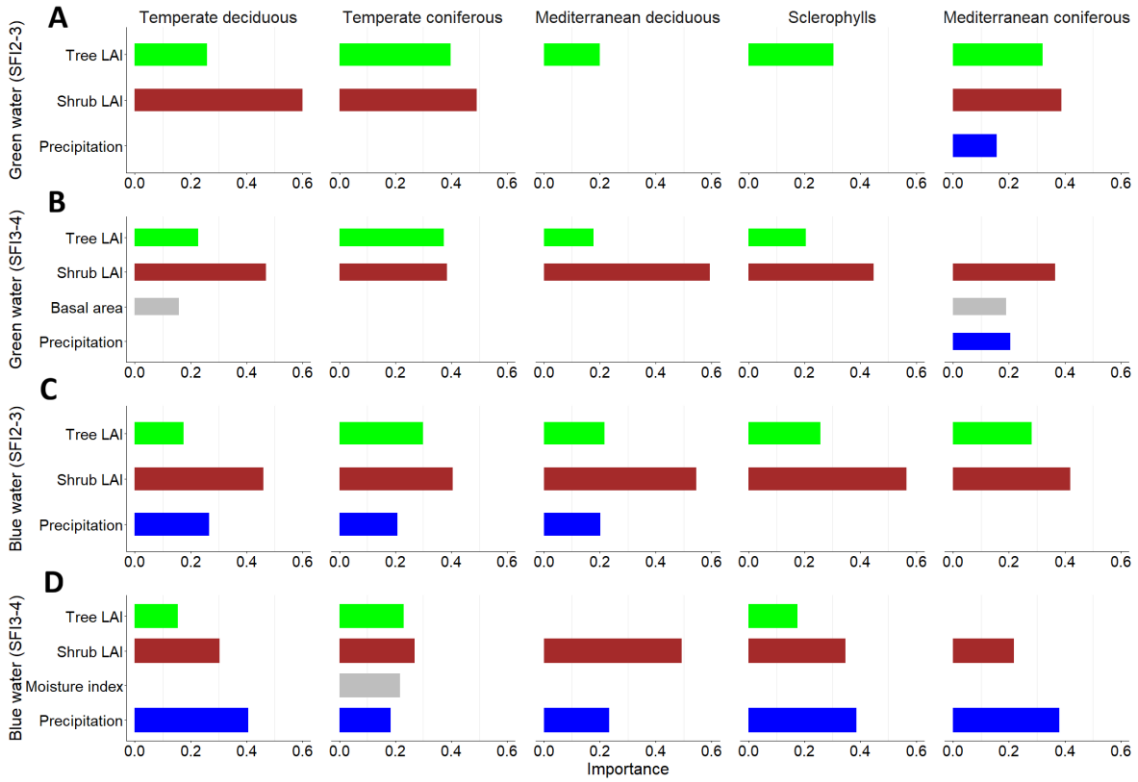



Figure 3. Importance of the most important variables (only variables with Importance > 0.15 in the models have been included) in the prediction of the green and blue water change for all functional forest types in the periods SFI2-SFI3 (above) and SFI3-SFI4 (below) according to the results obtained in the XGBoost regressions carried out by machine learning.

The changes of tree and shrub LAI (almost always both at the same time) were also the main drivers (although the shrub LAI was more important than tree LAI) of the changes in blue water between SFI2 and SFI3, together with precipitation (Figure 3; negative and positive effects, respectively, see Figure S2). In the SFI3-SFI4 change, precipitation changes were more important than in the previous period. and even greater than changes in shrub LAI in three forest types (Mediterranean coniferous, Temperate deciduous and Sclerophylls). Tree LAI change was only a significant driver in three functional types and with low importance in all of them. Moisture index was included as driver but with low importance in Temperate coniferous (Figure 3).

### 3.3. Effect of basal area reductionon the components of the water cycle

Green water was lower in the basal area reduction forests than in the forest plots without basal area reduction in all forest functional groups except in the Temperate and Mediterranean deciduous (Two-way repeated measures ANOVA, Table S4). The interaction between basal area reduction and SFI survey was significant in the Coniferous and Sclerophyll functional groups (Table S4, Figure 4). In Temperate coniferous plots we found a reduction of green water from SFI2 to SFI3 in managed plots but a quick recovery in SFI4. In Sclerophylls and Mediterranean coniferous there was a small increment from SFI2 to SFI3 but a higher increment from SFI3 to SFI4, approaching the values of non-

basal area reduction plots, which slowed down its increase between SFI3 and SFI4 (Figure 4).

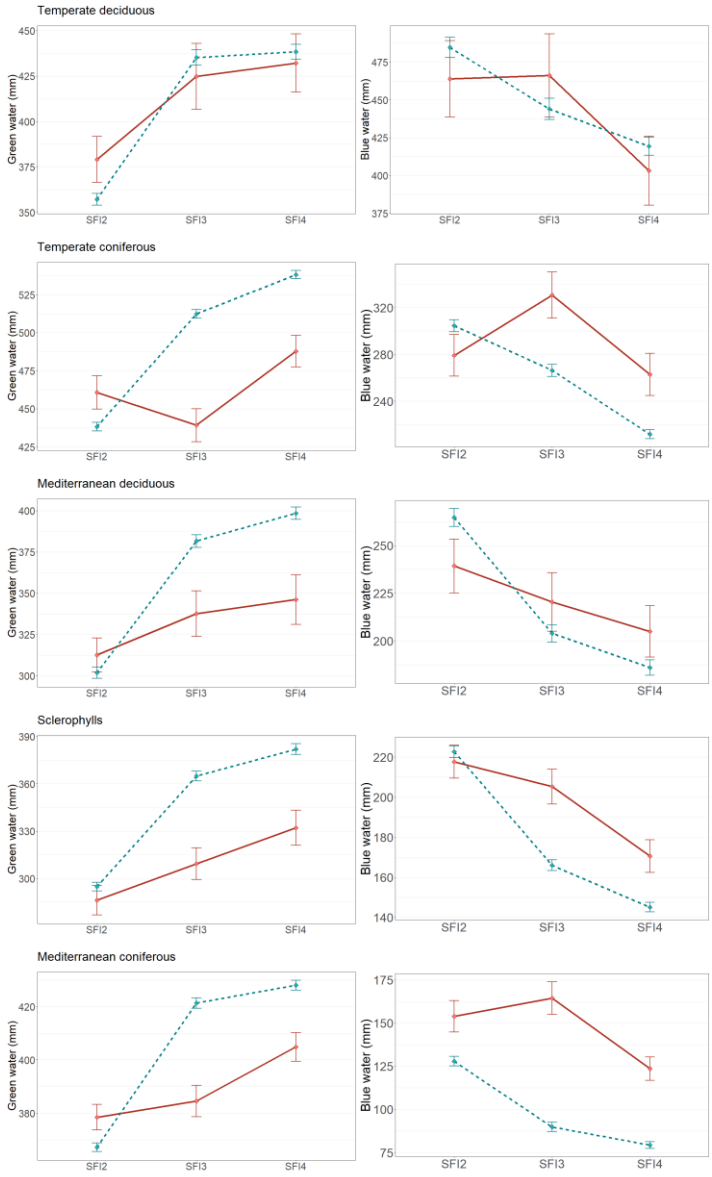



Figure 4. Mean (± standard error) of green and blue water values by forest functional group in the three SFI surveys for disturbed (red and solid lines) and undisturbed stands (blue and broken lines).

On the other hand, blue water was, as expected, higher in basal area reduction plots than in non-basal area reduction plots in Temperate coniferous, Sclerophyll and, especially, Mediterranean coniferous forests, but this pattern was not observed in the two deciduous functional types (Table S4). The interaction between Management and SFI survey was significant in all functional groups except in Mediterranean deciduous (Table S4, Figure 4). Thus, as indicated in previous sections, in non-basal area reduction plots there was a sustainable reduction of blue water from SFI2 to SFI3 and to SFI4. Besides, in basal area reduction plots there was a smaller reduction, or even an increment, of blue water yield compared to not basal area reduction plots from SFI2 to SFI3 (Figure 4). However, in these basal area reduction plots from all forest types there was a strong reduction of blue

water from SFI3 to SFI4 approaching or even being lower in the case of Temperate deciduous, the values of the non-basal area reduction plots (Figure 4). Basal area reduction forests showed a decrease in tree LAI but not in shrub LAI between the SFI2 to SFI3 (Figure 5), and an increase in both tree and shrub LAI between SFI3 to SFI4. Non-basal area reduction forest showed a generalized increase in both tree and shrub LAI between SFI2, SFI3 and SFI4.

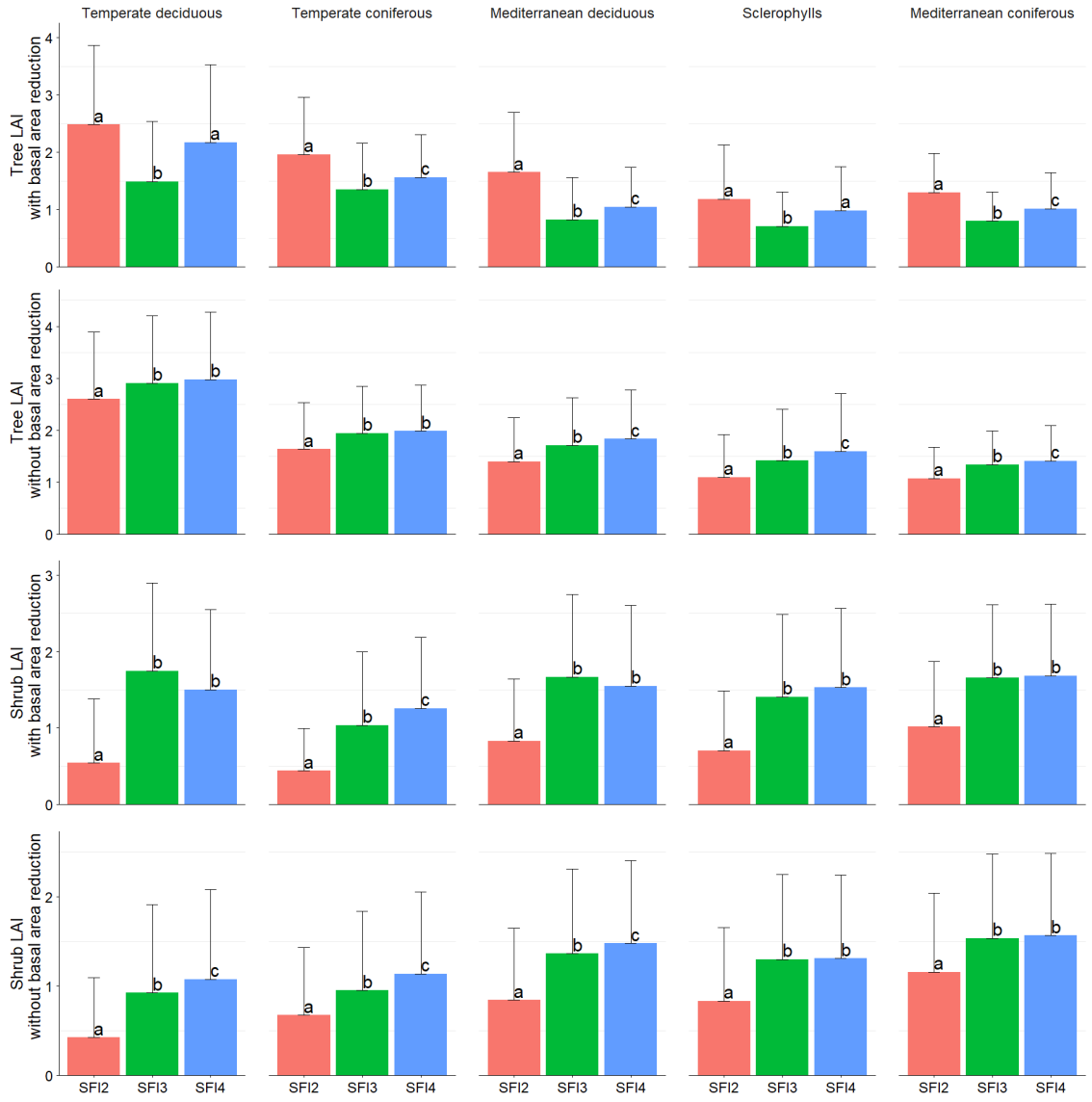



Figure 5. Mean (±standard error) values of tree and shrub LAI in the five functional forest types and the three SFI surveys in disturbed and undisturbed plots. Different letters denote significant differences ($p < 0.05$) among SFI surveys after Bonferroni post hoc test.

## 4. Discussion

### 4.1. Water cycle changes in Spanish forests

Our results indicate that blue water has decreased during the last decades in Spanish forests of all functional groups and across the country, except in few areas. Conversely, green water has increased in the same period with similar patterns. These patterns have also been found in other forest regions like in the oceanic temperate North American, China or the Alps and Boreal region in Europe (Caldwell et al., 2016; Jaramillo et al., 2018; Liu et al., 2016; Mastrotheodoros et al., 2020), where a generalized decrease in blue water and an increase in green water have been described. In our study, the increase of green water (and the concomitant decrease of blue water) was bigger in the first (SFI2-SFI3) than the second period (SFI3-SFI4) (Figure 2). There were not significant differences among forest functional groups since this pattern was the same in all of them. The increase of green water was higher in the north (Atlantic region and Pyrenees mountains) than in south of Spain. The predominant forests in the north of Spain are Temperate deciduous and coniferous (e.g., *Fagus sylvatica*, *Pinus sylvestris*), which have greater transpiration rates than Mediterranean trees and, consequently, produce greater amount of green water (Sánchez-Dávila et al., 2024).

### 4.2. Effects of climate and stand structure on changes in the water cycle

As expected, changes of LAI of the stand and changes in total precipitation are the main drivers of water cycle changes in Spanish forests (Table S3) (Sánchez-Dávila et al., 2024), but the importance of these variables differs among the SFI periods and between green and blue water. For green water, our work indicates that stand structure changes have greater importance than climatic changes in increasing green water, as found previously for drought stress (De Cáceres et al., 2015). Thus, the main driver was mainly the change in shrub and tree LAI and not the climatic changes (Figure 3). In many studies, the increase in evaporative demand raises transpiration and therefore green water (Caldwell et al., 2016; Mastrotheodoros et al., 2020). In contrast, climatic changes (represented by changes in moisture index, mean annual temperature or annual rainfall) had null importance to explain green water changes in our study. These results can be explained by the different magnitude of climatic and structural changes over the study period. Climatic variation included a steady increase in temperature over the study period, while precipitation increased in the first decade and decreased in the most recent decade (Figure S1). So far, the Mediterranean region has not experienced a sustained decline in precipitation in the long term and only in short periods of time (Peña-Angulo et al., 2020). In contrast, during the last decades in Spanish forests there has been a generalized increase in basal area and tree and shrub LAI in all forest types (Figure S1). Moreover, the stand LAI change is not due to the climate change (Table S5). Spanish forests have experienced this generalized increase in the development of stand structure due to a generalized abandonment of forest treatments and wood extraction (Améztegui et al., 2010). This forest development has increased the basal area of the trees (Vayreda et al., 2012) as well as the canopy leaf surface and shrub cover (Martín-Alcón et al., 2015). The increase of green water is due more to the increase in canopy leaf surface than to an increase in the evaporative demand of vegetation (Mastrotheodoros et al., 2020). LAI (shrub or tree LAI) had greater importance than basal area, which is only important in a few functional groups in the two periods analyzed. Basal area can be a proxy of stand transpiration, but LAI is a direct measure and it is a better driver. Furthermore, according to our results, the increase in shrub LAI may have had greater importance than the increase in tree LAI across all forest functional groups and in the two periods (Figure 3). Shrubs can develop faster than trees, colonizing the understory in the early stages of post-disturbance forest succession or after management practices. However, shrub cover is modulated by topography, and

the tree layer overstory has a negative effect on shrub cover due to light competition between strata (Coll et al., 2011; Gracia et al., 2007). Shrub LAI could reach a plateau until the tree layer fully develops, at which point shrub cover will decrease as the tree layer increases competition for light and water resources. Spanish forests have shown a generalized increased in tree and shrub cover in the last decades but it is expected that this increase will reach the plateau in the future when competition will be stronger. The unique functional group that showed some importance of the climate for green water change was the Mediterranean coniferous. Mediterranean coniferous is the functional group more sensitive to the precipitation change in the Spanish forests (Sánchez-Dávila et al., 2024).

For blue water, changes in stand LAI were the main driver in the first period. However, in the last decade changes in precipitation increased in importance, reaching or surpassing stand LAI as the main driver across the different forest types (Figure 3). Blue water can decrease due to a reduction in precipitation or an increase in canopy leaf surface, i.e., in evaporative demand. In the first period, although precipitation was higher, the increase in stand LAI offset the greater availability of water. Precipitation change did not show an important effect on the blue water change for Mediterranean coniferous and sclerophylls in the first decade since these forest groups showed a lower precipitation change than the other groups (Figure S1). In the second period, there was a combined effect of reduced precipitation and increased stand LAI. The decrease in blue water over time in ecosystems has traditionally been attributed to increasing droughts, while green water remains stable or decreases to a lesser extent (Mastrotheodoros et al., 2020; Orth and Destouni, 2018). However, our results indicate that blue water decreased even in a context of increasing precipitation (SFI2-SFI3), due to the remarkable rise in shrub and tree LAI. The increase in transpiration resulting from forest development outweighs the additional water provided by rainfall. Under a scenario of decreasing precipitation (SFI3-SFI4), forest development has a synergistic effect with drought, further reducing blue water. Therefore, the expansion and development of forests play a key role in the water cycle and have been probably more important, until now, than climatic changes in Iberian Spain.

### 4.3. Effect of basal area reduction on the components of the water cycle in the mid-term

In this study we have found that basal area reduction showed only a short-term improvement in blue water supply when basal area was reduced (between SFI2 and SFI3). Previous studies based on field and modelling approaches have also observed the improvement of the blue water yield with thinning when tree LAI decreases is reduced by more than 30% (del Campo et al., 2018; Hawthorne et al., 2013; Sun et al., 2015). However, our results indicate that the recovery of stand LAI after basal area reduction is relatively quick, so that the effect in changing blue water production lasts a short period of time. The increment of blue water was diluted in the mid-term (~ 20 years) since it decreased in the second period (SFI3-SFI4, Figure 4), although plots with lower basal area remained with greater blue water supply than non-managed ones (except in Temperate deciduous forests due to the increasing of the shrub cover). This is also due to the fact that the conditions generated by forest with basal area reduction (i.e., higher availability of resources like light, nutrients and ground space) and the lower competition from the trees cause the LAI of shrubs to increase very quickly in all forest types (Figure 5). This increase of shrub LAI reducing blue water after thinning has been also observed at local scale from Norway to Spain (Gebhardt et al., 2014; Molina et al., 2021). In Spain, our results indicate that basal area reduction has different importance in blue water supply depending on the forest

types: basal area reduction has increased its availability in sclerophyllous, Mediterranean coniferous and, to a lesser extent Temperate coniferous forests from SFI2 to SFI4, but there was no significant effect in Temperate deciduous forests and a small effect in Mediterranean deciduous forests. In these forests, the shrub LAI growth was higher than in evergreen forests (Figure 5), counterbalancing the reduction in tree LAI.

Although basal area reduction has been highlighted for its potential to increase blue water yield (Simon and Ameztegui, 2023), its long-term effect may be diminished due to increasing droughts (Hawthorne et al., 2013). Additionally, our results show that understory development can reduce the advantages of basal area reduction, and basal area reduction does not prevent the long-term decline in blue water as forest structure recovers. Basal area reduction can improve blue water yield if there is repeated thinning over time, including understory clearing (as a rough estimate, every 5 years). But, in addition to the fact that the field costs of these repeated actions can be very high, an intensive basal area reduction can have negative impacts on forest biodiversity conservation (Verschuyl et al., 2011).

### 4.4. Limitations

Model simulations to estimate water flows are not equivalent to direct observation in the field and may lead in some cases to misleading results. The model MEDFATE has been validated in multiple forest types at local scale with field ground data, but it has not been validated at country scale in all the possible forest types. It is possible that MEDFATE has lower accuracy in some climates or forest types that we have not evaluated. Despite acknowledging these limitations, the scarcity of field data at larger scales often necessitates the use of models to investigate and take important conclusions on water flows at the country or continental level.

### 4.5. Implications for the future of forests in Spain

Spanish forests showed a generalized increase in green water and a decrease in blue water across forest functional groups during the last three decades. Although climate change has been broadly studied as a driver of changes in the water cycle in forests, forest abandonment and growth could have a more important role on water cycles . The growth of forests in Spain (including both trees and shrubs) has been sustained over the past few decades (Vadell et al., 2016; Vayreda et al., 2012). However, the precipitation regime has become more unstable, increasing in the first decade and decreasing in the second one (Figure S1), although a generalized decrease in the precipitation (around 10-20%) in Spain have been pointed out in projections for the next decades (Lorenzo and Alvarez, 2020). We show in this study that the increase in leaf area due to forest growth is more important than climate change in influencing the dynamic of water cycle of Spanish forests. Even in the context of higher precipitation (period SFI2-SFI3), the increase in stand LAI and green water surpasses the greater water availability in the forest ecosystem. The reduction in leaf area through basal area reduction increases water yield, but its effect is short-lived (about 10-15 years), and the rapid and subsequent increase in shrub understory counteracts it. However, the growth of trees and shrubs will likely reach a maximum in the future due to spatial limits and tree-shrub competition. At that point, it could be that LAI will not increase and that climate change will become the main driver of future changes in the water cycle, by regulating both LAI and water fluxes.

Nevertheless, changes in other stand structure over time, such as shifts in forest species composition, can have more influence on the water cycle than climate change (Ford et al., 2011). In Spanish forests, there has been an increase in deciduous and evergreen broadleaf tree species compared to conifers (Vayreda et al., 2013), with deciduous species being more productive in terms of blue water (Sánchez-Dávila et al., 2024). The combined effects of forest cover, species composition, and climate change can either counterbalance or amplify each other, influencing the water cycle in multiple ways over time (Caldwell et al., 2016). Thinning can improve the blue water yield in the short term although the forecasts for the next decades in the Mediterranean indicate an increase of the temperature (i.e. evaporative demand) but also the torrentiality (Drobinski et al., 2018) that can improve the blue water yield because the precipitation will likely become mostly runoff. This study highlights those changes in stand structure, particularly those of shrub cover, play a significant role in altering the water cycle and should be monitored alongside climate change.

## Data availability statement

Spanish forest inventory data are available at

https://www.miteco.gob.es/es/biodiversidad/temas/inventarios-nacionales/inventario-forestal-nacional/. The model code of MEDFATE is available at https://github.com/emf-creaf/medfate. The MEDFATE model code is explained in De Cáceres et al. (2023).

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# Supplemental Material

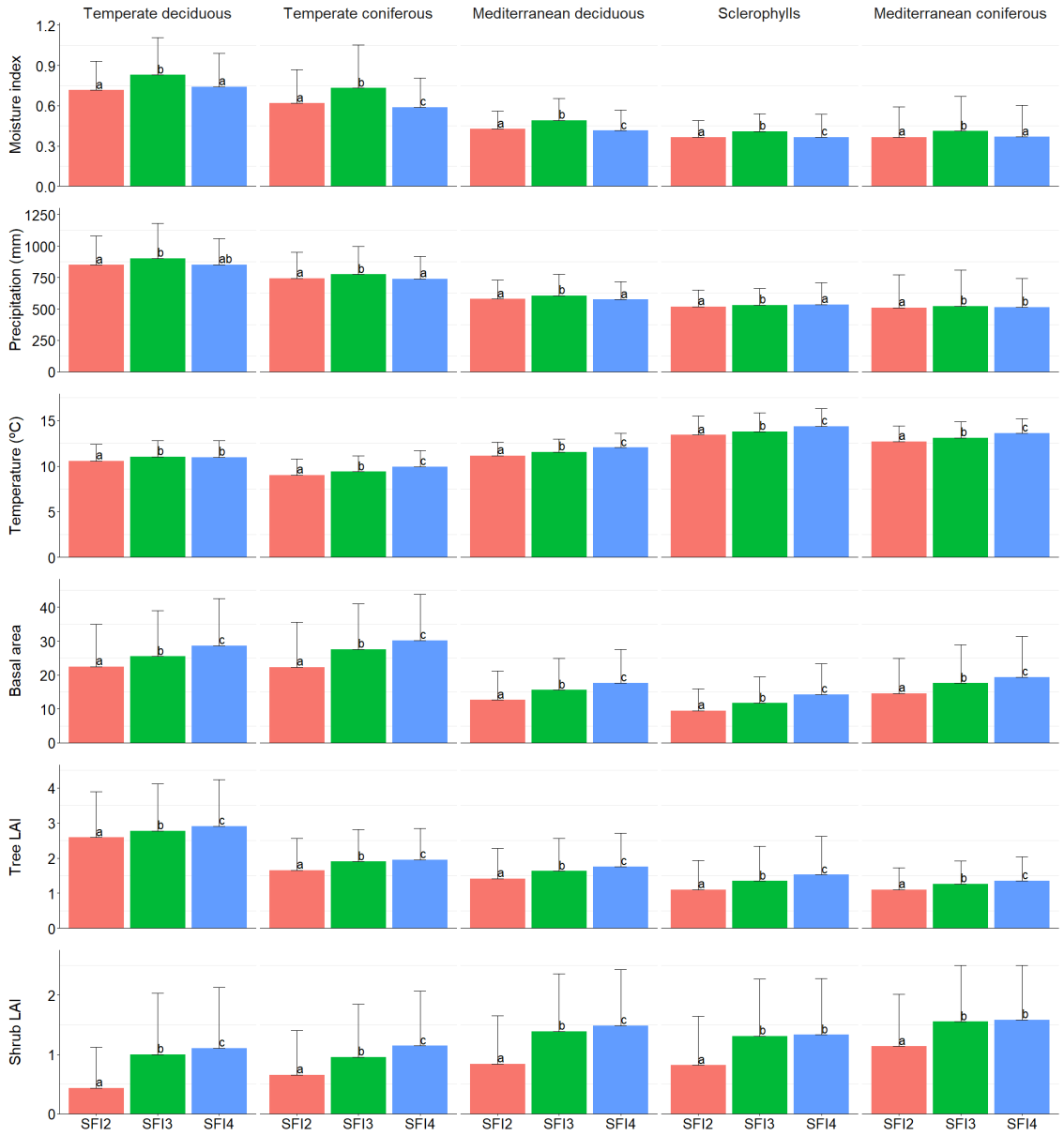



Figure S1. Mean (±standard error) values of moisture index, precipitation, temperature, basal area, tree LAI and shrub LAI per functional forest types and SFI survey. Different letters denote significant differences ($p < 0.05$) among SFI surveys after Bonferroni post hoc test.

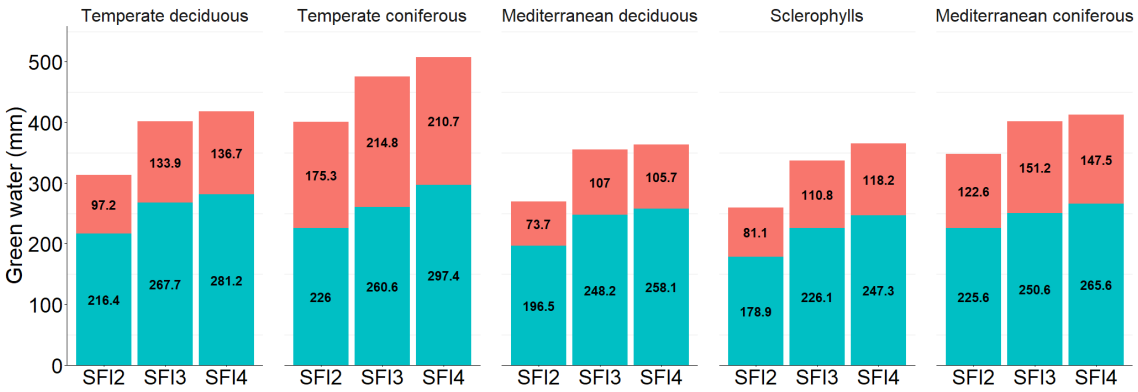



Figure S2. Decomposition of mean values of interception (red) and transpiration (blue) from green water per functional forest types and SFI survey.

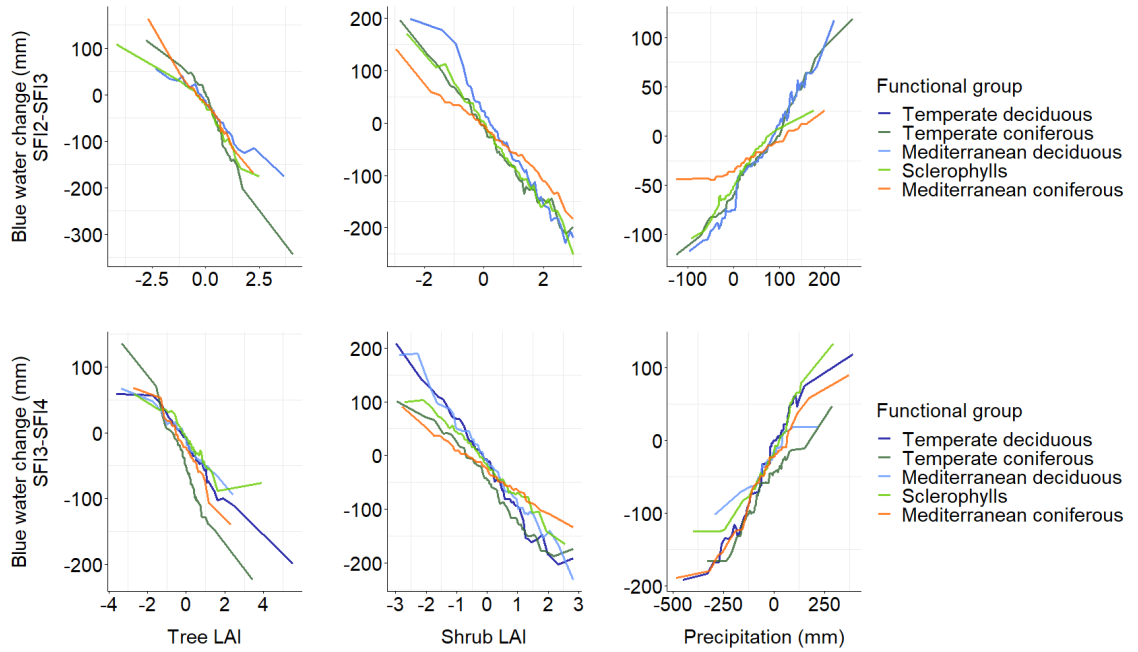



Figure S3. Partial dependence plots for the three main predictor variables and their effect on blue water change by SFI change period for the different functional groups.

**Table S1.** Classification into functional groups of the predominant tree species in the study area and the number of plots of each of them by SFI period of survey.

| SFI survey | Functional group | Predominant specie | Nº of plots |
|---|---|---|---|
| SFI2 | Temperate coniferous | Abies alba | 84 |
| SFI3 | Temperate coniferous | Abies alba | 102 |
| SFI4 | Temperate coniferous | Abies alba | 83 |
| SFI2 | Sclerophyll | Arbutus unedo | 142 |

| | | | |
|---|---|---|---|
| SFI3 | Sclerophyll | Arbutus unedo | 177 |
| SFI4 | Sclerophyll | Arbutus unedo | 177 |
| SFI2 | Temperate deciduous | Betula pendula | 2 |
| SFI3 | Temperate deciduous | Betula pendula | 2 |
| SFI4 | Temperate deciduous | Betula pendula | 2 |
| SFI2 | Temperate deciduous | Castanea sativa | 264 |
| SFI3 | Temperate deciduous | Castanea sativa | 274 |
| SFI4 | Temperate deciduous | Castanea sativa | 287 |
| SFI2 | Temperate deciduous | Fagus sylvatica | 586 |
| SFI3 | Temperate deciduous | Fagus sylvatica | 594 |
| SFI4 | Temperate deciduous | Fagus sylvatica | 762 |
| SFI2 | Mediterranean coniferous | Juniperus thurifera | 395 |
| SFI3 | Mediterranean coniferous | Juniperus thurifera | 402 |
| SFI4 | Mediterranean coniferous | Juniperus thurifera | 356 |
| SFI2 | Mediterranean coniferous | Pinus halepensis | 1824 |
| SFI3 | Mediterranean coniferous | Pinus halepensis | 1838 |
| SFI4 | Mediterranean coniferous | Pinus halepensis | 1856 |
| SFI2 | Mediterranean coniferous | Pinus nigra | 1335 |
| SFI3 | Mediterranean coniferous | Pinus nigra | 1347 |
| SFI4 | Mediterranean coniferous | Pinus nigra | 1319 |
| SFI2 | Mediterranean coniferous | Pinus pinaster | 2546 |
| SFI3 | Mediterranean coniferous | Pinus pinaster | 2475 |
| SFI4 | Mediterranean coniferous | Pinus pinaster | 2124 |
| SFI2 | Mediterranean coniferous | Pinus pinea | 833 |
| SFI3 | Mediterranean coniferous | Pinus pinea | 841 |
| SFI4 | Mediterranean coniferous | Pinus pinea | 592 |
| SFI2 | Temperate coniferous | Pinus sylvestris | 2093 |
| SFI3 | Temperate coniferous | Pinus sylvestris | 2097 |
| SFI4 | Temperate coniferous | Pinus sylvestris | 2087 |
| SFI2 | Temperate coniferous | Pinus uncinata | 293 |
| SFI3 | Temperate coniferous | Pinus uncinata | 296 |

| | | | |
|---|---|---|---|
| SFI4 | Temperate coniferous | Pinus uncinata | 288 |
| SFI2 | Temperate deciduous | Populus tremula | 6 |
| SFI3 | Temperate deciduous | Populus tremula | 6 |
| SFI4 | Temperate deciduous | Populus tremula | 8 |
| SFI2 | Mediterranean deciduous | Quercus canariensis | 1 |
| SFI3 | Mediterranean deciduous | Quercus canariensis | 3 |
| SFI2 | Mediterranean deciduous | Quercus faginea | 397 |
| SFI3 | Mediterranean deciduous | Quercus faginea | 399 |
| SFI4 | Mediterranean deciduous | Quercus faginea | 390 |
| SFI2 | Sclerophyll | Quercus ilex | 1969 |
| SFI3 | Sclerophyll | Quercus ilex | 2035 |
| SFI4 | Sclerophyll | Quercus ilex | 2004 |
| SFI2 | Temperate deciduous | Quercus petraea | 169 |
| SFI3 | Temperate deciduous | Quercus petraea | 176 |
| SFI4 | Temperate deciduous | Quercus petraea | 166 |
| SFI2 | Mediterranean deciduous | Quercus pyrenaica | 923 |
| SFI3 | Mediterranean deciduous | Quercus pyrenaica | 914 |
| SFI4 | Mediterranean deciduous | Quercus pyrenaica | 682 |
| SFI2 | Temperate deciduous | Quercus robur | 319 |
| SFI3 | Temperate deciduous | Quercus robur | 342 |
| SFI4 | Temperate deciduous | Quercus robur | 328 |
| SFI2 | Sclerophyll | Quercus suber | 407 |
| SFI3 | Sclerophyll | Quercus suber | 415 |
| SFI4 | Sclerophyll | Quercus suber | 330 |

**Table S2.** Summary of the evaluation results for MEDFATE model simulations of Transpiration, Soil Water Content, and Evapotranspiration using field data. Evaluation metrics displayed include the variance explained ($R^2$), Spearman correlation (R), and Mean Absolute Error (MAE). We included the evaluation metrics available in the different articles. The evaluation site and country are also displayed. Transpiration data were measured at the tree level using sap flow methods, and Evapotranspiration was measured at the plot level using Eddy Covariance data. Soil water content was measured at the plot level with soil moisture sensors. Daily and monthly runoff was measured at watershed scale using river gauges.

| Variable | Site/Watershed | Reference | Tree species | $R^2$ | R | MAE |
|---|---|---|---|---|---|---|
| Transpiration | Vallcebre (Spain) | De Cáceres et al., 2015 | *Pinus sylvestris* | 0.61 | | |
| Soil water content | Vallcebre (Spain) | De Cáceres et al., 2015 | | 0.57 | | |
| Transpiration | Prades (Spain) | De Cáceres et al., 2015 | *Quercus ilex* | 0.69 | | |
| Soil water content | Prades (Spain) | De Cáceres et al., 2015 | | 0.62 | | |
| Transpiration | Prades (Spain) | De Cáceres et al., 2021 | *Pinus sylvestris* | | 0.65 | 0.08 |
| Transpiration | Prades (Spain) | De Cáceres et al., 2021 | *Quercus ilex* | | 0.83 | 0.11 |
| Transpiration | Puechabon (France) | De Cáceres et al., 2021 | *Quercus ilex* | | 0.77 | 0.15 |
| Transpiration | Fontblanche (France) | De Cáceres et al., 2021 | *Quercus ilex* | | 0.89 | 0.16 |
| Transpiration | Fontblanche (France) | De Cáceres et al., 2021 | *Pinus halepensis* | | 0.51 | 0.08 |
| Transpiration | Can Balasc (Spain) | De Cáceres et al., 2021 | *Arbutus unedo* | | 0.71 | 0.15 |
| Transpiration | Can Balasc (Spain) | De Cáceres et al., 2021 | *Pinus halepensis* | | 0.23 | 0.12 |
| Transpiration | Can Balasc (Spain) | De Cáceres et al., 2021 | *Quercus pubescens* | | 0.36 | 0.19 |
| Transpiration | Can Balasc (Spain) | De Cáceres et al., 2021 | *Quercus ilex* | | 0.75 | 0.18 |
| Transpiration | Armallones (Spain) | De Cáceres et al., 2021 | *Pinus nigra* | | 0.51 | 0.23 |
| Transpiration | Armallones (Spain) | De Cáceres et al., 2021 | *Quercus faginea* | | 0.8 | 0.35 |
| Transpiration | Armallones (Spain) | De Cáceres et al., 2021 | *Quercus ilex* | | 0.8 | 0.29 |
| Soil water content | Prades (Spain) | De Cáceres et al., 2021 | | | | 0.1 |
| Soil water content | Puechabon (France) | De Cáceres et al., 2021 | | | | 0.08 |
| Soil water content | Fontblanche (France) | De Cáceres et al., 2021 | | | | 0.1 |
| Soil water content | Can Balasc (Spain) | De Cáceres et al., 2021 | | | | 0.15 |
| Soil water content | Armallones (Spain) | De Cáceres et al., 2021 | | | | 0.26 |
| Evapotranspiration | It-Col (Italy) | Saponaro et al., 2025 | *Fagus sylvatica* | 0.77 | | |
| Evapotranspiration | Fr-Hes (France) | Saponaro et al., 2025 | *Fagus sylvatica* | 0.69 | | |
| Evapotranspiration | Dk-Sor (Italy) | Saponaro et al., 2025 | *Fagus sylvatica* | 0.62 | | |
| Transpiration | Hesse (France) | De Cáceres et al., 2022 | *Fagus sylvatica* | | 0.72 | 0.27 |
| Transpiration | Fontainebleau (France) | De Cáceres et al., 2022 | *Quercus petraea* | | 0.87 | 0.24 |
| Transpiration | Font-Blanche (France) | De Cáceres et al., 2022 | *Pinus halepensis* | | 0.51 | 0.18 |
| Transpiration | Font-Blanche (France) | De Cáceres et al., 2022 | *Quercus ilex* | | 0.89 | 0.05 |
| Transpiration | Mitra (Portugal) | De Cáceres et al., 2022 | *Quercus ilex* | | 0.83 | 0.63 |
| Transpiration | Rinconada (Spain) | De Cáceres et al., 2022 | *Quercus pyrenaica* | | 0.66 | 0.08 |
| Transpiration | Vallcebre-Barrol (Spain) | De Cáceres et al., 2022 | *Quercus pubescens* | | 0.57 | 0.38 |
| Transpiration | Prades (Spain) | De Cáceres et al., 2022 | *Quercus ilex* | | 0.83 | 0.08 |
| Transpiration | Ronda (Spain) | De Cáceres et al., 2022 | *Abies pinsapo* | | 0.75 | 0.24 |
| Daily runoff | Aiguadora (Spain) | González-Sanchis et al. (in preparation) | | 0.57 | 0.75 | |
| Monthly runoff | Aiguadora (Spain) | González-Sanchis et al. (in preparation) | | 0.75 | 0.87 | |
| Daily runoff | Siurana (Spain) | González-Sanchis et al. (in preparation) | | 0.36 | 0.60 | |
| Monthly runoff | Siurana (Spain) | González-Sanchis et al. (in preparation) | | 0.67 | 0.82 | |

**Table S3.** Importance of the variables retained in the XGBoost models and their $R^2$ by functional group for the two SFI changes (SFI2-SFI3 and SFI3-SFI4).

**Blue water change (SFI2-SFI3)**

**Temperate coniferous ($R^2$=86.6)**

| Variable | Gain | Cover | Frequency |
|---|---|---|---|
| Shrub LAI | 0.481 | 0.413 | 0.325 |
| Tree LAI | 0.25 | 0.3 | 0.345 |
| Precipitation | 0.21 | 0.227 | 0.189 |
| Basal area | 0.052 | 0.056 | 0.107 |
| Temperature | 0.003 | 0.001 | 0.016 |
| Winter precipitation | 0.002 | 0.002 | 0.009 |

**Blue water change (SFI3-SFI4)**

**Temperate coniferous ($R^2$=86.7)**

| Variable | Gain | Cover | Frequency |
|---|---|---|---|
| Moisture index | 0.388 | 0.173 | 0.090 |
| Shrub LAI | 0.202 | 0.293 | 0.315 |
| Precipitation | 0.193 | 0.201 | 0.159 |
| Tree LAI | 0.162 | 0.242 | 0.284 |
| Basal area | 0.027 | 0.042 | 0.065 |
| Winter precipitation | 0.015 | 0.022 | 0.034 |

**Green water change (SFI2-SFI3)**

**Temperate coniferous ($R^2$=83.8)**

| Variable | Gain | Cover | Frequency |
|---|---|---|---|
| Shrub LAI | 0.545 | 0.504 | 0.426 |
| Tree LAI | 0.385 | 0.402 | 0.406 |
| Basal area | 0.051 | 0.068 | 0.087 |
| Summer precipitation | 0.009 | 0.012 | 0.036 |
| Precipitation | 0.008 | 0.010 | 0.030 |
| Temperature | 0.002 | 0.003 | 0.009 |
| Spring precipitation | 0.001 | 0.001 | 0.006 |

**Green water change (SFI3-SFI4)**

**Temperate coniferous ($R^2$=79.9)**

| Variable | Gain | Cover | Frequency |
|---|---|---|---|

| | | | |
|---|---|---|---|
| Shrub LAI | 0.441 | 0.418 | 0.296 |
| Tree LAI | 0.381 | 0.364 | 0.376 |
| Autumn precipitation | 0.085 | 0.118 | 0.122 |
| Basal area | 0.042 | 0.044 | 0.060 |
| Moisture index | 0.021 | 0.018 | 0.042 |
| Precipitation | 0.012 | 0.019 | 0.035 |
| Summer precipitation | 0.007 | 0.009 | 0.020 |
| Winter precipitation | 0.005 | 0.005 | 0.023 |
| Temperature | 0.003 | 0.003 | 0.014 |
| Spring precipitation | 0.002 | 0.004 | 0.011 |

**Blue water change (SFI2-SFI3)**

| **Mediterranean coniferous ($R^2$=79,15)** | | | |
|---|---|---|---|
| **Variable** | **Gain** | **Cover** | **Frequency** |
| Shrub LAI | 0.503 | 0.469 | 0.289 |
| Tree LAI | 0.236 | 0.319 | 0.287 |
| Basal area | 0.093 | 0.078 | 0.137 |
| Precipitation | 0.089 | 0.096 | 0.129 |
| Summer precipitation | 0.066 | 0.03 | 0.108 |
| Temperature | 0.008 | 0.006 | 0.021 |
| Spring precipitation | 0.006 | 0.003 | 0.03 |

**Blue water change (SFI3-SFI4)**

| **Mediterranean coniferous ($R^2$=82,7)** | | | |
|---|---|---|---|
| **Variable** | **Gain** | **Cover** | **Frequency** |
| Precipitation | 0.519 | 0.39 | 0.234 |
| Shrub LAI | 0.181 | 0.214 | 0.259 |
| Tree LAI | 0.086 | 0.166 | 0.173 |
| Winter precipitation | 0.079 | 0.083 | 0.067 |
| Basal area | 0.062 | 0.07 | 0.139 |
| Spring precipitation | 0.044 | 0.026 | 0.065 |
| Moisture index | 0.019 | 0.047 | 0.034 |

| | | | |
|---|---|---|---|
| Summer precipitation | 0.009 | 0.004 | 0.025 |
| Temperature | 0.001 | 0.001 | 0.004 |

**Green water change (SFI2-SFI3)**

**Mediterranean coniferous ($R^2$=79,7)**

| Variable | Gain | Cover | Frequency |
|---|---|---|---|
| Shrub LAI | 0.449 | 0.436 | 0.279 |
| Tree LAI | 0.242 | 0.317 | 0.405 |
| Precipitation | 0.165 | 0.159 | 0.146 |
| Summer precipitation | 0.09 | 0.039 | 0.063 |
| Temperature | 0.039 | 0.042 | 0.07 |
| Spring precipitation | 0.015 | 0.008 | 0.038 |

**Green water change (SFI3-SFI4)**

**Mediterranean coniferous ($R^2$=73,6)**

| Variable | Gain | Cover | Frequency |
|---|---|---|---|
| Shrub LAI | 0.372 | 0.374 | 0.351 |
| Basal area | 0.235 | 0.198 | 0.139 |
| Precipitation | 0.208 | 0.197 | 0.209 |
| Tree LAI | 0.102 | 0.173 | 0.149 |
| Spring precipitation | 0.042 | 0.014 | 0.048 |
| Summer precipitation | 0.024 | 0.025 | 0.056 |
| Winter precipitation | 0.005 | 0.005 | 0.017 |
| Autumn precipitation | 0.004 | 0.008 | 0.011 |
| Temperature | 0.004 | 0.003 | 0.016 |
| Moisture index | 0.003 | 0.001 | 0.005 |

**Blue water change (SFI2-SFI3)**

**Sclerophylls ($R^2$=68,98)**

| Variable | Gain | Cover | Frequency |
|---|---|---|---|
| Shrub LAI | 0.718 | 0.555 | 0.421 |
| Tree LAI | 0.173 | 0.254 | 0.344 |
| Precipitation | 0.072 | 0.132 | 0.139 |
| Basal area | 0.017 | 0.026 | 0.041 |
| Spring precipitation | 0.008 | 0.008 | 0.028 |
| Moisture index | 0.008 | 0.013 | 0.013 |
| Autumn precipitation | 0.003 | 0.011 | 0.011 |
| Temperature | 0 | 0 | 0.003 |
| Summer precipitation | 0 | 0 | 0.001 |

**Blue water change (SFI3-SFI4)**

| **Sclerophylls ($R^2$=76,86)** | | | |
|---|---|---|---|
| **Variable** | **Gain** | **Cover** | **Frequency** |
| Precipitation | 0.453 | 0.367 | 0.341 |
| Shrub LAI | 0.353 | 0.368 | 0.319 |
| Tree LAI | 0.113 | 0.178 | 0.237 |
| Moisture index | 0.061 | 0.076 | 0.056 |
| Summer precipitation | 0.013 | 0.01 | 0.03 |
| Temperature | 0.008 | 0.001 | 0.016 |

**Green water change (SFI2-SFI3)**

| **Sclerophylls ($R^2$=83,86)** | | | |
|---|---|---|---|
| **Variable** | **Gain** | **Cover** | **Frequency** |
| Shrub LAI | 0.764 | 0.611 | 0.441 |
| Tree LAI | 0.197 | 0.311 | 0.404 |
| Basal area | 0.018 | 0.035 | 0.059 |
| Precipitation | 0.012 | 0.023 | 0.048 |
| Temperature | 0.006 | 0.015 | 0.021 |
| Spring precipitation | 0.003 | 0.004 | 0.017 |
| Summer precipitation | 0.001 | 0.001 | 0.009 |

**Green water change (SFI3-SFI4)**

| **Sclerophylls ($R^2$=68,98)** | | | |
|---|---|---|---|
| **Variable** | **Gain** | **Cover** | **Frequency** |
| Shrub LAI | 0.525 | 0.472 | 0.344 |
| Tree LAI | 0.184 | 0.213 | 0.217 |
| Basal area | 0.112 | 0.121 | 0.169 |
| Summer precipitation | 0.091 | 0.103 | 0.102 |
| Precipitation | 0.077 | 0.08 | 0.126 |
| Spring precipitation | 0.009 | 0.008 | 0.03 |
| Temperature | 0.002 | 0.002 | 0.009 |
| Moisture index | 0.001 | 0.001 | 0.003 |

**Blue water change (SFI2-SFI3)**

| **Mediterranean deciduous ($R^2$=82,64)** | | | |
|---|---|---|---|
| **Variable** | **Gain** | **Cover** | **Frequency** |
| Shrub LAI | 0.713 | 0.548 | 0.374 |
| Precipitation | 0.14 | 0.209 | 0.254 |
| Tree LAI | 0.125 | 0.22 | 0.307 |
| Summer precipitation | 0.022 | 0.023 | 0.065 |

**Blue water change (SFI2-SFI3)**

**Mediterranean deciduous ($R^2$=82,64)**

| Variable | Gain | Cover | Frequency |
|---|---|---|---|
| Shrub LAI | 0.713 | 0.548 | 0.374 |
| Precipitation | 0.14 | 0.209 | 0.254 |
| Tree LAI | 0.125 | 0.22 | 0.307 |
| Summer precipitation | 0.022 | 0.023 | 0.065 |

**Blue water change (SFI3-SFI4)**

**Mediterranean deciduous ($R^2$=74,89)**

| Variable | Gain | Cover | Frequency |
|---|---|---|---|
| Shrub LAI | 0.605 | 0.505 | 0.371 |
| Precipitation | 0.197 | 0.242 | 0.26 |
| Basal area | 0.085 | 0.095 | 0.149 |
| Tree LAI | 0.077 | 0.111 | 0.139 |
| Moisture index | 0.036 | 0.046 | 0.082 |

**Green water change (SFI2-SFI3)**

**Mediterranean deciduous ($R^2$=82,81)**

| Variable | Gain | Cover | Frequency |
|---|---|---|---|
| Shrub LAI | 0.809 | 0.627 | 0.465 |
| Tree LAI | 0.114 | 0.219 | 0.268 |
| Basal area | 0.053 | 0.102 | 0.153 |
| Moisture index | 0.008 | 0.02 | 0.034 |
| Winter precipitation | 0.008 | 0.015 | 0.033 |
| Precipitation | 0.005 | 0.014 | 0.024 |
| Temperature | 0.003 | 0.004 | 0.023 |

**Green water change (SFI3-SFI4)**

**Mediterranean deciduous ($R^2$=74,58)**

| Variable | Gain | Cover | Frequency |
|---|---|---|---|
| Shrub LAI | 0.719 | 0.611 | 0.451 |
| Basal area | 0.132 | 0.139 | 0.165 |
| Tree LAI | 0.108 | 0.193 | 0.23 |
| Precipitation | 0.031 | 0.047 | 0.104 |
| Spring precipitation | 0.01 | 0.009 | 0.051 |

**Blue water change (SFI2-SFI3)**

**Temperate deciduous ($R^2$=85,03)**

| Variable | Gain | Cover | Frequency |
|---|---|---|---|
| Shrub LAI | 0.516 | 0.483 | 0.381 |
| Precipitation | 0.298 | 0.258 | 0.242 |
| Tree LAI | 0.109 | 0.193 | 0.223 |

| | | | |
|---|---|---|---|
| Basal area | 0.071 | 0.058 | 0.133 |
| Summer precipitation | 0.006 | 0.009 | 0.021 |

**Blue water change (SFI3-SFI4)**

| **Temperate deciduous ($R^2$=86,26)** | | | |
|---|---|---|---|
| **Variable** | **Gain** | **Cover** | **Frequency** |
| Precipitation | 0.557 | 0.376 | 0.285 |
| Shrub LAI | 0.253 | 0.332 | 0.324 |
| Tree LAI | 0.087 | 0.131 | 0.246 |
| Winter precipitation | 0.08 | 0.118 | 0.075 |
| Moisture index | 0.022 | 0.043 | 0.069 |

**Green water change (SFI2-SFI3)**

| **Temperate deciduous ($R^2$=85,78)** | | | |
|---|---|---|---|
| **Variable** | **Gain** | **Cover** | **Frequency** |
| Shrub LAI | 0.775 | 0.606 | 0.416 |
| Tree LAI | 0.155 | 0.28 | 0.34 |
| Basal area | 0.05 | 0.07 | 0.157 |
| Precipitation | 0.014 | 0.035 | 0.051 |
| Summer precipitation | 0.006 | 0.008 | 0.035 |

**Green water change (SFI3-SFI4)**

| **Temperate deciduous ($R^2$=76,68)** | | | |
|---|---|---|---|
| **Variable** | **Gain** | **Cover** | **Frequency** |
| Shrub LAI | 0.576 | 0.495 | 0.335 |
| Tree LAI | 0.19 | 0.239 | 0.254 |
| Basal area | 0.138 | 0.128 | 0.21 |
| Spring precipitation | 0.036 | 0.041 | 0.05 |
| Summer precipitation | 0.025 | 0.032 | 0.056 |
| Autumn precipitation | 0.02 | 0.036 | 0.047 |
| Moisture index | 0.01 | 0.017 | 0.029 |
| Winter precipitation | 0.003 | 0.009 | 0.008 |
| Temperature | 0.002 | 0.003 | 0.012 |

**Table S4.** Results of the two-way repeated measures ANOVA by forest functional forest group for forest management and SFI survey on green and blue water. p-values are refereed as (ns > 0.05, ∗ p < 0.05, ∗∗ p < 0.01, ∗∗∗ p < 0.001)

| Functional forest groups | Term | Green water | | Blue water | |
|---|---|---|---|---|---|
| | | F | p-value | F | p-value |

| | | | | | |
|---|---|---|---|---|---|
| Temperate deciduous | Management | 0.1 | ns | 2.1 | ns |
| | SFI | 141.8 | *** | 60.0 | *** |
| | Management x SFI | 1.3 | ns | 2.7 | * |
| Temperate coniferous | Management | 28.6 | *** | 8.0 | ** |
| | SFI | 330.1 | *** | 95.2 | *** |
| | Management x SFI | 21.1 | *** | 7.0 | *** |
| Mediterranean deciduous | Management | 0.1 | ns | 0.1 | ns |
| | SFI | 141.9 | *** | 87.3 | *** |
| | Management x SFI | 1.3 | ns | 2.5 | ns |
| Sclerophylls | Management | 39.7 | *** | 15.2 | *** |
| | SFI | 218.1 | *** | 231.5 | *** |
| | Management x SFI | 6.0 | ** | 6.5 | ** |
| Mediterranean coniferous | Management | 31.4 | *** | 136.8 | *** |
| | SFI | 305.1 | *** | 91.0 | *** |
| | Management x SFI | 24.4 | *** | 11.8 | *** |

**Table S5.** Summary of the $R^2$ of the XGBoost regressions for the stand LAI change by the climatic change variables in each SFI change period and forest group.

| Functional forest group | SFI2-3 | SFI3-4 |
|---|---|---|
| Mediterranean deciduous | 3.16 | 3.66 |
| Mediterranean coniferous | 11.23 | 0.71 |
| Temperate deciduous | 8.17 | 2.01 |
| Temperate coniferous | 9.40 | 10.83 |
| Sclerophylls | 7.11 | 3.59 |

# Capítulo 3

## Three decades of tree carbon losses from wildfires in Spain: the influence of forest type, carbon hotspots and drivers

Jesus Sánchez-Dávila, Judit Lecina, Jordi Vayreda, Javier Retana

**Three decades of tree carbon losses from wildfires in Spain: the influence of forest type, carbon hotspots and drivers**

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## Abstract

Forest carbon stocks are increasingly threatened by wildfires globally. However, the quantification of carbon losses across different forest types, their temporal evolution, and their underlying environmental drivers remain poorly understood at the national scale. We analyzed carbon losses due to fires in Spanish forests—one of the most fire-affected regions in Europe—using national inventories (1990–2025) integrated with wildfire perimeters and climatic and stand-structure predictors. Forests were classified into carbon stock "hotspots" and "non-hotspots," and carbon losses were calculated by decade, forest type, and hotspot status. Our results indicate that while carbon losses have decreased over time, the rate of change varies significantly by forest type. In the 2000s, losses were concentrated in Mediterranean pine forests; however, by the 2010s, significant increases occurred in both pines and exotic species within the wetter Atlantic region of northern Spain. Furthermore, while carbon loss decreased in most Mediterranean forests, it was disproportionately high in hotspot areas of sclerophyll forests. Notably, half of the forest plots showed no carbon loss following wildfires, and losses were minimal in deciduous forests and temperate pines. Environmental drivers exhibited no consistent pattern, as neither climatic nor stand-structure predictors were uniform across forest types or study periods.

**Keywords:** biomass, carbon, climate, forest, hotspot, wildfires

## 1. Introduction

Forests are the main terrestrial carbon sink (Pan et al., 2011). They sequester the carbon as woody biomass at the global scale at a rate of ~0.5 Gt $CO_2$ $yr^{-1}$ in the period 2000–2020 (Grassi et al., 2023). Forest carbon storage has increased in the last decades in temperate forests but has declined in the tropical and boreal forests due to disturbances such as deforestation or wildfires (Pan et al., 2024). In Europe the largest forest carbon stocks are in Atlantic and Central Europe, where the precipitation is highest (Nabuurs & Schelhaas, 2003). For this reason, the hotspots of forest carbon stock, that is, those stands where more carbon is stored, are concentrated in Atlantic-Central Europe (Neidermeier et al., 2025), although individual stands with very high carbon stock may be found in other biomes.

Wildfires are a natural or human-induced disturbance in many ecosystems worldwide. Nevertheless, in the last decades there has been an increase in the number and extent of wildfires in some regions of the world such as North America, Brazil, or Siberian Russia (Bousfield et al., 2023; MacCarthy et al., 2024). Wildfires can reduce the carbon sink stored in forests depending on the fire intensity and meteorological conditions. Thus, wildfires generate large losses of forest carbon storage in tropical forests, where they occur in a context of deforestation (van Wees et al., 2021). In other regions, such as North America or Europe, wildfire occurs in the context of rural abandonment or climate change (Balch et al., 2017), but they also produce high carbon losses

(MacCarthy et al., 2024). Wildfires can have different effects on forests carbon losses depending on regional differences: deciduous forests have lower occurrence of wildfires than evergreen forests (Krawchuk et al., 2006), with wildfires differing in extent and severity according to the dominant tree species (Miller et al., 2012). Wildfire occurrence also varies depending on climate (Holden et al., 2018; Turco et al., 2014) or fuel load and structural conditions (Hakkenberg et al., 2024; Wilson et al., 2022). In Europe, wildfires are mainly concentrated in the Mediterranean basin and have decrease in number and burned area in recent decades (1980–2010) due to increased efforts in fire suppression (Urbieta et al., 2019). However, in recent years there has been an increase in extreme fires in the region (Rodrigues et al., 2023) and fire severity has also increased (Alvarez et al., 2024).

Forest carbon losses by wildfires have been evaluated with remote sensing data at large scales as continents (Clarke et al., 2022; Fan et al., 2023). However, remote sensing products usually have low accuracy for quantifying both forest carbon stocks and losses due to disturbance. In contrast, national forest inventories that measure forest carbon stocks through time with repeated surveys include forest species information and stand structure characteristics and may have better accuracy. In Europe the effect of wildfires on forest carbon has been evaluated with field data at small local scales (Kelly et al., 2024; Molina et al., 2019). The effect of fires at regional scale like country is less known since field data is hard to obtain, although there are local field studies across large extensions in North America or using national forest inventory data (Ghimire et al., 2012; Walker et al., 2020). The role of the macroenvironmental factors and local conditions in forest carbon losses have not been unravelled. Local topography (Viedma et al., 2015) and the accumulation of shrub vegetation and trees (Fernandes, 2013; Oliveira et al., 2014) can increase fire severity. Climatic variables such as droughts and heatwaves (Xiao & Zhuang, 2007) or an increase in vapor pressure deficit (Sedano & Randerson, 2014) also have been pointed out as factors increasing fire ignition or severity. However, the role of these and other predictors on tree carbon losses have been evaluated in few scenarios.

In this work, we analyze carbon losses of the tree stratum by wildfires on Spanish forests through the past three decades, using repeated forest inventory data (1990–2025). Spanish forests are divided into Mediterranean species (evergreen broadleaf trees and pines), which are predominant around the Mediterranean Sea and inland, and temperate species (deciduous trees and pines) around the Atlantic Ocean and in the higher areas of the Mediterranean mountains. In Spain, forest carbon hotspots are mainly located in deciduous forests in the Atlantic biome (Vayreda, Martinez-Vilalta, et al., 2012). Spain is a country deeply affected by wildfires being, together with Portugal, the European country with more annual burned area (San-Miguel-Ayanz et al., 2018). The effect of wildfires in forest carbon stocks (including the carbon hotspots) across a gradient of different forest types and biomes at country scale with accurate field data from national forest inventory have not been evaluated. We have analyzed the total forest carbon losses by wildfires in Spanish forests through the last decades. We have classified forests with highest carbon stocks as hotspots and analyzed the effect of wildfires on them such as the possible drivers of the losses. Specifically, we addressed the following questions: 1) How much carbon has been lost in Spanish forests in recent decades due to fires and what are the differences between forest types and over time? 2) Are there differences in terms of carbon loss between hotspots and other forests in recent decades? 3) What are the environmental drivers affecting carbon losses in Spanish forests due to fires?

## 2. Material and methods

### 2.1. Spanish National Forest Inventory (SFI)

Our study area includes the forested areas of peninsular Spain and Balearic Islands, located between 36°3’ and 43°44’ latitude North and -9°16’ and 4°17’ longitude East. The Spanish forests are located in two climatic biomes: the Atlantic biome around the Atlantic Sea influence in the northern coast of Spain, where the climate is temperate and wet, and the Mediterranean biome in

the rest of the territory, where the climate is cold and hot and with seasonal drought in summer (Rivas-Martínez et al., 2017).

We used the repeated permanent field plot data from the Spanish national forest inventory (SFI) to identify tree species composition and carbon stock across the study area and through time. The SFI covers the forested areas of Spain with a sampling density of ~1 plot/km$^2$. SFI field plots have four concentric circular sub-plots with radii of 5, 10, 15 and 25 m. Trees were identified and measured within variable circular size plots (5 m radius for trees with diameter at breast height (DBH) ≥ 7.5 cm, and trees with 2.5 ≤ DBH ≤ 7.5 cm are counted; 10 m radius for trees with DBH ≥ 12.5 cm; 15 m radius for trees with DBH ≥ 22.5 cm; and 25 m radius for trees with DBH ≥ 42.5 cm). We used data from the second (SFI2, 1986-1996), third (SFI3, 1997-2008), and the fourth (SFI4, 2009-2025) inventories.

Aboveground biomass of live trees was computed from DBH using species-specific allometric equations developed by (Gracia et al., 2004) and (Montero et al., 2005) for Spanish tree species. We classified the plots according to the dominant tree species into seven functional groups: Temperate deciduous (e.g., *Quercus robur; Fagus sylvatica*), Mediterranean deciduous (e.g., *Quercus pyrenaica; Quercus faginea*), Temperate coniferous (e.g., *Pinus sylvestris; Pinus uncinata*), Mediterranean coniferous (e.g., *Pinus halepensis; Pinus pinaster*), Atlantic coniferous (Mediterranean coniferous species that live around the Atlantic sea like *Pinus pinaster*), Sclerophylls (e.g., *Quercus ilex; Quercus suber*) and Foreign (non native species like *Eucalyptus* spp. or *Pinus radiata*). Temperate deciduous are predominant in the north and west part of the Iberian Peninsula with Atlantic Sea influence, where the climate is wetter than Mediterranean (> 1000 mm). Mediterranean deciduous are dominant in the wetter and colder regions of the Mediterranean area (about 800 mm). Temperate coniferous are dominant in the highest altitudes of the Spanish mountains (> 1500 m), where the climate is subalpine, with cold winters and fresh summers. Sclerophylls and Mediterranean coniferous are dominant in the hotter and drier regions of the Mediterranean area (about 400-600 mm) but also there are some Mediterranean coniferous species (e.g., *Pinus pinaster*) that form large forests in the Atlantic biome. Foreign species are located mainly in the Atlantic biome where there are forest plantations for the pulp and paper industry. We excluded the plots with forest management and those dominated by riparian species. Overall, we selected 38,362 SFI plots.

### 2.2. Wildfire database

We obtained perimeters of wildfires from 1985 to 2023 from the regional Spanish agencies responsible of their compilation (see Appendix A in (Alvarez et al., 2024) for the sources of fire perimeters from each Spanish Autonomous Community). They were complemented by MODIS data (GlobFire database, which is based on MODIS Collection-6, (Artés et al., 2019)). These perimeters included complete dates (year/month/day). We finally obtained a database of 5,726 wildfires of more than 5 ha.

### 2.3. Quantifying tree carbon loss due to wildfires

We calculated the tree carbon stock of each SFI plot in the three inventories as the total aboveground tree biomass (Mg/ha) computed for the sum of all living trees. For each forest functional group, we classified as hotspots in both the SFI2 and the SFI3 the SFI plots located in the highest 20th percentile (Armenteras et al., 2015), which defines 20% of the plots with the highest values of total tree biomass.

To select the SFI plots affected by fires, we overlapped the distribution maps of the SFI plots with the wildfire perimeters and considered all SFI plots included in these perimeters. We calculated tree carbon stock change as the difference between the tree carbon stock values of the two inventories between which the fire was located. For instance, if an SFI plot was surveyed in 1995

(SFI2) and 2003 (SFI3) and burned in 1997, the tree carbon change was calculated as the difference between their values in SFI2 and SFI3. Thus, we obtained two periods (SFI2-3, between SFI2 and SFI3, and SFI3-4, between SFI3 and SFI4) of tree carbon change through time. Although the difference between the date of the fires and the dates of surveys could be closer to the first or the second survey, we did not carry out any correction because we considered that the growth of the Spanish forests is low (mean growth tree carbon rate: 1,5 Mg $ha^{-1}$ $yr^{-1}$; (Vayreda, Gracia, et al., 2012)).

We classified the SFI plots affected by fires into two groups: those that did not show loss of tree carbon stock (similar carbon stock between two consecutive surveys) and those that showed loss of tree carbon stock (less carbon stock in the last survey). In this second case, we calculated the total tree carbon lost in hotspot and in non-hotspot plots by period (SFI2-3 and SFI3-4) and forest group, and the average tree carbon loss (% of carbon loss respect of the total carbon of the plot) in each burned SFI plot. We did not evaluate the shrub or herb carbon losses since there is no information of their carbon values in the SFI plots.

### 2.4. Environmental predictors

We used climatic variables as predictors because higher temperatures and lower precipitations are drivers of fire occurrences in Spain (Jiménez-Ruano et al., 2017). We downloaded daily total precipitation, potential evapotranspiration (PET), vapor pressure deficit (VPD) and mean temperature in the months of July and August for the years affected by fires on the SFI plots from ERA5-Land Daily data at 0.1°x 0.1° (~9 km) (Muñoz Sabater et al, 2024). We calculated the moisture index (i.e., total precipitation/total PET) as a measure of how the temperature (through PET) modifies the water available. We averaged the daily values of mean temperature, annual precipitation, VPD and moisture index of the summer months (July and August) in a unique value for each SFI plot affected by fires (see summary in Table S1).

We also calculated topographic variables since a higher slope and solar radiation (in the south aspect) increase the severity of the fires (Viedma et al., 2015). Topographic variables of slope (%), aspect (º) and altitude (m) were derived from a digital elevation model (DEM) at 25 m of the PNOA Spanish project through the IGN website (downloaded on 09/02/2024; https://centrodedescargas.cnig.es/CentroDescargas/index.jsp#). Aspect was transformed with cosine to obtain the northness.

Shrub vegetation has a positive effect on fire occurrences in the Mediterranean because it increases surface fuel load, which increases fire intensity and connect understory and overstory fuel layers (Oliveira et al., 2014). In the SFI plots, shrub species within the 10-m-radius subplot were measured with a percent cover value and a mean height. Shrub phytovolume was estimated using shrub height and cover, assuming an allometric relationship between crown volume and shrub foliar biomass. The model uses a constant Specific Leaf Area (SLA) for each species (see details in (De Cáceres et al., 2023)). Shrub phytovolume ($m^3/m^2$) from each SFI plot was calculated with the *Medfate* R package (De Cáceres et al., 2023).

Finally, we assessed fire severity through satellite images using the Relativized delta normalized burn ratio (RdNBR, (Miller & Thode, 2007)) which is a good predictor of fire severity (Veraverbeke et al., 2010). We generated Landsat-based fire severity maps for each fire using the Google Earth Engine (GEE) platform, following the methodology of (Parks et al., 2018) and the following equation:

$$NBR = \left(\frac{NIR - SWIR}{NIR + SWIR}\right) \quad (1)$$

$$dNBR = (NBR_{prefire} - NBR_{postfire}) \times 1000 \quad (2)$$

$$RdNBR = \left\{ \begin{array}{c} \frac{dNBR}{|NBR_{prefire}|^{0.5}}, |NBR_{prefire}| \geq 0.001 \\ \frac{dNBR}{|0.001|^{0.5}}, |NBR_{prefire}| < 0.001 \end{array} \right\} \quad (3)$$

where NIR (Eq. 1) represents the near-infrared band and SWIR (Eq. 1) corresponds to the shortwave infrared band. We employed the mean compositing approach outlined in Parks et al. (2018), where all valid pixels (e.g., cloud-free observations) within a predefined date range are stacked, and the mean value for each pixel across the stack is computed to generate the final fire severity dataset. To avoid post-fire management effects (e.g., salvage logging) and early regeneration, we utilized images acquired after the fire (the date range spans from September to October for post-fire periods).

### 2.5. Statistical analysis

We carried out a post-hoc Tukey's test for pairwise comparisons for the mean total tree carbon loss and relative loss by forest type and SFI inventory. We selected functional groups with sufficient sample size (at least 10 SFI plots with tree carbon losses by fires in a period of time; see Table 1) to carry out the analyses: Mediterranean (in SFI2-3 and SFI3-4) and Atlantic coniferous (SFI3-4), Mediterranean and Temperate deciduous (SFI3-4), Foreign species (SFI3-4) and Sclerophylls (SFI2-3 and SFI3-4).

We analyzed the effects of environmental variables on the total tree carbon lost per plot (Mg C/ha) using Generalized Linear Models (GLMs). RdNBR, wildfire area (ha), slope, aspect, mean temperature, precipitation, moisture index, vapor pressure deficit, pre-fire SFI biomass and pre-fire shrub phytovolume were used as predictor variables, together with the hotspot condition (i.e., hotspot, non-hotspot). We analyzed all the SFI plots affected by fires including plots both with carbon losses and without losses. GLMs were fitted to a gaussian distribution. Predictor variables were standardized to a mean of 0 and the best model was selected based on the lowest Akaike Information Criterion (AIC). Previously, we removed the predictors with a variance inflated factor (VIF) > 2 in each GLM. Then, we did not include the mean temperature and precipitation in the GLMs. We ran GLM models for each forest type in each of the two SFI change periods (SFI2-3 and SFI3-4) separately. Also, we did the GLMs for the relative tree carbon lost per plot since the total tree carbon lost could be affected for the pre-fire SFI biomass (Table S2).

## 3. Results

### 3.1. Tree carbon losses by wildfires over time

The number of SFI plots affected by fires decreased between periods from 647 in SFI2-3 (1.7% of the SFI plots) to 389 in SFI3-4 (1.1% of the SFI plots) (Table 1), although with different patterns in the different forest types. In the first period, Mediterranean coniferous was the most affected group, with 335 (2.1% of the Mediterranean coniferous plots), followed by Sclerophylls and the other types with much lower numbers, including the absence of fires in the Temperate coniferous type. In the second period, Mediterranean coniferous was again the most affected

forest type, followed by Sclerophylls and Foreign. Less of half of the Mediterranean deciduous and coniferous and Sclerophyll plots affected by fires showed carbon loss in the first period, with lower values for the other types except for the Temperate deciduous (Table 1). In the second period, the percentage of plots with carbon losses were high in the Mediterranean coniferous (increased), Atlantic coniferous and Temperate deciduous (decreased), with lower values for the other groups (Table 1).

Table 1. Total number of plots, number of plots affected by fires (in parentheses, % of the total number of plots per forest group), and number of plots with tree carbon losses (in parentheses, % of the total number of plots affected by fires) for the forest types.

| **Forest types** | **Total N plots** | **N plots affected by fires (% of the total number of plots per forest group)** | | **N plots with tree carbon losses (% of the total number of plots affected by fires)** | |
|---|---|---|---|---|---|
| | | **SFI2-3** | **SFI3-4** | **SFI2-3** | **SFI3-4** |
| Temperate deciduous | 4,160 | 12 (0.3) | 29 (0.7) | 8 (66.6) | 12 (41.4) |
| Temperate coniferous | 3,947 | 0 | 0 | 0 | 0 |
| Atlantic coniferous | 1,058 | 1 (0.01) | 56 (5.3) | 0 | 30 (53.6) |
| Mediterranean deciduous | 3,107 | 80 (2.6) | 59 (1.9) | 28 (35) | 16 (27.1) |
| Mediterranean coniferous | 16,285 | 335 (2.1) | 132 (0.7) | 140 (41.8) | 67 (50.7) |
| Sclerophylls | 8,234 | 182 (2.2) | 78 (0.8) | 56 (30.7) | 20 (25.6) |
| Foreign | 1,571 | 23 (1.5) | 60 (3.6) | 5 (21.7) | 17 (28.3) |
| Overall | 38,362 | 647 (1.7) | 389 (1.1) | 239 (36.9) | 164 (42.1) |

Mean carbon loss per plot did not show a significant change over time in the forest type exexceptor Mediterranean deciduous and Foreign that increased (Figure 1). The pattern was similar in the relative carbon loss per plot (Figure 1). The highest percentages of carbon loss were in the Atlantic coniferous (around 75%) followed by the rest of forest types (around 50%) although Temperate deciduous were highest (around 75%) in one period.

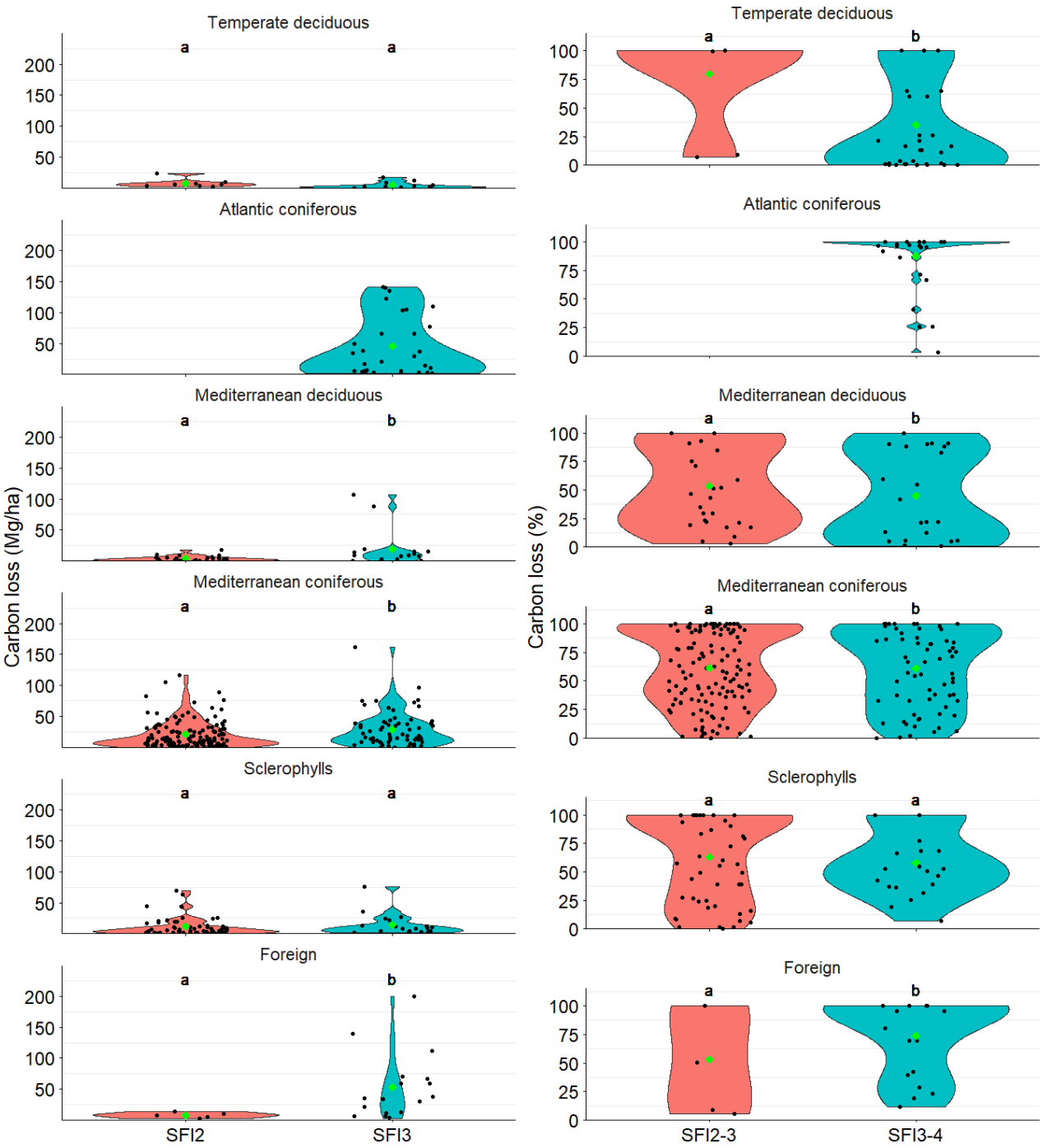



Figure 1. Mean total carbon loss (Mg C/ha) and relative carbon loss (%) per forest group and SFI period (only plots with carbon loss have been considered). Different letters denote significant differences ($p < 0.05$) between periods with the Tukey post hoc test.

Carbon lost due to wildfires showed a different spatial distribution in the two periods. Plots with losses were more concentrated from south to northeastern Mediterranean in the first decade (SFI2-3), but from central Spain to the northwestern Atlantic area in the second decade (SFI3-4) (Figure 2). Total tree carbon loss in each forest type (computed as the sum of all plots with tree carbon losses) was considerably higher in the Mediterranean coniferous than in the other groups, followed by the Atlantic coniferous in the second period (Figure 3). The relative contribution of the losses by forest type was also predominantly higher in the Mediterranean coniferous with a

contribution of 77.6% of the losses in the first period and of 33.9% in the second. In percentage, these values are considerably higher than what the two types of forest represent in terms of stock although lower in the second period (Table 2). In the first period, Sclerophylls were slightly overrepresented in the carbon losses compared to carbon stocks (16.9% versus 8%). In the second period both the Atlantic coniferous and the Foreign species were overrepresented in carbon losses (28.1% versus 5.3% in Atlantic coniferous, and 18.7% versus 8.5% in Foreign species).

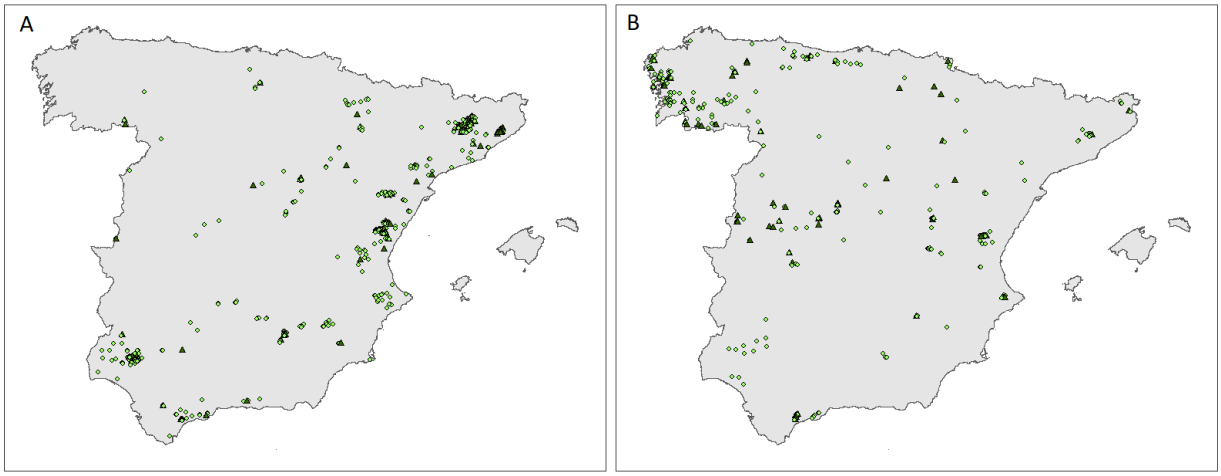



Figure 2. SFI plots affected by fires and hotspot condition (circle-non hotspot and triangle-hotspot) in the first (SFI2-3) and second period (SFI3-4).

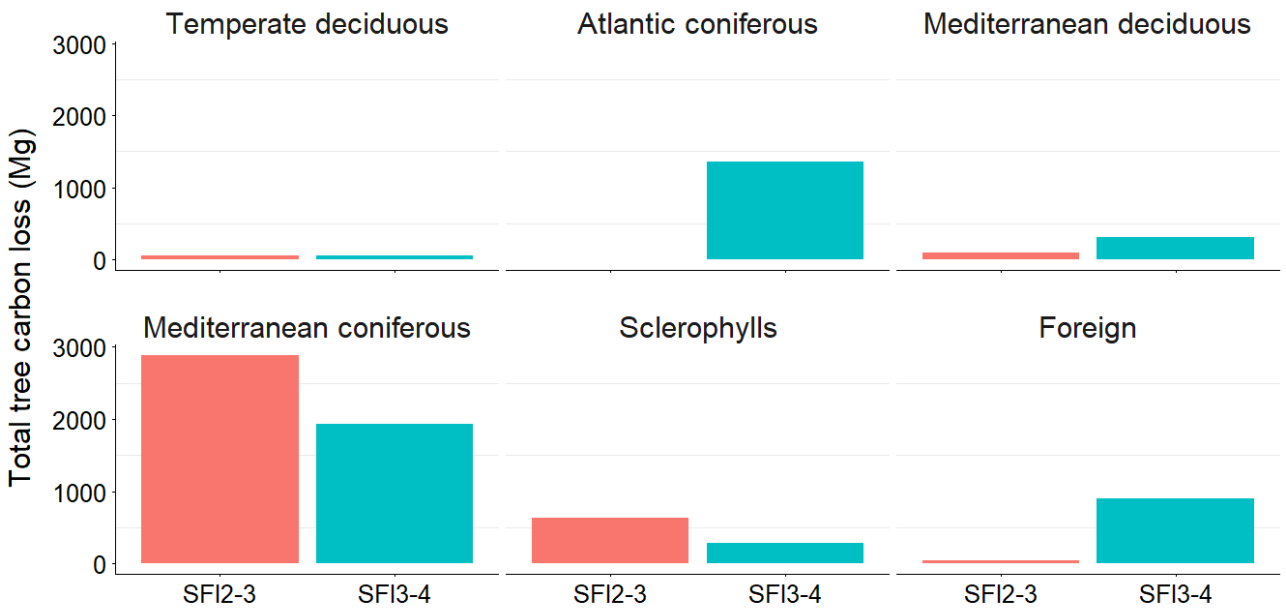



Figure 3. Total tree carbon losses per forest group and SFI period.

Table 2. Tree carbon stock stored (%) and tree carbon loss by fires (%) per forest type and SFI period. The percentages of losses that are higher than the corresponding stock percentages for that forest type and period are indicated in bold.

| **Forest type** | **Tree carbon stock stored (in %)** | | **Tree carbon losses by fires (%)** | |
|---|---|---|---|---|
| | **SFI2** | **SFI3** | **SFI2-3** | **SFI3-4** |
| Temperate deciduous | 16.3 | 15.2 | 1.7 | 1.1 |
| Temperate coniferous | 19.9 | 19.6 | 0 | 0 |
| Atlantic coniferous | 7.4 | 5.3 | 0 | **28.1** |
| Mediterranean deciduous | 9.7 | 9.6 | 2.8 | 6.4 |
| Mediterranean coniferous | 29.9 | 32.3 | **77.6** | **39.9** |
| Sclerophylls | 8 | 9.6 | **16.9** | 5.8 |
| Foreign | 7.7 | 8.5 | 1.1 | **18.7** |

### 3.2. Tree carbon losses in carbon hotspots

In the SFI2-3 period, the greatest number of affected hotspot plots was in the Mediterranean coniferous followed by the Sclerophylls (Table 3). In SFI3-4, the highest number of hotspot plots affected by fires was again in the Mediterranean coniferous, followed Foreign and Sclerophylls (Table 3). Most of the hotspot plots (around 30-40%) had not tree carbon losses in the forest types affected by fires, while in the SFI3-4 period increased in Mediterranean coniferous and Foreign but decreased in Temperate deciduous and Sclerophylls (Table 3).

Table 3. Total number of plots affected by fires, number of hotspot plots affected by fires (in % the total number of plots affected by fires), and number of plots with tree carbon losses (in % the total number of hotspot plots affected by fires) for different forest types and periods.

| **Forest types** | **N plots affected by fires** | | **N hotspot plots affected by fires (% of the total number of plots affected)** | | **N hotspot plots with tree carbon losses (% of the N of hotspot plots affected)** | |
|---|---|---|---|---|---|---|
| | **SFI2-3** | **SFI3-4** | **SFI2-3** | **SFI3-4** | **SFI2-3** | **SFI3-4** |

| | | | | | | |
|---|---|---|---|---|---|---|
| Temperate deciduous | 12 | 29 | 8 (66.6) | 12 (41.4) | 5 (62.5) | 1 (8.3) |
| Atlantic coniferous | 1 | 56 | 0 | 30 (53.6) | 0 | 7 (23.3) |
| Mediterranean deciduous | 80 | 59 | 28 (35) | 16 (27.1) | 1 (3.5) | 8 (50) |
| Mediterranean coniferous | 335 | 132 | 140 (41.8) | 67 (50.7) | 44 (31.4) | 17 (25.4) |
| Sclerophylls | 182 | 78 | 56 (30.8) | 20 (25.6) | 16 (28.6) | 4 (20) |
| Foreign | 23 | 60 | 5 (21.7) | 17 (28.3) | 1 (25) | 4 (23.5) |
| Overall | 647 | 389 | 237 | 162 | 67 | 41 |

Hotspots accounted for 40–60% of the total carbon lost in Spanish forests, with Mediterranean coniferous storing the highest carbon proportion in hotspots (Table S3). Mediterranean coniferous and Sclerophylls showed a decrease in the total carbon lost in hotspots (Figure 4), while in the Sclerophylls, carbon losses in hotspots were proportionally higher in both periods. In the Foreign and Mediterranean deciduous, carbon losses in hotspots increased over time.

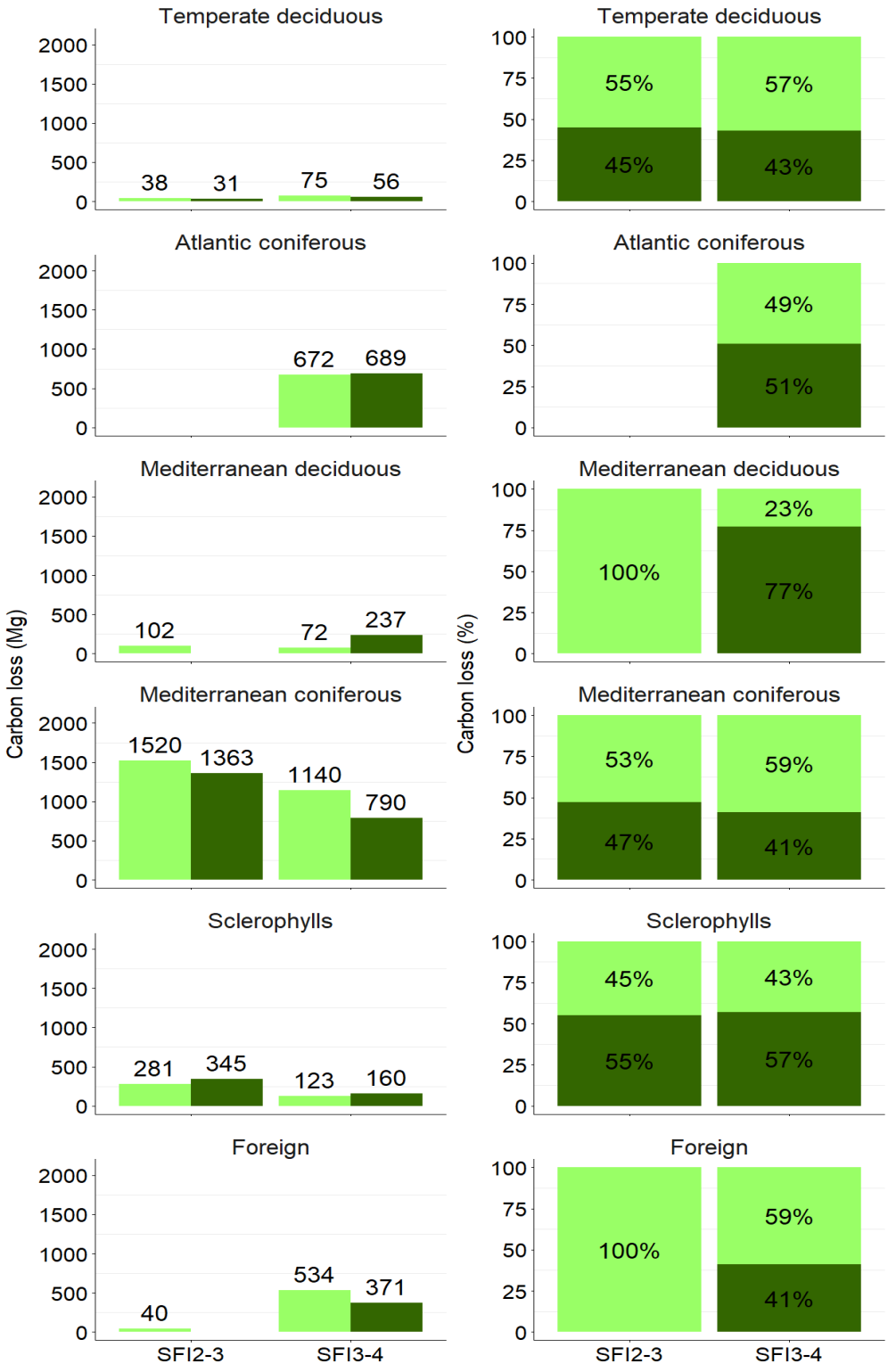



Figure 4. Total carbon loss (Mg) and % of loss in non-hotspot and hotspot plots (green and dark green, respectively) by forest types and periods.

### 3.3. Factors affecting tree carbon losses

GLMs indicated that the predictors of carbon loss are different in each forest type (Table 4). Atlantic and Temperate deciduous, and Mediterranean coniferous had a good performance in the GLM (25-40% of $R^2$). Atlantic coniferous had up to four predictors retained in the model: VPD was the most important predictor (with a negative effect), followed by moisture index (negative effect), hotspot condition (non-hotspot had a negative effect) and phytovolume (also negative effect). Temperate deciduous had the moisture index as main predictor (negative) followed by shrub phytovolume (negative). Mediterranean deciduous had the slope (positive effect for non-hotspot) as the only predictor retained in the first period. In the second period there was the northness aspect (negative) and moisture (positive). Mediterranean coniferous had the biomass (negative) and hotspot condition (negative) as the main predictors in the first period (SFI2-3) whereas in the second period was again the biomass and hotspot. Sclerophylls predictors were biomass (negative), moisture (positive) and hotspot condition (non-hotspot had a negative) in the first period and slope (positive) and moisture (negative) in the second. Foreign group was the worst type in model performance, with only hotspot retained as predictor.

Table 4. Results of the GLM models for the absolute tree carbon losses by forest type and SFI period. For each model effects, total variance explained ($R^2$) and coefficient, significance levels ($* \ p < 0.05$, $** \ p < 0.01$, $*** \ p < 0.001$) and variance explained (in brackets) of the variables retained are given.

| | Temperate deciduous | Atlantic coniferous | Mediterranean deciduous | | Mediterranean coniferous | | Sclerophylls | | Foreign |
|---|---|---|---|---|---|---|---|---|---|
| Period | SFI3-4 | SFI3-4 | SFI2-3 | SFI3-4 | SFI2-3 | SFI3-4 | SFI2-3 | SFI3-4 | SFI3-4 |
| Slope | | | 0.1±**0*** | | | | | 0.1±**0*** (6.9) | |
| Aspect | | | | -0.7±**0.3*** (10.5) | -0.3±**0.1*** (1.5) | | | | |
| VPD | | -1.3±**3.6**** (14.3) | | | | | | | |
| Phytovolume | -1.2±**0.6***(10.8) | -1.3±**0.3*** (4.4) | | | | | | | |
| Biomass | | | | | -0.1±**0***** (30.2) | -0.1±**0*** (21.6) | -0.3±**0.1**** (10.1) | | |
| Moisture | -4.4±**1.6**** (22.5) | -1.6±**0.6**** (8.5) | | **2±1.5*** (2.6) | 5.3±**2.3**** (1.3) | | 2.5±**2.8*** (0.5) | -0.6±**1.7*** (0.5) | |
| Hotspot | | -1.3±**0.6*** (6.6) | | | -1±**0.1***** (17.1) | -1.4±**0.3**** (17.2) | -0.7±**0.2**** (8) | | -0.9±**0.5*** |
| $R^2$ (%) | 26.6 | 26 | 6.4 | 13 | 39.6 | 28.2 | 13.3 | 7.1 | 6.2 |

## 4. Discussion

Our results indicate that the number of forest plots affected by fires has decreased over the last decades in Spanish forests, as has the number of forests experiencing carbon losses (Table 1). In the first period Mediterranean coniferous was the main group affected by fires followed by Sclerophylls. Nevertheless, there has been an increase in tree carbon losses in the last decade in

Atlantic forests. Coniferous forests in the Atlantic biome (mainly *Pinus pinaster*) and Foreign forests composed of non-native species (*Eucalyptus* sp., *Pinus radiata*) are the main sources of new carbon losses in the most recent decade. This is in accordance with the pattern of burned area, since the increase in wildfires in the recent decades has been concentrated specifically in the north-west of Spain and represented 40% of the total burned area in Spain (Arellano Pérez et al., 2018). In contrast, Mediterranean forests decreased in the number of forest plots and in the amount of carbon losses.

Mediterranean deciduous forests are weakly affected by fires in Spain (Moreno et al., 2011), and although was the third type most affected in the first period decreased in the most recent decade, in accordance with other studies (Urbieta et al., 2019). Nevertheless, Temperate and Mediterranean deciduous forests showed very low carbon losses due to fires. Therefore, our results showed that wildfires have a very limited effect on them. Temperate deciduous forests exhibit higher resilience to fires than coniferous forests or Foreign forests in Atlantic Spain (Cruz et al., 2024), and in this work we also show that fires themselves have a low impact on them, resulting in minimal carbon losses.

Forest hotspots (defined in this study as the 20% of the plots with the highest values of total tree biomass) represent half of the carbon stock in Spanish forests, confirming that they are very valuable in terms of climate mitigation in the Spanish forest ecosystems. Forest hotspots showed concordance (respect to their carbon stock) losses in Mediterranean coniferous forests whereas in the Atlantic forests were lower. In the Sclerophylls, carbon losses from hotspot forests were overrepresented in comparison with their contribution as carbon sinks since they are the main source of carbon loss (55-60%) when they store half of the carbon (Table S3). In contrast, in Atlantic Forest groups (Foreign species and Atlantic coniferous forests), carbon losses were underrepresented or similar in hotspots. Therefore, there is a mismatch in the effect of fires on carbon hotspots at the national scale, since the main Spanish carbon hotspots are concentrated in the Atlantic area (Vayreda, Martinez-Vilalta, et al., 2012), whereas carbon losses are overrepresented in the Sclerophylls although not in the coniferous forests. This is particularly detrimental because, given that the growth rate of Mediterranean forests is slower (high temperatures and low rainfall) than that of Atlantic forests, the recovery time of pre-fire stocks will be slower (Vayreda, Gracia, et al., 2012).

GLMs did not show a similar pattern of environmental predictors on carbon losses, neither between the different forest types nor periods. As expected, biomass was the main predictor in Mediterranean coniferous during the first period. In these Mediterranean pines, carbon loss was higher in forest plots with higher biomass but in the rest of groups biomass was not retained in the models except to Sclerophylls in the first period. Moreover, the relative carbon loss was not explained by the previous biomass available in neither group including the Mediterranean coniferous (Table S2). Hotspot condition that indicates a bigger amount of biomass had a positive effect on the carbon losses but was a minor predictor in the GLMs. Biomass reduction in forests has been proposed as a fire control measure in Mediterranean regions due to the reduction of fuel components (Fernandes, 2013), including shrub cover (Marino et al., 2011). Nevertheless, contrary to expectations, our analyses indicated that shrub phytovolume did not explain carbon losses. In contrast, in Atlantic forests with higher biomass concentrated and were also it was the increase of carbon losses in the recent years, the biomass was not retained in the model. Therefore, it is unclear whether forest management practices such as the reduction of tree biomass or shrub cover have a truly positive effect on decreasing carbon losses during wildfires. However, its management entail high economic costs. Moreover, shrubs play an important role in forest ecosystems as sources of food or refuge for animals (Ellis & Betts, 2011; Heinze et al., 2011) and in tree regeneration (Castro et al., 2004). RdNBR, used as a proxy for fire severity, was not retained in either forest type. Although fire severity has increased in recent decades in Spain (Alvarez et al., 2024), forests have not been strongly affected by this increase in fire severity. Spanish forests can have a big resistance to fire severity or occurrence by their bark thickness (Madrigal et al., 2019) or their resprouting capacity (Puerta-Piñero et al., 2012; Quevedo et al., 2007).

Climatic variables (VPD and moisture index) did not show an important effect on most forests, only in the Atlantic coniferous and Temperate deciduous. In these forests, regions with lower moisture index showed higher carbon loss. Thus, carbon losses were greater in drier regions (lower moisture index), also with largest losses occurred in the Atlantic coniferous when VPD was lower (air wetter). This suggests a combined effect of a wetter local air and a hotter macroenvironment where carbon loss was highest. For Mediterranean deciduous or Foreign forests, the performance of the model was very low, indicating that carbon loss in these forests was not well explained by stand conditions (biomass and shrub cover) or by climate. Climatic variables (VPD and moisture index) did not show great differences over time or between forests with carbon or non-carbon losses (Table S1).

The heterogeneity in the retained predictors and the lack of climatic or stand factors in explaining carbon losses can be because of wildfires in Spain are mainly of human origin (90% of occurrences; (Ganteaume et al., 2013)), either intentional or due to negligence. For instance, wildfire occurrence in the north-western region of Galicia—the region with the highest number of fires in Spain over the last decade and where the increase in forest carbon losses is concentrated—has been identified as a social problem, as fire ignitions are not randomly distributed and are influenced by land ownership conflicts (Fuentes-Santos et al., 2013) and by landscapes close to human settlements, where 90% of wildfires have a human origin (Chas-Amil et al., 2013). Therefore, environmental conditions (macroclimate or local forest conditions) do not appear to play a significant role in the increase of tree carbon losses in north-western Spain and in the increase of tree carbon loss in the recent decade.

There were several limitations of the study. Thus, the analyses of factors affecting tree carbon losses might be limited by the lack of local environmental data that are difficult to obtain at the country scale, such as forest understory microclimate or the local wind conditions in the day of the fires (moreover we used a climatic source at coarse resolution of 9 km), or stand-level conditions such as herbaceous biomass. In addition, intrinsic tree characteristics not considered in this study, such as bark thickness, resprouting capacity (Brando et al., 2012) or the vertical structure and fuel types within the forest (Alvarez et al., 2012) could explain their vulnerability to fires. Moreover, we did not have information about carbon losses in the soil and shrubs layers, so that we cannot have complete forest carbon losses in. However, we consider that the evaluation of tree carbon loss caused by fires and its change over time, together with its decomposition into forest groups and hotspot conditions, provides important results about the effects of fire on forest carbon stocks.

## 5. Conclusions

Forest carbon losses in Spanish forests have showed a decrease in recent years, although with an increment concentrated in the north-western part of Spain, specifically in Atlantic coniferous and Foreign forests. Nevertheless, we have also shown that fires only produce carbon losses in half or even less of the forest plots, indicating that forests (or landscapes, or both) have a high resistance to fire damage. The recent decades have shown an increment in tree carbon loss that is concentrated in Atlantic evergreen forests (Atlantic coniferous and Foreign species), and they represent all the new carbon losses. In contrast, Mediterranean forests are stable or decreasing in terms of tree carbon losses, but there has been an overconcentration of carbon losses in the hotspots of Sclerophylls in the recent decade.

The main drivers of these carbon losses remain unclear at the country scale, since in Mediterranean coniferous forests the main factor was biomass, in Atlantic coniferous forests it was climate, and in Deciduous and Foreign forests the performance of the models was poor. In Mediterranean forests climate did not have an effect although the conditions are drier and hotter than at the country scale. In Atlantic forests, where the increase in carbon loss occurred mainly in the last decade, the biomass or shrub amount did not show a relationship with carbon losses. These

results indicate that the drivers of carbon losses may be harder to explain using macroenvironmental predictors, or that more information at the local stand scale is needed. Additionally, the role of human pressure may mislead the interpretation of the real influence of macro- or microenvironmental conditions on fire incidence and impact, since the occurrence of fires in Spain is mainly of human origin (Ganteaume et al., 2013).

## Author Contributions

**Jesús Sánchez Dávila:** conceived the research idea and design and wrote the manuscript with the support of the rest of the authors. All authors discussed the results and edited the manuscrip


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## Data Availability Statement

Spanish forest inventory data are available at https://www.miteco.gob.es/es/biodiversidad/temas/inventarios-na cionales/inventario-forestal-nacional/.

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## Supplemental Material

Table S1. Mean and standard deviation of the climatic variables per forest group, SFI survey and affected plots by wildfires with carbon losses (0-No, 1-Yes).

| Forest group | SFI | Carbon loss | Precipitation | Temperature | VPD | Moisture index |
|---|---|---|---|---|---|---|
| Sclerophylls | SFI3 | 0 | 13.8±12.9 | 25.8±1.7 | 1.8±0.5 | 0.1±0.1 |
| Sclerophylls | SFI3 | 1 | 23.3±15.7 | 25.6±1.9 | 1.6±0.6 | 0.1±0 |
| Sclerophylls | SFI4 | 0 | 48.5±38 | 22.4±3.1 | 1.4±0.6 | 0.2±0.2 |
| Sclerophylls | SFI4 | 1 | 20±16.3 | 23.9±3.1 | 1.8±0.6 | 0.1±0.1 |
| Temperate deciduous | SFI3 | 0 | 28.6±31.3 | 22.7±2.5 | 1.2±0.4 | 0.1±0.2 |
| Temperate deciduous | SFI3 | 1 | 0±0 | 24.8±0.7 | 1.6±0.4 | 0±0 |
| Temperate deciduous | SFI4 | 0 | 69.2±27.7 | 17.7±1.9 | 0.5±0.2 | 0.4±0.2 |
| Temperate deciduous | SFI4 | 1 | 51±36 | 18.6±3.2 | 0.6±0.4 | 0.3±0.2 |
| Foreign | SFI3 | 0 | 8.3±9.8 | 26.6±0.5 | 2±0.1 | 0±0 |
| Foreign | SFI3 | 1 | 16.7±20.8 | 25.8±1.4 | 1.7±0.6 | 0±0 |
| Foreign | SFI4 | 0 | 68±27.1 | 19.7±1.1 | 0.7±0.2 | 0.3±0.2 |
| Foreign | SFI4 | 1 | 64±9.7 | 19.9±1.1 | 0.8±0.2 | 0.3±0 |
| Mediterranean coniferous | SFI3 | 0 | 19.2±13.5 | 24.3±1.5 | 1.4±0.4 | 0.1±0.1 |
| Mediterranean coniferous | SFI3 | 1 | 26.3±20.7 | 24±1.2 | 1.3±0.4 | 0.1±0.1 |
| Mediterranean coniferous | SFI4 | 0 | 29.8±21.9 | 24.1±2.6 | 1.6±0.5 | 0.1±0.1 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Mediterranean coniferous | SFI4 | 1 | 32.9±21.5 | 24.1±1.9 | 1.6±0.4 | 0.1±0.1 |
| Atlantic coniferous | SFI4 | 0 | 69.2±51.8 | 19.1±1.3 | 0.7±0.2 | 0.4±0.3 |
| Atlantic coniferous | SFI4 | 1 | 56±34 | 19.3±0.9 | 0.6±0.2 | 0.3±0.2 |
| Mediterranean deciduous | SFI3 | 0 | 25±14.3 | 22.3±2 | 1.2±0.3 | 0.1±0.1 |
| Mediterranean deciduous | SFI3 | 1 | 30±25.8 | 23.2±1.4 | 1.4±0.5 | 0.1±0.1 |
| Mediterranean deciduous | SFI4 | 0 | 26.4±25.3 | 21.3±3.3 | 1.3±0.7 | 0.1±0.1 |
| Mediterranean deciduous | SFI4 | 1 | 30±34.3 | 21.1±3.6 | 1.2±0.7 | 0.2±0.2 |

Table S2. Results of the GLM models for the relative tree carbon losses by forest type and SFI period. For each model effects, total variance explained ($R^2$) and coefficient and significance levels (ns > 0.05, $*$ $p < 0.05$, $**$ $p < 0.01$, $***$ $p < 0.001$) of the variables retained are given.

| | Temperate deciduous | Atlantic coniferous | Mediterranean coniferous | | Mediterranean deciduous | Sclerophylls | | Foreign |
|---|---|---|---|---|---|---|---|---|
| Period | SFI3-4 | SFI3-4 | SFI2-3 | SFI3-4 | SFI3-4 | SFI2-3 | SFI3-4 | SFI3-4 |
| RdNBR | 0.1±0 ns | | 0.1±0 ** | | | | | 0.1±0 ns |
| Surface wildfire | | 0.1±0.1 ns | | | | 0.1±0 ns | | |
| Slope | | | -0.1±0 ns | | | -0.1±0 ns | | |
| Aspect | | -0.7±0.4* | | -0.9±0.4* | | | | |
| VPD | | | | | | -0.6±0.3 * | | |
| Moisture | | | | -3.4±1.3** | | | | |
| Hotspot | | | | 1.3±0.5* | -0.1±0.2 ns | | | |
| $R^2$ (%) | 0.2 | 48.2 | 24.3 | 38.1 | 0.1 | 14.5 | - | 17.27 |

Table S3. Total carbon (Mg/ha) by forest group and SFI survey and hotspot condition (0-non hotspot, 1-hotspot) and their relative proportion.

| Forest group | SFI | hotspot | Total carbon | % |
|---|---|---|---|---|
| Sclerophylls | SFI2 | 0 | 54298.83 | 51.00 |
| Sclerophylls | SFI2 | 1 | 52151.16 | 48.99 |
| Temperate deciduous | SFI2 | 0 | 105657.6 | 55.54 |
| Temperate deciduous | SFI2 | 1 | 84578.2 | 44.45 |
| Mediterranean coniferous | SFI2 | 0 | 211521.5 | 47.43 |
| Mediterranean coniferous | SFI2 | 1 | 234369.5 | 52.56 |
| Mediterranean deciduous | SFI2 | 0 | 49591.51 | 42.76 |
| Mediterranean deciduous | SFI2 | 1 | 66374.36 | 57.23 |
| Temperate coniferous | SFI2 | 0 | 122528.2 | 51.60 |
| Temperate coniferous | SFI2 | 1 | 114907.4 | 48.39 |
| Atlantic coniferous | SFI2 | 0 | 52697 | 59.58 |
| Atlantic coniferous | SFI2 | 1 | 35750 | 41.80 |
| Foreign | SFI2 | 0 | 52752 | 57.31 |
| Foreign | SFI2 | 1 | 39280.1 | 42.68 |
| Sclerophylls | SFI3 | 0 | 66744.37 | 43.16 |
| Sclerophylls | SFI3 | 1 | 87867.50 | 56.83 |
| Temperate deciduous | SFI3 | 0 | 114969.8 | 47.74 |
| Temperate deciduous | SFI3 | 1 | 125807.3 | 52.25 |
| Mediterranean coniferous | SFI3 | 0 | 239608.8 | 39.58 |
| Mediterranean coniferous | SFI3 | 1 | 365706.9 | 60.41 |
| Mediterranean deciduous | SFI3 | 0 | 56625.92 | 36.78 |
| Mediterranean deciduous | SFI3 | 1 | 97308.17 | 63.21 |
| Temperate coniferous | SFI3 | 0 | 142845.6 | 45.31 |
| Temperate coniferous | SFI3 | 1 | 172349.2 | 54.68 |
| Atlantic coniferous | SFI3 | 0 | 49236.8 | 58.19 |
| Atlantic coniferous | SFI3 | 1 | 35364.6 | 41.80 |
| Foreign | SFI3 | 0 | 74355.1 | 54.32 |
| Foreign | SFI3 | 1 | 62512.5 | 45.67 |

# Capítulo 4

## Forest degradation in Spanish forests: changes in canopy cover in the last decades.

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# Forest degradation in Spanish forests: changes in canopy cover in the last decades.

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## Abstract

Forest expansion has been a trend in Europe in the last decades due to rural abandonment in contrast with the deforestation of tropical countries. But degradation is harder to measure than deforestation and we do not have measures at country scale either over time in European forests. In this work, we used LiDAR to measure forest expansion and degradation across Spanish forests over time to know the level of degradation at detailed scale. We obtained the forest canopy cover, gaps and leaf area density (LAD) from three consecutive LiDAR flights over time (2008-2025) and across Spanish forests using the last two National Forest Inventory plots. Forests were classified in five forest types and forest cover was used as measured of expansion and gaps and LAD were integrated as a measure of forest degradation. The number of forest plots per level of expansion and degradation and their changes over time were calculated. Climatic variables were calculated to know if they were drivers of expansion or degradation. Results indicate that there was a generalized increase of the forest cover (expansion) across forest types and time periods but also an increase in the degradation (around 20% of the Spanish forests). Greater degradation occurred for any forest type except for Temperate deciduous species. Climatic variables did not show a good performance then they are not the source of the greater degradation in the Spanish forests. In summary, we have shown that in the Spanish forests degradation has increased greatly in recent years even in a context of continuous forest expansion, indicating that the state of forests is probably worse than suggested by the low mortality rates registered until now.

**keywords:** climate, degradation, expansion, forest, gaps, LiDAR

## Introduction

During the last decades, forests in many Northern Hemisphere countries have mainly expanded due to the abandonment of traditional practices such as livestock grazing and wood extraction (Garbarino et al., 2020; Navarro & Pereira, 2012; Palmero-Iniesta et al., 2021). Thus, the forest area in Europe has increased by 25% on average since the mid-20th century (Fuchs et al., 2015). Moreover, as an additional consequence of this abandonment, different studies have shown a generalized increase in forest tree size and density in recent decades (Mönkkönen et al., 2022; Spiecker et al., 2012; Vayreda et al., 2012). On the contrary, in other regions of the world, such as tropical forests, forest loss has been highlighted, with tropical deforestation realizing 1-2 billion tons of carbon per year (Pearson et al., 2017). These studies on deforestation are frequent, since forest deforestation is easily estimated with remote sensing products like satellite images across

spatial and temporal scales (Joshi et al., 2015). In contrast with these tropical regions, deforestation is not common in Europe, which explains the local expansion of forests in the region.

Another process directly related to forest loss but much less known is forest degradation. Although its importance has been highlighted for years, making it part of the proposed mechanism for reducing emissions from deforestation and forest degradation (REDD), the concept of forest degradation is much less clear, both from a scientific point of view and from its practical application. Existing definitions are based on a negative trend in land condition or a reduction in the production of ecosystem goods and services, but fail to address how, when and to what degree this reduction ultimately leads to degradation of a forest. Degradation is expressed as long-term reduction or loss of at least one of the following scopes: structure, species composition, biological productivity, ecological integrity, value to humans or functions upon which the vigor and resilience of a forest is based (Vásquez-Grandón et al., 2018). However, the practical application of this type of definition is limited, because there is no clear consensus on how to apply it. In the few cases where it has been measured, mainly in the tropics, forest degradation has been found a major source of greenhouse gas emissions by an order of magnitude similar to deforestation (Pearson et al., 2017).

As indicated above, forest degradation can be estimated in many ways, although stand structure changes, losses in species, and lack of regeneration are the most used (Dupuis et al., 2020). Changes in stand structure are measured through stand characteristics such as tree growth, canopy gaps, or tree attributes like leaf area, height, etc. While tree biomass has increased in European forests, canopy gaps and tree attributes are less well-known at large scales. Forest gaps are open spaces of variable size (from just a few to tens of square meters) within the tree canopy or between tree crowns. Small and medium gaps can occur naturally due to the partial or total death of canopy trees caused by disturbances such as droughts, pests or windstorms. Large gaps can occur through major disturbances such as fires or hurricanes. Canopy gaps are a natural process, and their presence alone is not an indicator of a degraded forest. However, their increase over time can indicate a decline in forest health, being a sign of forest degradation (Reis et al., 2022). Changes in tree characteristics such as defoliation can also indicate degradation. Changes in leaf area density (LAD; the total leaf area per unit of volume) is an indicator of tree growth and productivity and can be used to monitor forest degradation (Milodowski et al., 2021). Finally, the replacement or reduction of dominant tree or shrub species by others may be also a sign of degradation (Janssen et al., 2020), although successional processes in forests might be a confounding factor (Norden et al., 2015).

Monitoring stand structure changes through field measurements is expensive, but remote sensing techniques such as LiDAR can detect these changes at a fine scale of a few square meters. Repeated LiDAR data over time allow for the analysis of stand structure changes and the detection of trends such as the dominant height of vegetation, allowing the identification of tree cover expansion or decline at local and regional scales (Guo et al., 2017; Ucar et al., 2018). Moreover, it can detect finer-scale stand structure changes in gaps or LAD, which can serve as indicators of forest degradation due to natural canopy decline or disturbances. Previous studies have analysed vegetation cover (Guo et al.,

2017; Ucar et al., 2018), forest gaps (Krüger et al., 2024), and LAD (Kamoske et al., 2019; Milodowski et al., 2021) using LiDAR, but mostly at small regional scales or only in specific regions at big scale (Reis et al., 2022). Nevertheless, there is still a lack of knowledge about fine-scale stand structure changes at larger scales that can be indicators of degradation, such as national-level assessments, where multiple combinations of forest types, climate and structural characteristics may interact. In these cases, remote sensing can be combined with national forest inventories where forest species composition and many structural variables are measured across the country.

In this work, we aim to assess forest degradation in Spanish forests analysing changes in stand structure and canopy using LiDAR and the national forest inventories. Spanish forests have expanded spatially in recent decades (Améztegui et al., 2010), and tree size has increased (Vayreda et al., 2012) due to the partial abandonment of forest management. Nevertheless, although there is an increased mortality (Natalini et al., 2016; Prieto-Recio et al., 2015; Sánchez-Cuesta et al., 2021) and defoliation (Navarro-Cerrillo et al., 2022; Prieto-Recio et al., 2015) has also risen in recent years, there are not information about forest degradation in the whole country. We ask the following questions: 1) how has forest degradation in Spanish forests changed in recent decades, overall and by forest types? 2) What are the effects of climate, stand structure and forest types on these changes? Specifically, we aim to explore potential differences in forest degradation across different forest types and regions within Spanish forests, as well as to understand the role of climate change and stand structure as drivers of forest degradation.

## 2. Material and methods

### 2.1. Forest inventory data

We carried out our study in the forested areas of Spain, excluding the Canary Islands. We used the permanent field plot data from the Spanish National Forest Inventory (SFI) to characterize tree species composition and stand structure variables across the study area. The SFI covers the forested areas of Spain with a density of ~1 plot/km². SFI field plots have four concentric circular sub-plots with radii of 5, 10, 15, and 25 m. Trees were identified and measured within variable circular size plots (5 m radius for trees with diameter at breast height (DBH) ≥ 7.5 cm, and trees with 2.5 ≤ DBH ≤ 7.5 cm were counted; 10 m radius for trees with DBH ≥ 12.5 cm; 15 m radius for trees with DBH ≥ 22.5 cm; and 25 m radius for trees with DBH ≥ 42.5 cm). We used the plots of the fourth inventory (SFI4) carried out from 2009 to 2024 to calculate the basal area and selected plots with more than 70% of basal area of one species corresponding to the dominant native tree species. We classified each plot according to this dominant tree species into five forest functional groups: Temperate deciduous (e.g., *Fagus sylvatica*, *Quercus robur*), Mediterranean deciduous (e.g., *Quercus pyrenaica*), Temperate coniferous (e.g., *Pinus sylvestris*), Mediterranean coniferous (e.g., *Pinus halepensis*), and Sclerophylls (e.g., *Quercus ilex*). We removed plots with evidence of human management or loss due to recent natural disturbances. Overall, we selected 19,224 permanent forest plots sampled in the Spanish forest inventory (see Figure S1 for plot distribution across Spain): 2,347 Temperate deciduous; 1,523 Mediterranean deciduous; 2,932 Temperate coniferous; 6,228 Mediterranean coniferous and 6,194 Sclerophylls.

### 2.2. LiDAR data

LiDAR data were downloaded from the PNOA-LiDAR Spanish project through the Instituto Geográfico Nacional website. The PNOA-LiDAR project is an Airborne laser scanning that covers the Spanish territory. Three flights in 2008–2015, 2015–2021, and 2021–2025 were performed, and the point cloud had a point density of about 0.5, 1.5, and 5 points/m², respectively. LiDAR data were distributed in 2 × 2 km tiles for the first flight and 1 × 1 km tiles for the second and third flights. LiDAR tiles covering the SFI plots were downloaded for each flight. We extracted the LiDAR point clouds around the center of every SFI plot in a radius of 25 m (~1964 m²), since it is the maximum radius of the plot in the SFI.

A digital elevation model (DEM) of 1 $m^2$ resolution was generated from filtered ground returns and used to normalize the height of the returns in each flight. Then, we created a canopy height model (CHM) from the normalized data at 1 $m^2$ resolution. We classified the CHM pixels into two cover types according to the height: understory vegetation corresponding to ground-shrubs (height<3 m) and overstory vegetation corresponding to trees (height> 3 m). We calculated the percentage of vegetation cover for the two types by flight in each SFI plot. We classified the CHM pixels of ground-shrubs as gaps when the pixels were surrounded by pixels classified as tree cover (see example in Figure 1). All the pixels of adjoining gaps were gathered in a singular gap element.

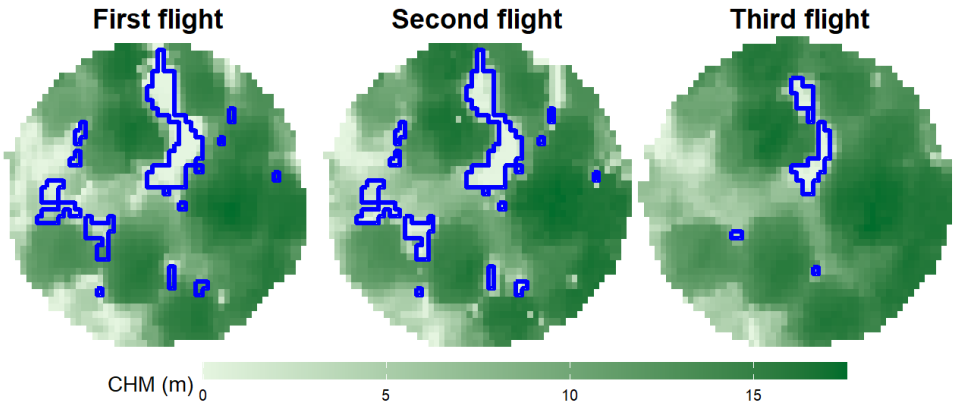



Figure 1. Canopy Height Model of a SFI plot in the three LiDAR flights. Canopy gaps detected are indicated with blue lines.

We calculated the gap cover (%) as the sum of the gap areas divided by the total area of gaps and tree cover combined. If there is an increase in the tree cover it is more likely to contain more gaps due to having more canopy available. Then, we used the gap cover as a percentage to assess the relative extent of gaps rather than their absolute area, since larger forest areas are more likely to contain gaps.

We estimated the LAD ($m^2/m^3$) with the method of Bouvier (Bouvier et al., 2015). This method assesses the number of laser points that reached the layer z+dz (being z a vector of positive z coordinates and dz the thickness of the layers used) and those that passed through the layer [z, z+dz]. Then it computes the log of this quantity and divides it by the extinction coefficient k as described in Bouvier et al. (2015). Since layer 0 (the ground) always returns infinity, it is removed from the results. LAD is calculated in 1-m slices from 3 m height above the ground up to a maximum. To avoid biases in the LAD calculation, we homogenized the second and third LiDAR flight with the first flight reducing the point cloud to 0.5 points/m². We processed the LiDAR data

with the "lidR" R package (Roussel et al., 2020). We calculated the average LAD per SFI plot and LIDAR flight from the LAD slices.

We calculated the average mean of forest cover, gap cover and LAD by forest functional group and by LiDAR flight. We calculated the difference of forest cover, gap area and LAD between flights to obtain the change over time in each SFI plot in the two periods between flights, 1-2 (P1-2) and 2-3 (P2-3). As the dates of the flights varied by region and flight, we divide the absolute changes of these three variables by the number of years between flights. We calculated the median of change of forest cover, gap cover and LAD of each forest functional group. We used the 10% around the median as the threshold to classify the plots that did not change (neutral) over time. Then, the SFI plots with increasing or decreasing values bigger than the 10% of the median were considered as SFI plots with forest development or degradation in that period, respectively. By functional groups and periods, we calculated the number of plots maintained, decreased or increased forest cover, gap area and LAD.

For the forest cover we classified the plots into three categories of canopy expansion. We used the 10% around the median as the threshold to classify the plots that did not change (neutral) over time. Then, the SFI plots with increasing or decreasing values bigger or smaller than 10% of the median were considered as SFI plots with forest cover increase or decrease in that period, respectively. For the gap cover and LAD we combined both variables because they are indicators of the quality of the canopy: more gap cover and less LAD are indicators of canopy degradation, and vice versa, less gap cover and more LAD are indicators of canopy development. We created 5 classes of gradient between degradation and development using a combination of gap cover and LAD: Degraded: increase gap-decrease LAD; Slightly degraded: increase gap-neutral LAD or neutral gap-decrease LAD; Neutral: neutral gap-neutral LAD or increase gap-increase LAD or decrease gap-decrease LAD; Slightly developed: decrease gap-neutral LAD or neutral gap-increase LAD; Developed: decrease gap-increase LAD.

### 2.4. Forest degradation drivers

We extracted climatic data from ERA5-Land Daily data (temporal range of 2008–2025) at 0.1°x 0.1° (~9 km) (Muñoz Sabater et al, 2024). Specifically, we downloaded: Temperature of air at 2 m above the surface of land, annual precipitation and potential evapotranspiration (PET, mm/year). We average the daily data of temperature, precipitation and PET in a mean annual data from the range 2008-2025. We also calculated the mean annual moisture index as the ratio between the precipitation and PET and the mean annual SPEI index with the R package SPEI (Begueria et al., 2017).

### 2.6. Statistical analysis

We carried out two-way ANOVA tests to analyze the effects of the LiDAR flight and forest type and their interaction on forest expansion (forest cover) and degradation (gap area and LAD). Where the ANOVAs were significant, we did a post-hoc Tukey's test for pairwise comparisons.

We carried out an ordered logistical regression (OLR) model with the five factor categories of degradation as response variable. We did the OLR for each period of change (first-second flight and second-third flight). Then, we calculated the mean annual values of the climatic variables (Temperature, Precipitation, Moisture and SPEI index) within the interval between the flights (see the summary in Table S1). We used these climatic

variables as predictors together with the basal area of the plot. The OLRs were did with the "MASS" R package (Ripley et al., 2013). All network analyses were conducted in R v. 4.1.1

## 3. Results

### 3.1. Forest cover and degradation

Forest cover showed a generalized increase (Figure 2) in most plots, which values around 40% of increased in all the forest types, from 82% of plots in the Temperate deciduous to 91% in the Mediterranean deciduous and from 83% in the Temperate deciduous to the 89% in the Mediterranean deciduous between the second and third flight (Figure S2). Although this increment showed lower value over time. Nevertheless, the Decreased class was very low (around 10%) but also it was lower over time, indicating that Neutral was the class that increased the most overtime.

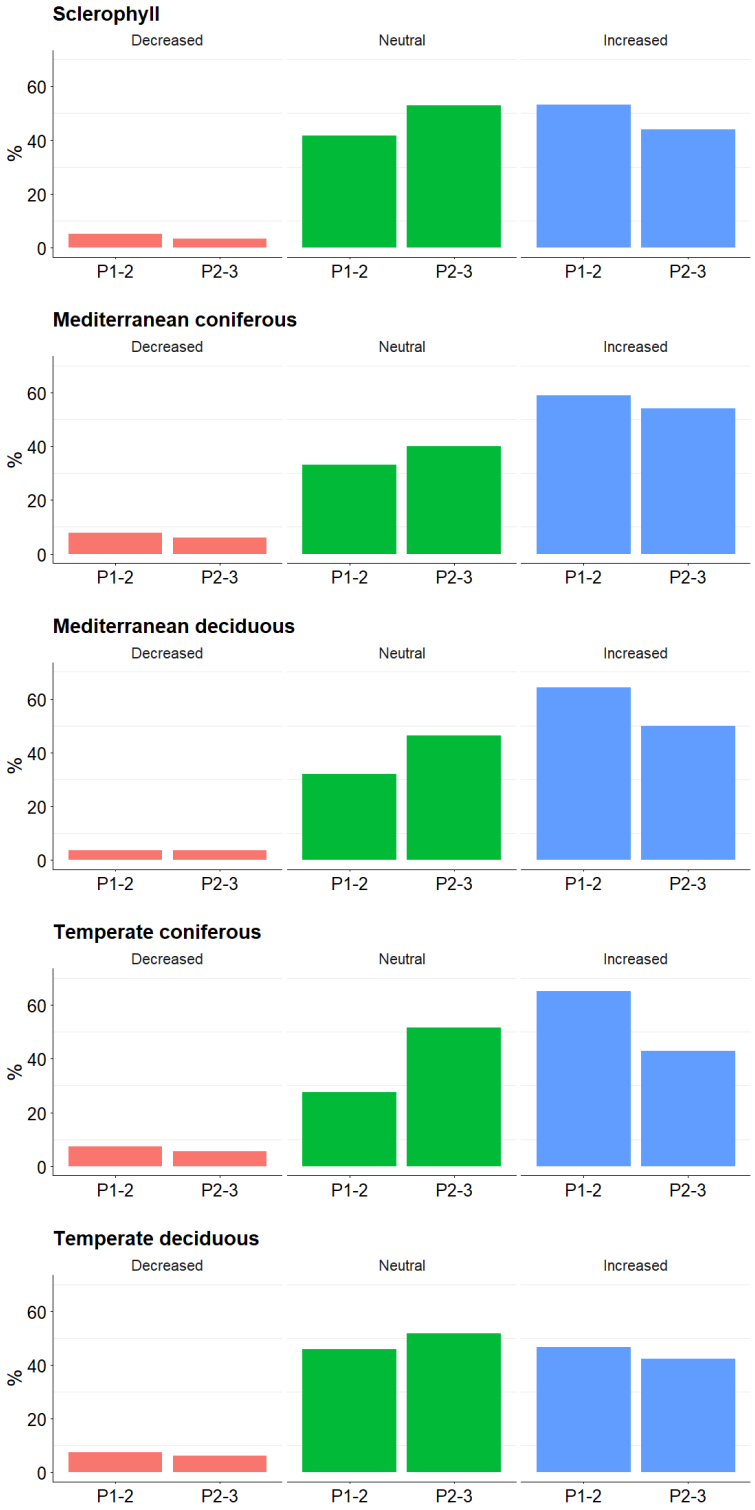



Figure 2. Percentage of SFI plots with decreased (decreasing forest cover), neutral (similar forest cover) and increased (increasing forest cover) by forest functional group and period.

Concerning degradation categories (Figure 3), forests Degraded was greater in the Sclerophylls in the first period (around 15-20% of the plots) followed by the Temperate deciduous and Mediterranean deciduous and coniferous (around 15%) and Temperate coniferous has the lowest

values (below 10%). In the second period all the forest increased except for the Temperate deciduous that decreased. Coniferous forests showed a greater increase to 20%. The forest Slightly degraded were the Mediterranean forest (around 15%) followed by the rest (around or below 10%). All the forest groups decreased in the second period by 3-5%. The Neutral forests represented the category with higher values, and they increased between the first and second period between 28-40% to 40-50%. The forest Slightly developed represented between the 10-15% in the forest groups in the first period and it decreased to around 5-10% in all the groups. Finally, the forests Developed increased in the Sclerophylls and Mediterranean deciduous (12% to 13% and 18 to 23%), but it is decreased in the Mediterranean (15% to 12%) and Temperate coniferous (29% to 18%) and Temperate deciduous (32% to 30%).

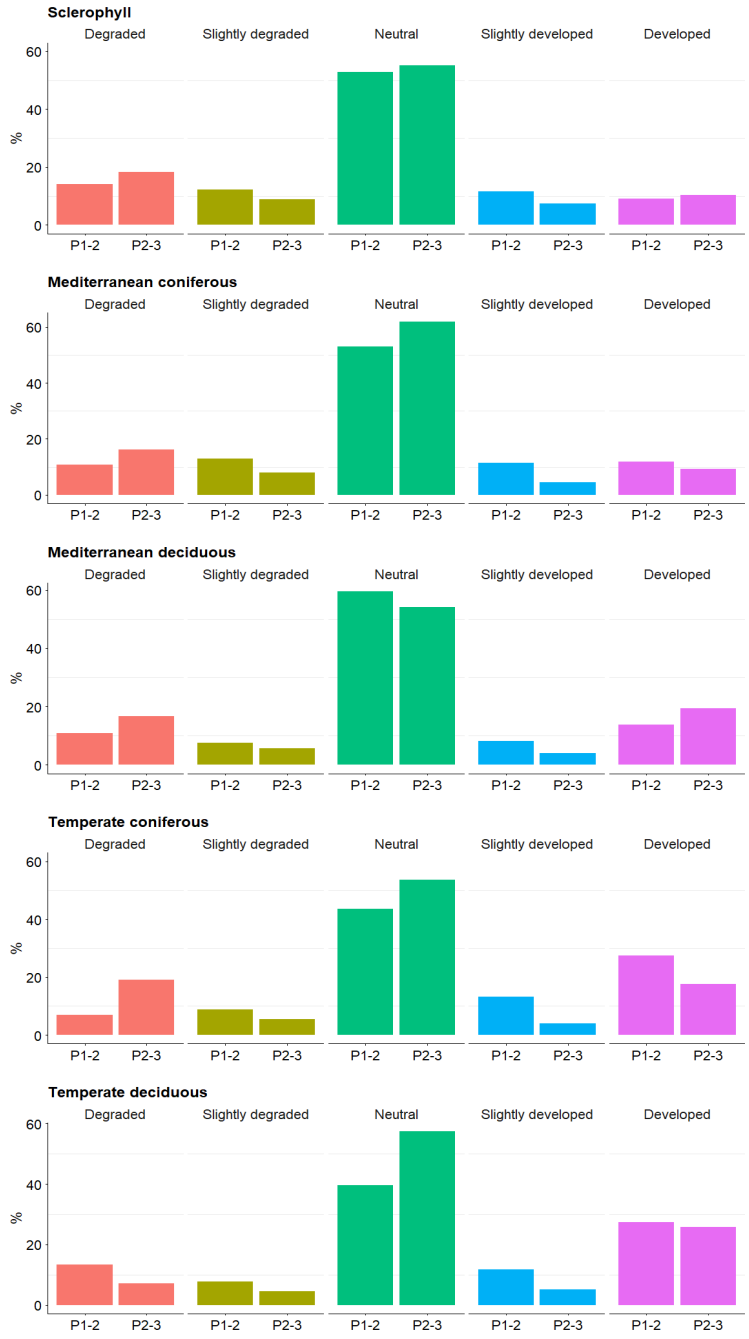



Figure 3. Percentage of SFI plots with degradation (increasing gap area and decreasing LAD), neutral (similar gap area and LAD) and developed (decreasing gap area and increasing LAD) by forest functional group and period.

There were significant differences among forest types and flights for forest development (forest cover) and degradation (gap cover and LAD) (Table 1). Thus, forest cover per plot showed a continuous increasing in all forest groups (from mean±standard deviation 44.8±29.3% in flight 1 to 51.6±29.2 and 55.2±28.8% in flights 2 and 3, respectively) with the Temperate deciduous forests having the highest forest cover (76.2±24.5%) followed by Temperate coniferous, Mediterranean deciduous and Mediterranean coniferous and Sclerophylls with the lowest value (37.6±25.7%). The interaction between the two factors was not significant (Table 1), indicating that the increase through flights was similar in the five forest types (Figure 4A).

Table 1. Two-way ANOVA tests of the effects of forest type, flight and their interaction on forest cover, gap cover and LAD. F values and significance levels (ns > 0.05, ∗ p < 0.05, ∗∗ p < 0.01, ∗∗∗ p < 0.001) are given for each test.

| Variable | Forest type | | Flight | | Forest x Flight | |
|---|---|---|---|---|---|---|
| Forest cover | 919.9 | *** | 256.9 | *** | 1.3 | ns |
| Gap cover | 284.2 | *** | 19.2 | *** | 26.9 | *** |
| LAD | 391.3 | *** | 126.8 | *** | 5.7 | *** |

Concerning gap cover, the two factors and their interaction were significant (Table 1). Thus, there was an increase from the first (3.4±4.2%) to the second flight (3.7±4.2%) but a decrease from the second to the third flight (3.4±4.0%). The forest type with the highest value of gap cover was Temperate coniferous (4.3±4.2%) followed by Mediterranean coniferous, Mediterranean deciduous, Temperate deciduous and Sclerophylls with the lowest value (2.3±3.5%) (Figure 4B). The average percentage of gaps showed an increase between the first and second flight and maintenance between the second and the third flight in Mediterranean coniferous, Mediterranean deciduous and Sclerophylls, but a maintenance between the first and the second flight and a decrease in the third flight in the two temperate forest types (Figure 4B).

In the LAD analysis, the two factors and their interaction were also significant (Table 1). LAD per plot was similar in the first two flights but decreased in the third one (Figure 4C). This variable was highest in Temperate deciduous and Temperate coniferous forests (0.12±0.07 and 0.11±0.06 $m^2/m^3$, respectively) and lowest in the Mediterranean coniferous and the Sclerophylls (0.08±0.06 in the two cases). The interaction between the two factors was significant: Temperate deciduous and Mediterranean deciduous increased from the first to the other two flights, while the other three groups decreased in the third flight (Figure 4C).

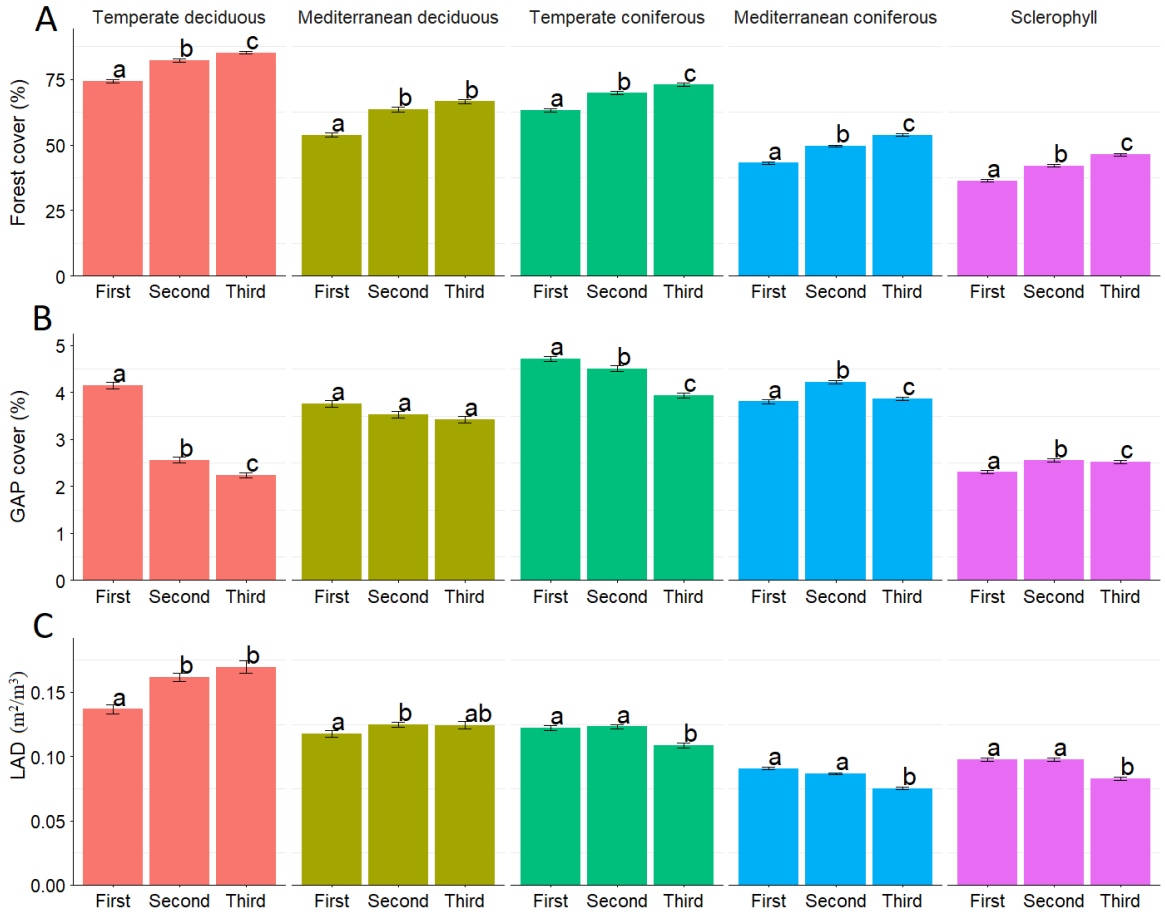



Figure 4. Mean (±standard error) values of forest cover (A), gap cover (B) and LAD (C) in the three LiDAR flights and the different forest types. Different letters denote significant differences among flights ($p$< 0.01) after Tukey's test.

### 3.2. Driver analysis

ORL models had very low $R^2$ (< 1%) indicating that the climatic and stand basal area change had a very low predictive power in the degradation changes. Temperature was the only significant predictor in the two periods, while SPEI index was also significant in the second period (Table 2).

Table 2. Results from the ORL models conducted for each flight period. R-Squared of the model (in brackets), coefficients, standard deviation and significance levels (ns > 0.05, * $p$ < 0.05, ** $p$ < 0.01, *** $p$ < 0.001) of the variables are displayed.

| | First period (0.13%) | Second period (0.12%) |
|---|---|---|
| Tmean | -0.23±0.05*** | 0.15±0.06** |
| Moisture | -0.00±0.02 ns | 0.03±0.03 ns |
| Prcp | -0.08±0.03 ns | 0.07±0.06 ns |
| Basal area | 0.08±0.03 ns | 0.19±0.04 ns |
| SPEI | 0.00±0.04 ns | 0.51±0.03 *** |

## 4. Discussion

Our results indicate that forest canopy cover has increased during recent years in Spanish forests across all functional groups and across the country (Figure 2 and Figure 4A). This generalised increase in canopy cover may be related to the growth of the forest after the abandonment of traditional human activities, such as firewood extraction or livestock grazing (Garbarino et al., 2020; Navarro & Pereira, 2012; Palmero-Iniesta et al., 2021). Our results are consistent with other works at the landscape scale that showed an increase in afforestation in Spanish (Ameztegui et al., 2010) and European forests (Palmero-Iniesta et al., 2021). Moreover, we have showed how the loss of forest canopy cover is very reduced in Spanish forests (< 10% of SFI plots) and did not increase, even reduces, over time. European forests have been historically deforested for human activities, and Spain for instance had a reduced extension of forests in the first decades of the 20$^{th}$ century with short and scattered trees (Valbuena-Carabaña et al., 2010). In this context of deforestation and small trees, Spanish forests have had the possibility to grow because there was a lot of space available. Nevertheless, we observed that there is a lower forest cover growth in the second period in comparison with the first flights (Figure 2). The increase of forest cover will be also increasing the tree competence among them and the forest cover growth will be each time lower. Temperate deciduous for instance show a very limited growth since their forest cover is already very high (> 90%) indicating that they are almost in a stage of competition more than growth (Figure 4A). Mediterranean forests have a lower forest cover (< 60%) then they can growth more in the next decades.

Despite this expansion of canopy cover throughout Spain and in the different types of forest, there has also been a degradation of part of this canopy. We measured the degradation as the decline of the quality of the canopy cover by their leaf density and the size of their gaps, being both indicators of stand productivity and health (Reis et al., 2022; Milodowski et al, 2021). In tropical countries, forest degradation is mainly derived from a bad exploitation such as excessive harvesting for timber or firewood (Hosonuma et al., 2012). An increase in the canopy gaps has been observed with multitemporal LiDAR at small scale in forests where there is logging exploitation (Rangel Pinagé et al., 2019). But in contrast with tropical forest where the degradation is conducted by loggings and there are larger canopy gaps (Rees et al., 2022), in Central Europe there is closure of the canopy gaps due to the abandonment of forest management (Krueger et al., 2024). In Spanish forests, mean gap cover showed both increases and decreases in recent years, whereas the LAD showed a decrease in the last flight (Figure 4B and 4C, respectively). However, the combination of both variables showed that forest degradation doubled in the number of plots during recent years affecting approximately 20% of Spanish forests (Figure 3). This increment of forest degradation is generalized across all forest functional groups except for Temperate deciduous.

Temperate deciduous was the only group with low canopy degradation values. Although Temperate deciduous species (*Fagus sylvatica* and *Quercus robur* mainly) are in the Spanish peninsula in their southern edge of their European distribution. These deciduous species have showed a bigger growth vulnerability to drought in their edge distribution in Spanish forests (Rozas et al., 2015) and climate niche predictions predict a future regression in the Spanish Peninsula (Serra-Diaz et al., 2012). Nevertheless, we have showed how they are increasing their canopy cover and they are not having symptoms of degradation for the period analysed. The niche of the species at the edge can be hard to model (Thuiller et al., 2003) and they can adapt well in the edge distribution by microenvironmental conditions as topographic characteristics (Rozas et al, 2015). Moreover, there has been an expansion of these temperate species in both the warm and dry and the cold and wet edges in Spain (Padullés Cubino et al., 2024; Vayreda et al., 2016). These Temperate deciduous species suffered in the paste a historical deforestation (Valbuena-Carabaña et al., 2012), and they are now recovering their original distribution (Padulles et al. 2024, Vayreda et al., 2016).

In contrast, Mediterranean forest types, together with Temperate coniferous, have showed a bigger degradation. Mediterranean forests have showed a greater defoliation and mortality in recent decades (Natalini et al., 2016; Sánchez-Salguero et al., 2012) and Temperate coniferous (mainly *Pinus sylvestris*) also have showed a decline in their regeneration and higher defoliation in Spain (Vilà-Cabrera et al., 2013). Nevertheless, the ORL models did not show that climate change had any effect on forest degradation for the period analysed (Table 2). Although climate change has been pointed out as a driver of tree mortality in Spanish forests (Prieto-Recio et al., 2015; Sánchez-Cuesta et al., 2021), forest degradation is a different symptom, since these forests have shown that they maintain their capacity for canopy growth, albeit with a more degraded tree canopy. Climate change in Spain has showed a positive trend in temperature (Brunet et al., 2007) but not a decline in precipitation in the long term in the Mediterranean region (Peña-Angulo et al., 2020). Also, precipitation have not showed a change in their torrentiality (Serrano-Notivoli et al., 2018) and the occurrence of droughts has not showed a positive effect on increasing degradation, since there are forests with severe droughts where there was not degradation, and forests without drought with greater degradation. Thus, macroclimate (temperature, precipitation or derived variables) is a poor predictor of canopy degradation, which is perhaps determined more by local environmental predictors such as soil depth, nutrient and ground water availability, or by small disturbances (windstorms, pest, etc) that we cannot monitor at a large scale due to the lack of accurate data in forest inventories. For instance, canopy gaps can increase and leaf area decline after windstorms (Chang et al., 2020; Liu et al., 2020) and insect pests (Perry et al., 2018; Solberg et al., 2006).

Surprisingly, this forest degradation is linked with a greater expansion of forest canopy cover. This result means that forests are occupying more space with their canopies, but their crowns are less dense (less LAD) and/or have more gaps inside or between neighbouring canopies. Less LAD could be interpreted as more defoliation and more gaps as partial dead of trees or branches (some parts of the canopy die). This simultaneous expansion and degradation indicate that Spanish forests have not lost their capacity for growth over the years, but that they are showing symptoms of degradation in their canopy structure. If this situation persists in the future, it could mean less vigour, less growth capacity and, ultimately, less ability to respond to extreme weather events, such as droughts or pests, in the future.

There are, of course, limitations of the novel study. In this work we have evaluated forest degradation through canopy measures of forest cover, gap cover and LAD. They are valuable field measures, and they can be indicators of forest degradation, but there is no doubt that it is only one aspect of forest degradation: the degradation process can reach a lot of biological processes like lack of tree regeneration, species replacement, ecosystem services productivity and others (Vásquez-Grandon et al. 2018). Moreover, the time window studied in this work is relatively short (around 15 years) as we cannot know if the trend observed in this work will be sustained in the next decades. Nevertheless, we highlight the utility of analyzing the concept of forest degradation through field measures of forest cover, gap cover and LAD across a country scale and over time.

## 5. Conclusions

Spanish forest has showed a generalized increase in their canopy cover but also a bigger degradation in the canopy. This increase of canopy degradation was observed in all Spanish forest types except the Temperate deciduous. We show in this study that climate change did not have an effect in this canopy degradation. We also show how the expansion and degradation can be easily monitored at country scale and over time with LiDAR, measuring forest canopy cover, gaps and LAD without expensive stand field surveys that can be unfordable at country scale. This one of

the first works at large scale about forest canopy degradation with high spatial resolution data (1 $m^2$) and their combination with forest inventory data can supply information of forest degradation across forest types and regions in a continuous monitoring over time. We have showed that in the Spanish forests degradation have increased greatly in the recent years even in a context of forest expansion, indicating that the state of forests is probably worse than the one suggested by the low mortality rates registered until now (Coll et al., 2013; Vayreda et al., 2013)

## Author Contributions

**Jesús Sánchez Dávila:** conceived the research idea and design and wrote the manuscript with the support of the rest of the authors. All authors discussed the results and edited the manuscript

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**Data Availability Statement**

Spanish forest inventory data are available at https://www.miteco.gob.es/es/biodiversidad/temas/inventarios-nacionales/inventario-forestal-nacional/. LiDAR data can download in: https://pnoa.ign.es/web/portal/pnoa-lidar/productos-a-descarga

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## Supplemental material

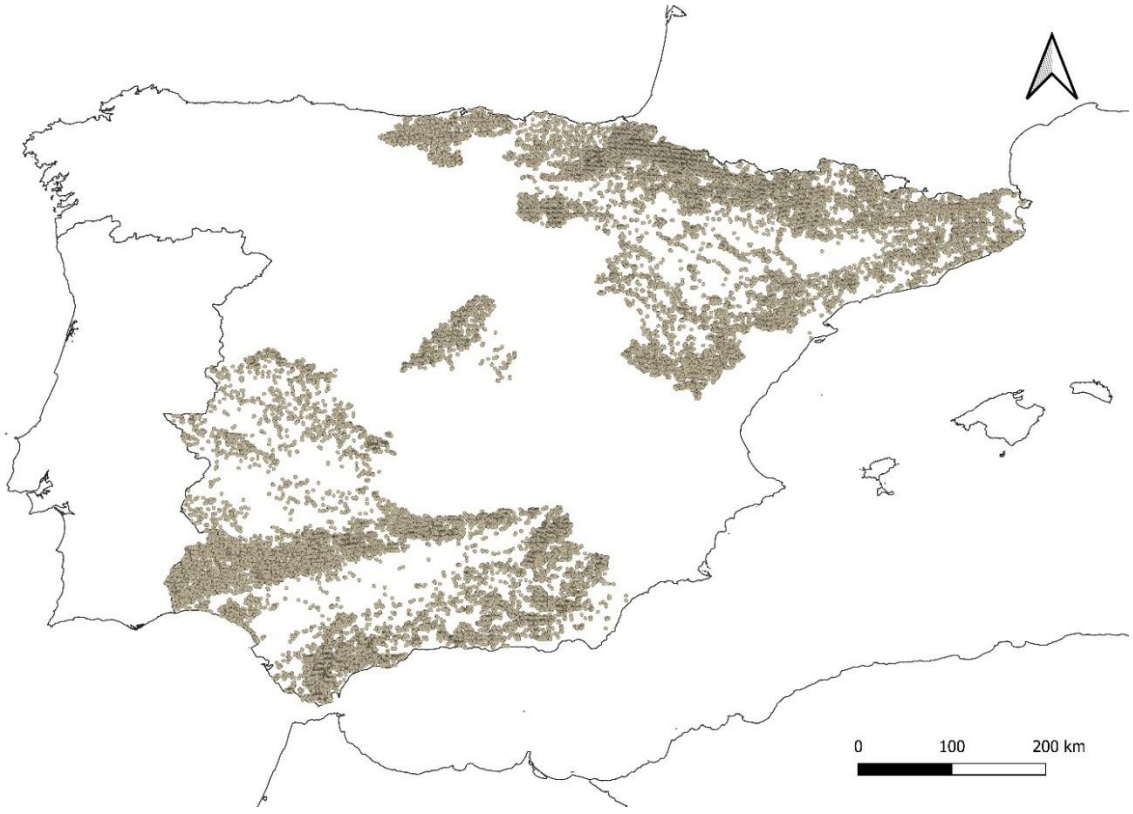



**Figure S1.** Distribution of the SFI plots analyzed across Spain.

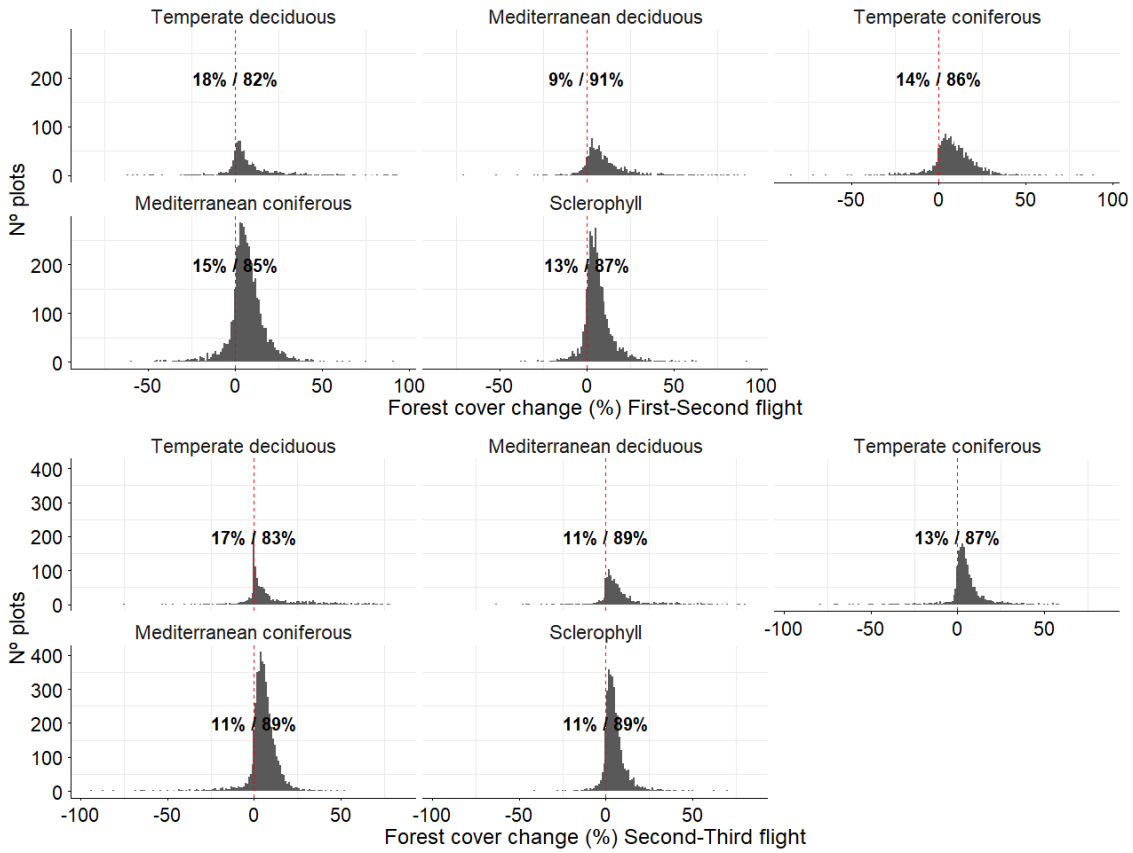



**Figure S2**. Histogram of forest cover change by LiDAR flight and forest types with negative/positive changes in percentage of plots.

**Table S1.** Average annual mean climatic variables per forest types and period (P1-P2: interval between first and second LiDAR flight and P2-P3 between second and third flight).

| | Temperature (ºC) | | Precipitation (mm) | | Moisture index | | SPEI | |
|---|---|---|---|---|---|---|---|---|
| Forest types | P1-P2 | P2-P3 | P1-P2 | P2-P3 | P1-P2 | P2-P3 | P1-P2 | P2-P3 |
| Temperate deciduous | 10.6 | 11.1 | 1219 | 1155 | 2.43 | 2.44 | 1.40 | 1.26 |
| Mediterranean deciduous | 12.3 | 12.4 | 807 | 790 | 0.83 | 0.74 | 0.29 | 0.25 |
| Temperate coniferous | 10.5 | 11.1 | 839 | 818 | 1.29 | 1.51 | -0.01 | -0.03 |
| Mediterranean coniferous | 13.6 | 14.2 | 569 | 574 | 0.42 | 0.48 | -0.24 | -0.23 |
| Sclerophylls | 14.9 | 15.1 | 600 | 590 | 0.48 | 0.48 | -0.27 | -0.31 |

# Conclusiones

En el primer capítulo de la tesis la modelización del ciclo hidrológico forestal en los bosques españoles muestra que el agua azul, tanto en valor absoluto como relativo, es mayor en las regiones húmedas de España, en los biomas atlántico y alpino. También se observa que la producción de agua azul se concentra en los meses de otoño-invierno mientras que el agua verde se concentra en primavera-verano. El Índice de Área Foliar (LAI) del bosque es la principal variable predictora del agua azul, teniendo una relación no lineal, ya que al aumentar el LAI disminuye el agua azul hasta alcanzar un valor más estable cuando el LAI es muy alto. Los bosques caducifolios presentan mayores cantidades de agua azul que los perennes (esclerófilas y coníferas) debido a la caída de la hoja en otoño-primavera, lo que reduce la interceptación del agua lluvia que es casi un tercio del agua evapotranspirada y porque dejan de transpirar durante este período. En conjunto, se muestra que hay un desacoplamiento en los componentes del ciclo hidrológico ya que el agua azul depende de la precipitación otoñal-invernal mientras que el agua verde depende de la demanda evaporativa de los árboles en los meses de primavera-verano.

En el segundo capítulo de tesis el análisis de los cambios del ciclo hidrológico forestal en los bosques españoles muestra que hay un incremento del agua verde y un decrecimiento del agua azul en las últimas décadas. El incremento del LAI de la vegetación debido al abandono de la gestión forestal muestra un efecto más importante que el cambio climático, ya que incluso en una década de crecimiento de precipitación (2000-2010), el aumento de demanda hídrica por el aumento del LAI sobrepasa la mayor disponibilidad de agua en el ecosistema. El aumento del LAI no solo se debe al crecimiento de los árboles sino también a los arbustos que muestran un aumento generalizado en todos los tipos de bosques. Cuando la precipitación disminuye en el periodo 2010-2020 el agua verde no se ve afectada y el agua azul sigue disminuyendo por un efecto combinado de menor precipitación y mayor LAI. La reducción de área basal, y por tanto de LAI, aumenta la producción de agua azul pero solo a corto plazo (10-15 años) ya que el crecimiento de los arbustos es muy rápido y el LAI vuelve a sus niveles originales muy rápido. Esto muestra que la gestión forestal, que es altamente costosa y difícil de aplicar si no se pueden macanizar los trabajos, es de poca utilidad para mantener valores elevados de agua azul ya que su efecto tiene una corta duración.

En el tercer capítulo de la tesis se muestra que el carbono perdido como consecuencia de los incendios ha disminuido en la última década respecto a la década anterior. Sin embargo, hay una diferencia marcada por tipos de bosques, mientras que ha disminuido en los bosques mediterráneos, ha aumentado en los bosques atlánticos, en particular en los pinares y los eucaliptales del noroeste. Los bosques que más carbono almacenan, los hotspots de carbono, no se ven particularmente afectados por los incendios excepto en los bosques mediterráneos de esclerófilas donde las perdidas en los hospots están sobrerrepresentadas y han aumentado ligeramente en las últimas décadas. Más de la mitad de los bosques españoles no muestra perdidas después de los incendios, y en el caso de los bosques caducos las pérdidas son mínimas, indicando de forma general que los bosques españoles tienen una gran resistencia a los incendios. Las variables climáticas o estructurales no tienen un patrón consistente de predicción, variando entre tipos de bosque y periodo analizado.

En el cuarto capítulo de la tesis sobre la monitorización de la degradación y expansión de los bosques españoles con LiDAR se muestra que los bosques se han expandido más pero también ha aumentado la degradación en la última década. Todos los tipos de bosque han aumentado su cubierta forestal, aunque hay una ralentización en los últimos años, probablemente porque el aumento de la competencia y la disminución del espacio limita el crecimiento de forma progresiva. La degradación también ha aumentado en todos los tipos de bosques, excepto en los bosques caducifolios atlánticos que se mantienen estables. Aunque los bosques caducos atlánticos están en el límite sur de su distribución europea se encuentran en una distribución disminuida de

su potencial distribución, por lo que incluso estando en los bordes puede que aun tengan potencial para aumentar su distribución sin mostrar síntomas de degradación. Los bosques mediterráneos y las coníferas templadas por contra tienen una degradación mayor, aunque el cambio climático o las variables forestales estructurales no explican el aumento de la degradación. El aumento de la degradación puede deberse a perturbaciones (tormentas, plagas) o condiciones (microclima, agua disponible en el suelo) locales de difícil medida a escala nacional.