# **Mediterranean forest resilience to**

# drought and climate change



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This dissertation is submitted for the degree of Doctor of Philosophy

## Declaration

This thesis is the result of my own work and includes nothing which is the outcome of work done in collaboration except as declared in the preface and specified in the text.

It is not substantially the same as any work that has already been submitted before for any degree or other qualification except as declared in the preface and specified in the text.

It does not exceed the prescribed word limit of 60,000 for the Biology Degree Committee.

Sacha Khoury April 2021

### **Summary**

### Mediterranean forest resilience to drought and climate change Sacha Khoury

Enhancing resilience to climate change is a key management goal for Mediterranean ecosystems. Typically, these management plans are based on ecological knowledge of species' tolerances derived from local studies limited in time and space. Remote sensing provides opportunities to study resilience over larger scales, but the tools needed to quantify the resilience of forests to drought and evaluate the effectiveness of management plans remain limited. This thesis examines how freely available satellite data can be used to quantify changes in forest canopies in response to climate variability. Using a combination of time-series and break-point analyses of satellite imagery I resolve limitations in forest resilience estimation and show that, for Spanish woodlands, the relative water availability during and following drought events are important in driving the canopy greenness loss and recovery. I show that despite increasing aridity, and examples of localised die-back events, Spanish forests are mostly becoming denser, with only 12% of locations analysed declining in greenness over the 18-year study period. This work demonstrates the importance of large-scale remote sensing analyses for obtaining an objective perspective on drought impacts. The thesis then explores the potential of remote sensing to map tree species in a region of regenerating woodlands near Madrid, providing the information needed for a nuanced understanding of resilience. I found that tree classification using high-resolution airborne hyperspectral imagery was highly accurate, while species maps produced using Sentinel 2 imagery (multispectral data with 10-m spatial resolution) were less successful at identifying species, with average agreement of 64% with the airborne derived map. Following on from this work, I used areas with high classification agreement between the airborne and spaceborne species information to study the effect of species composition on forest responses to droughts. I identify contrasting responses of the canopy greenness and wood production to drought. Specifically, wood production was found to be more sensitive to changes in water availability than canopy greenness. For the oak species, wood production was mirrored by changes in canopy greenness, but black pines reduced their wood production during droughts without substantial reduction in canopy greenness. I investigate the differences between the species and the mixing effects further by studying foliar compositions during

a dry summer in Spain. There were strong differences between pines and oaks in the stable isotope ratios of carbon, probably driven by underlying differences in water-use efficiency, and differences in the stable isotope ratios of nitrogen, probably driven by underlying differences in species' investments in the photosynthetic apparatus. I conclude by highlighting the implications of my research for studying the relationships between diversity and ecosystem functioning from space.

"Perplexity is the beginning of Knowledge"

"الحيرة بدء المعرفة"

Gibran Khalil Gibran

جبران خليل جبران

To my grandfather Maurice Karam & to my parents Arze Karam and Michel Khoury

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### **Publications and collaborators**

The analytical chapters presented in this thesis have been formatted as scientific papers to facilitate publication in academic journals. Co-authorship is attributed, reflecting contributions of collaborators to my research, in the form of supervisory support, logistic support, or contributions to data collection. Therefore, the collective pronoun "we" has been used throughout the text instead of the singular "I". Author contributions are as follows:

Chapter 1 is entirely my own work

• Chapter 2 is published: **Khoury S**, Coomes DA. 2020. Resilience of Spanish forests to recent droughts and climate change. *Global Change Biology* 26: 7078–7089.

### https://doi.org/10.1111/gcb.15268.

Assistance in planning and organization of the manuscript, discussion of analyses and supervision of the writing process was provided by David Coomes. Methodology design, data processing, analyses and writing were performed by me.

• Chapter 3 is in preparation for submission to *Remote Sensing*: **Khoury S**, Chan AHY, Bongalov B, Bentley L, Clewley D, Coomes DA. 2021. Mapping Mediterranean tree species using airborne hyperspectral and spaceborne multispectral remote sensing.

David Coomes, Laura Bentley, and I authored the grant application associated with the collection of remote sensing data, performed by the NERC Airborne Research Facility (project code ES17/126). Supporting georeferencing data was collected by Laura Bentley and I. Boris Bongalov, Daniel Clewley and myself were involved in processing the hyperspectral and LiDAR datasets. I conducted all data analyses and wrote drafts of the manuscript. We thank members of the NERC Airborne Research Facility and Data Analysis Node for the collection and processing of the data (project code ES17/126). Data processing was aided by the NERC JASMIN computing cluster. We acknowledge that LiDAR data were obtained from the Spanish National Centre for Geographic Information programme, under the direction of the Spanish Ministry of Public Works and Transport. Help on the ground was also provided by Fernando Valladares, Alicia Forner Sales, and David López Quiroga.

• Chapter 4 is in preparation for submission to the *Journal of ecology*: **Khoury S**, Jucker T, Bouriaud O, Valladares F, Coomes, DA. 2021. Different species, same droughts: Do treerings and canopies tell the same story?

Tommaso Jucker provided allometric analysis codes and collected initial field data along with Olivier Bouriaud. Giovanni Iacopetti provided the newest tree-ring increment dataset for Spain from the second FunDivEurope census. Fernando Valladares and his group helped with field management and data collection. I came up with the idea for the paper, performed analyses and wrote manuscript drafts.

• Chapter 5 is being prepared for submission to *Oikos*: **Khoury S**, Bentley L, Forner Sales A, Valladares F, Coomes DA. 2021. Effects of Mediterranean woodland diversity on leaf functional traits.

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• Chapter 6 is entirely my own work.

During my PhD, I was involved in the following manuscripts which were not included in this thesis:

- Nunes MH, Both S, Bongalov B, Brelsford C, Khoury S, Burslem D, ... Cutler M. 2019. Changes in leaf functional traits of rainforest canopy trees associated with an El Niño event in Borneo. *Environmental Research Letters*. <u>https://doi.org/10.1088/1748-9326/ab2eae</u>
- Ludovisi R, Tauro F, Salvati R, Khoury S, Mugnozza Scarascia G, & Harfouche A. 2017. UAV-Based Thermal Imaging for High-Throughput Field Phenotyping of Black Poplar Response to Drought. *Frontiers in Plant Science* 8, 1681. https://doi.org/10.3389/fpls.2017.01681
- Maesano M, Khoury S, Nakhle F, Firrincieli A, Gay A, Tauro F, & Harfouche A.
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- Streich J, Romero J, Gazolla JGFM, Kainer D, Cliff A, Prates ET, ... Khoury S, Harfouche AL. 2020. Can exascale computing and explainable artificial intelligence applied to plant biology deliver on the United Nations sustainable development goals? Current Opinion in Biotechnology. https://doi.org/10.1016/j.copbio.2020.01.010
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## Chapter 1 General Introduction

### **1.1** Mediterranean forests and climate change

### 1.1.1 Forests and climate change

The effects of climate change, such as the increase in frequency, duration and/or severity of drought and heat stress, are already shaping the forests of the world, and tree mortality and die-off events are co-occurring more frequently in most ecosystems. For instance, the 2012-2015 drought in California caused greater than 30% losses in canopy water over 1 million hectares, affecting about 58 million large trees (Asner *et al.*, 2015). In Algeria, Atlas cedar (*Cedrus atlantica*) die-off reached 100% in the driest mountains because of droughts in 1999-2012. A global overview of drought and heat-induced tree mortality reveals the complexity of tree responses to climate change. Climate-induced physiological stresses and interaction with other climate-mediated processes, such as insect outbreaks and wildfire, differ greatly across species and ecosystems (Allen *et al.*, 2010).

#### **1.1.2** Mediterranean forest and climate change

Mediterranean ecosystems are renowned biodiversity hotspots rich in endemic species, but this is threatened by climate change (Myers et al., 2000). Through millennia, these regions have been shaped by Mediterranean civilizations that exploited their multiple social, economic and environmental goods and services, such as provision of wood- and non-wood products, clean water, erosion and desertification control, carbon sequestration, biodiversity conservation and natural areas for recreation (Scarascia-Mugnozza *et al.*, 2000). With a rapidly growing population, human interactions with Mediterranean woodlands have not always been well planned, and species extinctions and loss of biodiversity have occurred (Scarascia-Mugnozza et al., 2000; Cuttelod et al., 2008). Biodiversity loss is likely to be aggravated by climate change, which is predicted to make the Mediterranean basin hotter and drier in the coming century (Lavorel *et al.*, 1998; Sala, 2000; FAO Plan Bleu, 2013), mainly due to a decrease in summer rainfall but also due to an increase in evaporation (Gao et al., 2006; Giorgi & Lionello, 2008; Dai, 2013), and by ongoing degradation arising from anthropogenic disturbances. Rapid climatic changes are already occurring in the Mediterranean basin, where temperature increase is 0.45°C higher than the global average since the end of the 19<sup>th</sup> century, and rainfall decrease exceeds 20% in some regions (Guiot & Cramer, 2016a). It is therefore essential to understand how these woodlands are reacting to these changes and predict their reaction to future changes. An improved understanding could contribute towards management strategies that maximize the resilience of these woodlands to extreme events.

#### 1.1.3 Mediterranean forest densification

Human management of woodlands varies greatly across the Mediterranean region. On the southern side of the Mediterranean Sea, a growing population has increased firewood extraction, grazing, and exploitation of land for agriculture, but in northern regions the abandonment of traditional management practices and urbanization has led to the regrowth of forests (Scarascia-Mugnozza *et al.*, 2000; Otero *et al.*, 2011, 2015; Fao & Plan Bleu, 2013). The regrowth pattern follows the forest transition concept formulated by Mather (1992) and Mather & Needle (1998).

Several studies have evaluated services/disservices provided by densification, a few of which have considered how those services may change with global warming. In terms of biodiversity, Peco et al. (2012) and Otero et al. (2015) agree that the abandonment of Mediterranean farmland and pasture land has led to forest transitions that disadvantaged non-forest habitats and eliminated some grassland and shrub species in favour of taller woody species, and that these transitions increase fire risks. Some ecologists argue that these perturbation-dependent ecosystems are approaching a new equilibrium state with more homogeneous landscapes negatively affecting species phenotypic and genotypic diversity (Pelorosso et al., 2011). For instance, managed woodlands in the mountains of Morocco exhibited 5% higher tree species diversity than unmanaged woodlands in Spain that are both populated by *Abies pinsapo* (Linares *et al.*, 2011). While forest densification may be considered damaging for its biodiversity in some studies, the secondary succession underway in Spanish forest is seen as restorative of the original Spanish landscape by others. As such, a study in Spanish forests dominated by Pinus nigra emphasized the need for sylvicultural practices to support the ongoing secondary succession by the recruitment of oaks in the understory which is also expected to provide higher resilience to disturbances and environmental changes (Martín-Alcón et al., 2015). The oaks are favoured for their resprouting ability which can provide faster recovery following fires (Puerta-Piñero et al., 2012). In other studies, however, fire-succession models for Mediterranean forests suggest that, although wildfire frequency might be lower in these denser forests, the chances of a catastrophic fire are much higher than for

forests that are regularly thinned (Tàbara et al., 2003). The simulation model used plantfunctional types to represent spatial and temporal competition for resources (water and light) in a rule-based modelling framework and showed that wildfire spread parameters have the greatest influence on two aspects of the landscape change: land-cover change and the wildfire regime (Tàbara et al., 2003); however, many drivers still need to be added for a more predictive Landscape Fire-Succession Model (Millington et al., 2009). As for water availability, Beguería et al. (2003) found a significant decrease in water discharge (30% reduction in mean annual water discharge) in the past 50 years in Spanish woodland that could be attributed to land-use and plant-cover changes. Similar effects on water runoff were observed in other studies (Molinillo et al., 1997; Gallart & Llorens, 2004; Lasanta et al., 2006). Finally, a review by García-Ruiz & Lana-Renault (2011) stressed the negative effects of land abandonment on hydrology and pointed out the need for more studies to understand the hydro-morphological consequences that depend on several factors, such as field type, climate, rate and characteristics of plant colonization, and soil features before management actions are taken. Densification can lead to 100% vegetation cover which increases interception of water, increases infiltration and water consumption leading to less run-off; the latter does however result in less erosion (García-Ruiz & Lana-Renault, 2011).

#### **1.1.4** Forest succession in the Iberian Peninsula: Oaks vs. pines.

In the Mediterranean region the process of forest succession is far more apparent than any effects of global warming, mainly because of the prevalent land abandonments, fire suppression and restricted management (Vayreda *et al.*, 2013; Carnicer *et al.*, 2014; Martín-Alcón *et al.*, 2015). Large-scale studies in the Iberian Peninsula report qualitatively different growth and recruitment trends (individuals with DBH < 7.5 cm growing in the subplots of 5m radius were identified as recruits), in response to increased temperature and drought of Mediterranean oaks and pines. For instance, *Quercus* species were found to be expanding in 41% of the plots surveyed, while *Pinus* species were advancing at a much smaller rate covering only 10% of the surveyed areas (Carnicer *et al.*, 2014). Similarly, *Quercus* had a 34% greater recruitment success than *Pinus* in the same ecosystems (Carnicer *et al.*, 2014). Contrasting trends between these two plant genera are found in many studies, however, it remains unclear which genus has higher phenotypic plasticity that might provide resilience in the face of drought. Conifers were found to have a higher growth rate in absence of competition while angiosperms performed better in mixed stands (Jucker et al., 2014a). The evergreen oak, Q. ilex, expanded massively in the last decade at the expense of several pine species due to its strategy of resource storage and conservative use of resources, allowing it to sustain very low growth rates under stress (Gómez-Aparicio *et al.*, 2011). Then again, oak mortality was found to be higher with advanced drought and heat stress (Ruiz-Benito et al., 2013). Surprisingly, temperature increase had a more severe effect on both pines and oaks than precipitation, and forest structure amplified these effects considerably, as these two genera have different defence mechanisms to resist heat. On one hand, pines close their stomata to prevent hydraulic failure by embolism, which leads to reduced transpiration and water use, but also could lead to carbon starvation (Ruiz-Benito et al., 2013). On the other hand, oaks have drought tolerance mechanisms that permit them to keep a relatively high transpiration rate that could finally lead to hydraulic failure in the long run (Ruiz-Benito *et al.*, 2013). This difference is primarily linked to the vertical rooting system: pines depend on a superficial rooting system, which means they are first to sense and suffer a water deficit, but also the first to absorb water from any summer rain. In contrast, it is the deep-rooting system that allows oaks to maintain high rates of transpiration by using water from deep soil layers as superficial layers dry out. It is therefore important to take into consideration forest structure, as well as climatic variations, in terms of frequency and severity, and water availability to explain better any observable trend in vegetation.

### **1.2** Ecosystem resilience to drought

### **1.2.1** Defining and measuring drought

Droughts are events characterized by water scarcity on land that affect the natural ecosystem in which they occur, and can lead to larger socio-economic impacts (Tramblay *et al.*, 2020). They account for most of the climate-caused variations in gross primary productivity globally and in the past two decades have converted in several instances carbon sinks to carbon sources (Allen *et al.*, 2010; Klein & Hartmann, 2018). Future climatic predictions point towards more severe and more frequent droughts that have a serious potential to hinder the capacity of forests to counter climate change (Anderegg *et al.*, 2020). Yet, following a review of the drought literature, Slette *et al.* (2019) highlighted that 68% of drought studies in ecology fail to define or quantify drought precisely, impeding our collective understanding of drought impacts. The authors recognized that

the issue stemmed from a lack of consensus between climatologists on a generalizable definition and quantification method of the phenomena. The difficulties surrounding the quantification of drought are related to the complexity of the water cycle; water arrival, for example through precipitation, is unequally absorbed by land features, and will be used by certain ecosystems more than others and in many cases by humans for their needs (Vicente-Serrano et al., 2010). This makes water availability highly variable between sources and relative to the studied system. Several routes are suggested to make ecological drought studies more comparable. One of these routes is using standardized drought indices, the Palmer Drought Severity Index (PDSI, Palmer, 1965) and the Standardized Precipitation Evapotranspiration Index (SPEI, Vicente-Serrano *et al.*, 2010) being the most used ones (Slette et al., 2019). Drought indices usually attempt to circumvent the aforementioned difficulties by making water availability relative to water needs at a site when computing the index. For instance, PDSI takes into account water supply and demand, the basic elements of a climatic water balance, by including runoff and evaporative demand in addition to precipitation. The more recent SPEI goes a step further, aggregating the water balance at different temporal scales, and standardizing these values with a reference time period, ultimately making drought comparable at large spatial scales (Vicente-Serrano *et al.*, 2010). Simply put, the computation of a monthly SPEI index is done by transforming a water balance (precipitation - potential evapotranspiration) time-series of each month separately following a log-Logistic distribution (i.e. standard Gaussian variate with zero mean and standard deviation of one). Since the probability distribution functions of the water balance data are not homogenous from month to month, the data is split into twelve series (one for each month) and independent probability distribution functions are fit to each series. They are then joined together to give a time-series of the probability of a specific month X being an extremely wet or dry event as compared to all reference months X in a specific time period (recommended to be > 15 years). These monthly values are then aggregate so that a scale 6, for instance, would imply that data from month X-5 to X will be added and used for computing the SPEI<sub>6</sub> of month X (Figure 1.1) (see Vicente-Serrano *et al.*, 2010, and Beguería et al., 2014, for more information on how SPEI is computed). Despite the importance of such indices, the proportion of studies in 2014-2019 using them to characterise studied droughts is still below 25% (Slette *et al.*, 2019). The lack of uptake might be due to some of their shortcomings (Zang et al., 2019). Specifically, while

accounting for the supply in the water balance equation is fairly straightforward (e.g. absolute precipitation values), computing water demand is not. For instance, demand in SPEI is potential evapotranspiration, the amount of water that could potentially be lost to evaporation over a vegetated surface given meteorological conditions at the time. But potential evapotranspiration can be computed in several ways; the simplest equation uses temperature data only (Thornthwaite, 1948), while the most widely adopted equation is dependent on the intensity of solar radiation, air temperature, humidity and wind speed (Monteith, 1965). Hence, different ways of computing evapotranspiration lead to different water demand values, affecting the end result and making the same drought index incomparable across studies. Furthermore, the relative nature of these indices, which makes them essential for large studies, can be wrongly interpreted (Zang et al., 2019); or seen as a disadvantage by researchers who find absolute climatic values more informative, especially for smaller studies. It is therefore recommended to use both an index and absolute values, as well as using high resolution datasets if possible instead of coarse, gridded datasets to overcome some the aforementioned issues (Zang *et al.*, 2019).



Figure 1.1 Standardised Precipitation Evapotranspiration Index. Data were taken from Khoury & Coomes (2020).

SPEI index computation starts by taking a seasonal water-balance (first panel) and separating each month into its own time-series before fitting probability distribution models and normalizing them using a reference period (>15 yrs) which leads to non-seasonal SPEI index (panel 3). Although water-balance trend (panel 2) and SPEI<sub>1</sub> trend (panel 4) look similar the first is a series of absolute values which can be used to check variation at that particular site only, while the latter can be used in larger studies and be compared to other SPEI values from different sites. The different scales allow to account for different water accumulation rates with the shortest scales corresponding to dry lands with high sensitivity to current precipitation while larger scales present lower sensitivity and often correspond to underground water basins which are not immediately impacted by lower precipitation. The blue line indicates 0 on the different scales. The red dots indicate two recognized drought years at scale 1 over Spain and how they lag when considering different SPEI timescales.

Another key aspect in drought studies is the identification of what constitutes droughtinduced damage. As mentioned earlier, droughts can result from a wide array of climatic conditions with direct and indirect effects on the water cycle (De Boeck & Verbeeck, 2011). Periods of low precipitation have direct effects, and periods of higher solar radiation, higher temperature and higher vapour pressure deficit, among others, are indirect. The combined effect of these environmental conditions and water scarcity may inflict different kinds of damage on trees, some of which is irreversible, or reversible at very different rates, leading to the so-called 'legacy effects' (Camarero *et al.*, 2018). Camarero *et al.* (2018) suggested that researchers should attempt to capture both short-term (1-5 years) and long-term (10-30 years) effects of droughts when possible as they can lead to different conclusions. However, many published studies limit their analysis to a specific period pre- and post-drought as suggested by Lloret *et al.* (2011) when they first proposed ways of computing drought resilience.

### 1.2.2 Defining and measuring resilience

There is a renewed interest in the resilience of ecosystems in the context of global changes (Parry et al., 2007; Standish et al., 2014; Craze, 2015; Nikinmaa et al., 2020; Schwarz et al., 2020; Albrich et al., 2020; Van Meerbeek et al., 2021) and the topic has sparked several conversations in the past decade (Hodgson et al., 2015b, 2016; Oliver et al., 2015, 2016; Yeung & Richardson, 2016). Briefly, 'resilience' has been conceptualized by scientists in various disciplines interested in how systems respond to disturbances or perturbations. In ecology, the term 'resilience' emerged in the early 1970s as a concept that either complements 'stability' of systems in non-equilibrium states, or as a component of system stability near equilibrium (Van Meerbeek et al., 2021). Studied systems include everything from small organisms to large ecosystems. Van Meerbeek et al. (2021) traced back the origins of the terms 'resilience' and 'stability' in ecology to two schools of thought centred on equilibrium and non-equilibrium stability concepts (Figure 1.2). Resilience is therefore related to many other concepts in the ecological literature such as shifts in ecosystem states and tipping points (Scheffer *et al.*, 2001, 2009; Biggs *et* al., 2009; Guttal & Jayaprakash, 2009; Barnosky et al., 2012), ecosystem collapse (Lindenmayer et al., 2016), ecological transitions (Kéfi et al., 2014), vicinity to a threshold (Wissel, 1984), critical transitions (Scheffer et al., 2009; Hirota et al., 2011; Dakos et al., 2012), alterations in ecosystem state and functions (Pulsford et al., 2016), and of course stability (Lehman & Tilman, 2000; Jucker et al., 2014b), to mention a few. In this thesis, we focus on quantifying the resilience of forests to droughts, but in this Introduction, we additionally visit the concepts of tipping points and ecosystem state shifts and how they are measured.



**Figure 1.2 Evolution of the equilibrium and non- equilibrium concepts of stability in ecology.** *Reprinted by permission from Springer Nature: Journal of Ecology, Unifying the concepts of stability and resilience in ecology. Van Meerbeek K, Jucker T, Svenning J. Copyright (2021).* "Central themes (with benchmark publications) are indicated in capital letters. Research foci are added in bullet points. SES, socio- ecological systems" (Van Meerbeek *et al.*, 2021). In ecology, the terms 'stability' and 'resilience' have taken multiple definitions over the years to describe the health of an ecosystem exposed to perturbations. Some of these definitions focused on the quantifiable behaviour relative to an equilibrium state of the ecosystem, while others focused on the qualitative description of an ecosystem behaviour rejecting the existence of one equilibrium state. Resilience, as most commonly used now, is highlighted in green, taking into account the whole response to a perturbation or disturbance (i.e. both the loss of and recovery of the system health).

### 1.2.2.1 Defining resilience in ecology

In search of a 'common currency', as Ingrisch & Bahn (2018) put it, researchers have argued over which definition, which component, and which name is the most useful. In a recent review, Nikinmaa *et al.* (2020) investigated the resilience literature related to forest ecosystem responses and identified three main concepts, ecological, engineering, and socio-ecological resilience. While the first two concepts are usually quantitative, derived from the equilibrium concept, the socio-ecological resilience is often qualitative and derived from the non-equilibrium concept (Figure 1.2 and 1.3a). They proposed that the three notions were nested within each other (Figure 1.3a) and showed the growing popularity of engineering resilience in the last decade (Figure 1.3b) (Nikinmaa *et al.*, 2020).


#### Figure 1.3 Resilience concepts.

a) Nestedness of the three resilience concepts. b) Increase in the number of studies related to the three resilience concepts in forest studies from 2000 to mid-August 2018. *Reprinted by permission from Springer Nature: Current Forestry Reports, Reviewing the Use of Resilience Concepts in Forest Sciences. Nikinmaa L, Lindner M, Cantarello E, Jump AS, Seidl R, Winkel G, Muys B. Copyright (2020).* 

Recently, scientists argued that the best approach to studying resilience is to use all the available concepts which have proved to be equally important and refrain from using restrictive labels (Hodgson *et al.*, 2016; Van Meerbeek *et al.*, 2021). They were mostly referring to the use of 'ecological' and 'engineering' resilience which are usually associated with resistance to disturbance and recovery from disturbance (Hodgson et al., 2015b; Ingrisch & Bahn, 2018). Below, in Figure 1.4, we present the major components of resilience, under low severity disturbance (also known as perturbation) and high severity disturbance, as well as the concept of tipping points (see Van Meerbeek et al., 2021, for a more complete set of resilience components and synonyms). From the two disturbance regimes we can identify (i) sensitivity: the capacity to withstand or absorb disturbance, which is defined as well as the inverse of resistance; (ii) recovery or adaptability: the capacity to return to a stable state; (iii) return time: the time taken to return to a stable state after a disturbance; (iv) recovery rate: the rate of return to the stable state (less commonly known as elasticity); (v) tipping line or tipping point: a threshold that once reached the system will be qualitatively different; and (vi) latitude: distance from un-disturbed state to the nearest tipping point.



#### a) High severity disturbance & resilient system b) Low severity disturbance & resilient system

#### Figure 1.4 Resilience and its components.

(a) Ecosystem response to a high severity disturbance. (b) Ecosystem response to a low severity disturbance or perturbation (c) Ecosystem transition into another state. Shaded in green, orange, and blue are three stable ecosystem states which can represent different ecosystems. Green solid lines represent resilient ecosystems, while the green dotted line represents a sensitive ecosystem transitioning into another stable state. Dotted in black is the tipping line, however, given its dynamic nature, it is surrounded by a zone of uncertainty (in grey). The black dot represents the tipping point which is simply the point at which the ecosystem crosses the critical threshold.

#### 1.2.2.2 Quantifying resilience

The other concepts mentioned in the introduction of Section 1.2.2, such as ecosystem state shifts, are not included in the reported numbers in Figure 1.3b. Most of these concepts focus on developing indicators to quantify latitude and identify tipping points (or lines). Quantifying latitude would allow managers to identify which systems are in danger of transitioning into another state and which level of disturbance is needed to tip the system (Yeung & Richardson, 2016). Despite the theoretical potential of latitude and its more direct applicability for management, methods to detect the distance from tipping points are lagging behind the theoretical framework, perhaps due to the difficulty of detecting tipping points which imply a binary and perhaps simplified view of ecological systems (Hodgson *et al.*, 2016). The most common approach is based on detecting a

slowing down in recovery rate after disturbances (i.e. 'early warning signals' or 'critical slowing down'). Some studies suggest that slowing down can be detected from elevated temporal autocorrelation (Verbesselt *et al.*, 2016) or an increase in the variance of ecosystem state variables (Carpenter & Brock, 2006). Dakos *et al.* (2012) review the range of available methods by testing them on simulated time-series and suggest that no one method is enough to identify critical slowing down. Many papers, however, criticize methods for critical slowing down detection for their inability to detect actual transitions when used on continuous data (Scheffer *et al.*, 2001; deYoung *et al.*, 2008; Schreiber & Rudolf, 2008; Hastings & Wysham, 2010; Boettiger & Hastings, 2013; Boettiger *et al.*, 2013; Dakos *et al.*, 2015; Lamsal, 2017). Others have even questioned the existence of a slowing down before state shifts (Dakos *et al.*, 2012b). Biggs *et al.* (2009) noted that even when those methods succeed in detecting critical slowing down, they do so too late when the regime shift has already initiated, rendering them useless to remediate or correct the situation.

Recent reviews indicate that most forest resilience studies are using indices suggested by Lloret et al. (2011) (Schwarz et al., 2020), and focus on resilience to fire and droughts, using basal area increments, vegetation cover, and tree density as their response variable (Nikinmaa et al., 2020; Albrich et al., 2020). Schwarz et al. (2020) demonstrate drawbacks in the computation of the most adopted resilience indices and discuss a new way to compute the indices as proposed by Thurm *et al.*, 2016, in three case examples (Figure 1.5). Briefly, the drawbacks in the original method are related to the adoption of a set period of time in which system change is measured, and the assumption of a linear response: that meant that values of resistance and recovery depended on how many years pre- and post- drought were considered in their computation, and on the regularity of the response being measured (Figure 1.5). Another issue is the start date of the disturbance or perturbation; as previously discussed in the case of drought in Section 1.2.1, it is hard to pinpoint when a drought starts for a particular region. While this particular issue can be circumvented by working at a coarser temporal scale, e.g. looking at dry years instead of dry months, this does not always solve the problem, it reduces the resolution of the information, and remains dependent on the spatial scale employed. For instance, at regional spatial scales or continental scales, droughts will occur at different times or with a considerable lag.



**Figure 1.5 Methods for measuring resilience components.** Reprinted by permission from Springer Nature: Current Forestry Reports, Quantifying Growth Responses of Trees to Drought—a Critique of Commonly Used Resilience Indices and Recommendations for Future Studies. Schwarz J, Skiadaresis G, Kohler M, Kunz J, Schnabel F, Vitali V, Bauhus J. Copyright (2020).

Three case studies in which the original method of computing resilience components failed to represent what is happening to the ecosystem. The original methods imply computed difference between the drought year and a specific period of time before and after to determine resistance and recovery (Lloret *et al.*, 2011). The proposed method by Thurm et al. (2016) computes recovery rate instead of recovery amount but does not resolve problems related to unusual behaviour in the pre-drought period.

# 1.3 Spaceborne and airborne remote sensing over the Mediterranean region

Earth observation (EO) is useful in many aspects, it collects data on the earth's atmosphere, often referred to top of the atmosphere (TOA) data, but also collects data on the earth's surface, essential for detecting surface changes at large scales (Liang *et al.*, 2019). Besides becoming essential for the earth energy budget computation, EO became a key component of the carbon flux monitoring with the first vegetation indices developed in the 1970s (Xiao *et al.*, 2019). The normalized difference vegetation index

(NDVI), based on a simple ratio using plant reflectance in the red zone and near-infrared zone of the electromagnetic spectrum, is to this day the most used vegetation index for detecting and monitoring vegetation cover (Xiao et al., 2019, Rouse et al., 1974), and is used in this thesis. Remote sensing has advanced rapidly; from satellite to close-range instruments (Lausch et al., 2016, 2017). With petabytes of free EO data now available (Woodcock et al., 2008; Nemani et al., 2011 to cite a few), researchers can map ecosystem properties at different geospatial and temporal scales and resolutions, using a range of active and passive sensors, efficiently complementing costly forest inventories. Advances in computing systems, including machine learning algorithms provide new opportunities for EO data analysis. One computing platform, Google Earth Engine (GEE), offers multipetabyte analysis-ready data and a cloud super-computing service, with which researchers can analyse data at a global scale within minutes. This speed is possible thanks to built-in parallelization and data distribution models which are optimized to deal with common temporal and geospatial tasks, such as mathematical operation on tiled images, aggregation of spatial data, time-series analysis, training of classifiers between others (Gorelick et al., 2017).

### **1.3.1** Time-series of Spaceborne data and change detection.

Over the past decades, space agencies developed key EO programmes that provide freely available and highly valuable multispectral imagery to scientists around them. We introduce them in this section.

# 1.3.1.1 High temporal resolution multispectral satellite data: MODIS

Launched in 2000 by the National Aeronautics and Space Administration (NASA), Moderate-resolution Imaging Spectroradiometer (MODIS), captures data in 36 spectral bands ranging in wavelength from 0.4 µm to 14.4 µm and at varying spatial resolutions (from 250 m to 1 km); seven of these bands were intended for land applications (Zhang *et al.*, 2003). MODIS-derived vegetation indices are also often used as the continuation of the lower ground-resolution National Oceanic and Atmospheric Administration Advanced very-high-resolution radiometer-derived NDVI (NOAA-AVHRR-derived NDVI) (Huete *et al.*, 2002; Brown *et al.*, 2008; Beck *et al.*, 2011; Fensholt & Proud, 2012). Mounted on two individual satellites, Aqua and Terra, MODIS images the entire earth every 1 to 2 days. Daily MODIS bidirectional surface reflectance values are controlled for quality, atmospherically corrected, and composited into 8-day and 16-day products. Despite the low spatial resolution, especially in comparison with 30 m Landsat pixels, the high temporal resolution of MODIS and the fact that it is not subject to orbital drift that can cause misleading results (Nagol et al., 2014) makes it highly valuable for large scale analysis. Time-series of MODIS data are often exploited to determine vegetation phenology with varying success depending on the biomes, agricultural cover, and methodology used (Zhang et al., 2003). In one study, MODIS-derived NDVI metrics captured the beginning of the spring greening and the onset of the autumn leaf yellowing with great precision (< 1-week difference between the ground measure and space detected) in deciduous forests, while in tropical rainforest the phenological patterns detected were mostly noise (Hmimina et al., 2013). More recent studies managed to elucidate vegetation phenological patterns even in rainforests using MODIS time-series (Pennec et al., 2011; Lara et al., 2018). MODIS time-series are also frequently used, alone (Verbesselt et al., 2009, 2010, 2016; le Maire et al., 2011; Lambert et al., 2013; Seddon et al., 2016; Uyeda et al., 2017; Kannenberg et al., 2019b) or in combination with other sensors (Hansen et al., 2013; Zhu et al., 2016), in global and local ecosystem studies based on change detection over vegetated landscapes. In a global study using MODIS, Seddon et al. (2016) identified which of the three main climatic drivers, temperature, water availability, and cloudiness, limits green ecosystems (Figure 1.6). Although the Mediterranean area was not specifically discussed, it is clear from the vegetation sensitivity index map that Mediterranean woodlands are mostly sensitive to water availability and temperature combined and less sensitive to cloudiness (Figure 1.6).





a) Sensitivity of vegetation productivity (MODIS-derived enhanced vegetation index) to climate variability. The created sensitivity index varies from 0 (low sensitivity, green) to 100 (high sensitivity, red). b) Climate drivers of green ecosystems' sensitivity across the globe. Barren lands are shown in grey in a) and black in b).

# 1.3.1.2 High ground resolution multispectral satellite data: Landsat and

# Sentinel 2

Landsat satellites consist of 7 successful satellite missions to date, a joint program between NASA and the United States Geological Survey (USGS), that collected and are still collecting multispectral data over our planet at 30 m ground resolution, allowing us to monitor land cover and land-use change efficiently for more than 40 years. The latest Landsat satellite, Landsat 9, is scheduled to be launched in 2021 continuing the Landsat legacy (Masek et al., 2020). Despite having the longest record of earth imagery, since 1972 (Xiao et al., 2019; Nguyen et al., 2020), the whole Landsat collection remains largely unused because of quality and orbital issues in the first 5 satellites, impeding the achievement of high-quality imagery (Tier 1) (Nguyen et al., 2020). Furthermore, while being by far the most employed for land cover mapping (Belward & Skøien, 2015), the Landsat series is much less used for inter- and intra-annual vegetation monitoring, owing to the low temporal resolution (16 days for any one Landsat satellite and 8 days when it is possible to combine data from two satellites). The disparity in Landsat data collection and processing globally, combined with the low temporal resolution makes a considerable portion of monthly composites useless for vegetation monitoring, severally affecting studies requiring more than one cloud-free pixel a year except over the USA (Ju & Roy, 2008). Originally, global Landsat data was downlinked to several international cooperative stations due to memory limitation at any one site, until the opening of the Landsat archive in 2008. However, the assimilation of all Landsat data by the archive is still ongoing with different regions being prioritized (Wulder et al., 2016). For instance, most of the imagery over Spain only got assimilate to the global Landsat archive in the past couple of years (see U.S. Geological Survey, 2016, 2020; the difference between the two maps indicate the number of scenes added to the archive). While ready to use Landsat products were made available over the USA since 2008, facilitating the use of the dataset for time-series analysis (Zhzu, 2019), a similar dataset was just made available last year for the rest of the world (Potapov et al., 2020). How useful is this new Landsat dataset going to be for time-series analysis remains to be seen.

Similar to MODIS offering a higher-resolution continuation to AVHRR, with its 13 bands and focus on landcover mapping Sentinel 2 is perceived as a higher resolution (10 m) continuation to Landsat (30 m) (Figure 1.7). Sentinel 2A, which was launched by the European Space Agency in June 2015, was followed by Sentinel 2B, in March 2017, with a spatial resolution of 10 to 60 m. The two satellites with a revisit period of 10 days, also offer a higher temporal resolution compared to Landsat, doubling the image capture over the same area, from on average 3 images/month (considering 2 Landsat satellites) to 6 images/month (considering 2 Sentinel satellites). The 10 m resolution is allowing for land cover mapping to the species level (Grabska *et al.*, 2019, 2020), while the short time-series of Sentinel 2 are already being used to detect changes in vegetation at local scales (Navarro *et al.*, 2019).



Figure 1.7 Radiometric characteristics of Sentinel 2, Landsat 7 and 8 satellites taken from USGS EROS Archive.

Sentinel 2 was by design created to be compatible with Landsat 8 bands (thermal bands excluded). It can be seen in the figure that bands 1-7 and band 9 in Landsat 7 and Landsat 8 align closely with some of the bands of Sentinel-2, both in wavelength and bandwidth, which allows for continuity in time-series analyses. While bands 5-7 were added in the vegetation red-edge which gives greater predictive capabilities for vegetation monitoring and the estimation of parameters such as the leaf area index, chlorophyll concentration, and carbon mass.

# 1.3.1.3 High spectral resolution satellite data: EnMAP

EnMAP, a future satellite by the German imaging spectroscopy mission, to be launched in 2022, is intended to provide 30 m hyperspectral data that could be promising for spectranomics (Guanter *et al.*, 2015). Unmatched in its spectral resolution by other spaceborne sensors, EnMAP is already drawing interest from forest researchers trying to analyse the sensitivity of such sensors in detecting canopy traits (Clasen *et al.*, 2015; Dotzler *et al.*, 2015). To date, hyperspectral sensors have been mostly used for proximal and airborne sensing (Lausch *et al.*, 2016, 2017).

# **1.3.2** Point clouds and spectral series of airborne data

Ground based and airborne based spectral sensors record radiance emanating from the measured object at numerous wavebands allowing scientists to uncover information on the properties of the object being measured. These properties or traits can be biochemical, physiological, morphological, structural, phenological, or functional and allow us to characterize and even identify measured objects (Lausch *et al.*, 2016). Using this technology, mounted on an airborne craft, in combination with easily accessible machine learning algorithms and high processing computational power has allowed scientists to map tree species over entire landscapes (Dalponte *et al.*, 2012), determine their canopy composition (Asner & Martin, 2009b) and determine their health status with high precision (Chan *et al.*, 2020). However, scaling up canopy traits from ground observations to landscape observations is not straightforward and while some studies were already successful at harnessing the power of such methods, many researchers are still trying to overcome all the challenges and limitations of these methods (Nunes *et al.*, 2017; Bongalov, 2019). These limitations range from the propagation of ground sampling bias to problems with spatial auto-correlation and independence assumption violations (Bongalov, 2019).

# 1.4 This thesis

# 1.4.1 Objectives and structure

This thesis explores how remote sensing approaches can be used to uncover information on Mediterranean forest resilience to drought and climate change at multiple spatio-temporal-scales: ranging from the regional level, that of Spain, down to the local tree species level; and from the decadal time scale down to the specific drought event scale. While several studies have looked at quantifying resilience to specific drought events, most are limited in their spatial and temporal scale making it hard to determine resilience drivers. This thesis aims to bridge these gaps in our understanding of forest resilience by looking both at the forest canopy from above and at the forest productivity and foliar composition on the ground. The main objectives are:

(i) Quantify forest canopy resilience to climate change and droughts from space and determine its drivers.

(ii) Compare forest canopy resilience to forest wood productivity resilience and understand how they relate to each other.

(iii) Determine how forest species mixing affect forest resilience to drought.

In **Chapter 2**, we combine time-series analysis of remotely sensed leaf area with spatial regression models and breakpoint analysis to quantify Spanish forest trends and determine drought resilience drivers, fulfilling the first objective. We consider both the long-term gradual change in water availability, made worse by climate change, and the short-term extreme drought events. We evaluate the effect of elevation, absolute water

availability, relative water availability, forest canopy density, dominant tree species group, the protected status of the forest, and land cover change pre-2000, on the longterm and short-term resilience of Spanish forests over 18 years of NDVI from more than 3000 MODIS pixels covering the whole of Spain.

In **Chapter 3**, we look at how machine learning algorithms can be trained on airborne hyperspectral and spaceborne freely available Sentinel 2 data to provide valuable species distribution maps to be used in bridging the gap between long-term high-resolution temporal data derived from satellites such as MODIS and the low spatial resolution of these datasets. This work is a steppingstone to achieving objectives ii and iii. It allows time-series analysis of long-term remotely sensed data to reach its full potential by uncovering species mixing effects which are a key driver of forest productivity and forest response to disturbance.

**Chapter 4** utilises species information from **Chapter 3** to uncover species mixing effects in Mediterranean landscapes on wood net primary production and leaf area, achieving objective ii. It also evaluates the potential of using remotely sensed leaf area to predict wood primary productivity which is highly valuable for uncovering carbon sequestration potential of forests yearly in light of climatic changes.

**Chapter 5** looks at canopy traits in mixed Mediterranean forest to evaluate the capacity of canopy composition in relaying information on plot level competition and uncover physiological and phenological differences between Mediterranean pines and oaks achieving objective iii.

In the last chapter, **Chapter 6**, we discuss how the different findings in this thesis inform each other and can all be combined to answer important methodological and ecological questions about the resilience of forests to climate change and disturbances. Further, we mention potential avenues to expand on this work looking at different ecosystems, different disturbances, and using other technological advances.

### 1.4.2 Methodological considerations and motivations

In **Chapter 2** we study Spanish forests because Spain has the largest forested area of all Mediterranean countries and several climatic regions which can be instrumental in understanding resilience (de la Guerra et al., 2017; FAO & Plan Bleu, 2013). We considered different analytical approaches to estimate resilience to drought and climate change in the short- and long-term. First, we looked at the difficulties researchers encounter when estimating drought (see section 1.2.1), we evaluated different climatic indices and datasets, and settled on the use of 1.1 km gridded SPEI data for Spain (Vicente-Serrano et al., 2017). Compared to other gridded drought datasets over Spain, this one had a higher spatial resolution, an appropriate temporal span for the study, and was computed specifically over Spain using daily climatic data from the National Spanish Meteorological Services (AEMET). As previously mentioned, the relative nature of drought indices is essential when researching questions at large spatial scales, however, used alone they do not allow to capture the effect of water balance gradients across a whole country. For these reasons, we decided to compute a climatic water balance like the one used for the index (precipitation – potential evapotranspiration) and included it in our models to account for the absolute differences in water availability across Spain as previously suggested (Zang et al., 2020). Second, given that forests are affected by drought at two temporal frames, short-term fluctuations in climate have short-term effects that last 1-5 years while long-term trends affect forests over 10-30 years (Camarero et al., 2018), we separate long- and short-term drought effects by studying the general trend in NDVI first (decadal-scale) and the fluctuations in NDVI second (monthly scale). Third, to estimate the resilience to extreme droughts, we looked at the most popular approaches to estimate resilience components, that of Lloret et al. (2011), and at the more recent approach by Thurm *et al.* (2016). Recognizing their shortcomings (Figure 1.5, Schwarz et al., 2020), we decided to approach the problem differently, making use of a recently developed package for break-point analysis (Jamali & Tomov, 2017), to automatically detect changes in vegetation instead of computing them over a set period. Using this change detection algorithm allowed us to extract a non-linear trend and segment it to detect the full and precise extent of the ecosystem response. Looking at the same cases studies presented by Schwarz et al., 2020, we demonstrate how our segmentation approach would detect the different segments used for the computation of the resilience metrics (Figure 1.8). In Section S3 of this thesis, we plot the resilience



metrics determined from the two methods over our dataset from Chapter 4 with a set



**Figure 1.8 Segmentation method used in this thesis to compute resilience metrics.** Illustration showing the three case studies used in Schwarz *et al.* (2020) with dotted segments in blue and black marking the magnitude of change considered using the Lloret *et al.* (2011) approach to compute resistance and recovery by averaging values over a set period (here 3 years) before and after the set event year (vertical red line). The purple line illustrates the non-linear trend that would be extracted by our segmentation approach if the ecosystem time-series in consideration has a seasonal and noise component or simply the segments computed over an annual time-series such as this one. In dashed orange and green we see the segments that would be used in the computation of the resilience indices in the period of time determined by us, allowing the disturbance event to be automatically detected (red dot).

In **Chapter 3**, we investigate how airborne hyperspectral and spaceborne multispectral satellite data can be used to assist researchers in identifying the species composition of large satellite pictures to open the door for the remote study of species diversity effects at large scales. Given that two-thirds of the forests worldwide are mixed forests it seems rather important that scientists studying these ecosystems from freely available satellite data know what is contained within those pixels. The limitations of Chapter 2 motivated this work. The dataset used for species identity in Chapter 2 specifies the dominant species but did not specify with certainty the proportion of those species in the landscape. While the Spanish inventory data used to validate the work had a huge difference in the spatial resolution that would similarly not allow the identification of precise species composition over those pixels. We, therefore, decided to harness the power of machine learning classification and big data to classify a regenerating forest landscape near Madrid using both a costly airborne data collection and freely available Sentinel 2 data for comparison.

In **Chapter 4** we study the effect of species mixing on forest response to drought using that information. We use the MODIS pixels that had a high agreement between the

airborne and spaceborne-derived classification and use the more precise hyperspectral dataset to estimate species proportions, i.e. the map validated against ground measurements of species composition in plots. Knowing the composition of each 250 m MODIS pixel we were able to infer species mixing effect on canopy variation and compare it to variation in wood productivities over the same landscape in central-east Spain. We used the same methodology from Chapter 1 to estimate the resilience of these Spanish forests to extreme droughts and determine the effect mixing had on wood productivity resilience and on leaf area resilience. Recognizing the potential for wood net primary productivity estimation, we relate the time series of wood production to that of remotely sensed leaf area and uncover species specific coupling between the two datasets.

In **Chapter 5**, we study the canopy composition of the Spanish plots we worked in (Chapters 3 & 4), in an attempt to reconcile the lack of diversity effect observed in the previous chapter with published data about diversity induced competition in these forests which usually does not include canopy data. We had three hypotheses in mind: (H1) tree leaf traits are not significantly different between mixed and single species plots, implying that underground competition and effect on wood production are not reflected in tree leaf traits: (H2) tree leaf traits are not significantly different between mixed and single species plots, implying that effect on wood production is indeed dependent on the variables being used to estimate said effect; (H3) tree leaf traits are dependent on plot diversity but using canopy horizontal area as a measure for species proportions and diversity does not allow us to capture these effects properly.

# Chapter 2 Mediterranean forests resilience to recent droughts and climate change

# Abstract

A widespread increase in forest cover is underway in northern Mediterranean forests because of land abandonment and decreased wood demand, but the resilience of these successional forests to climate change remains unresolved. Here we use 18-year time series of canopy greenness derived from satellite imagery (NDVI) to evaluate the impacts of climate change on Spain's forests. Specifically, we analysed how NDVI was influenced by the climatic water balance (i.e. Standardized Precipitation- Evapotranspiration Index, SPEI), using monthly time-series extracted from 3,100 pixels of forest, categorized into ten forest types. The forests increased in leaf area index by 0.01 per year on average (from 1.7 in 2000 to 1.9 in 2017) but there was enormous variation among years related to climatic water balance. Forest types varied in response to drought events: those dominated by drought-avoiding species showed strong covariance between greenness and SPEI, while those dominated by drought-tolerant species showed weak covariance. Native forests usually recovered more than 80% of greenness within the 18 months and the remainder within 5 years, but plantations of Eucalyptus were less resilient. Management to increase the resilience of forests-a key goal of forestry in the Mediterranean region—appears to have had a positive effect: canopy greenness within protected forests was more resilient to drought than within non-protected forests. In conclusion, many of Spain's successional forests have been resilient to drought over the past 18 years, from the perspective of space. Future studies will need to combine remote sensing with field-based analyses of physiological tolerances and mortality processes to understand how Mediterranean forests will respond to the rapid climate change predicted for this region in the coming decades.

# 2.1 Introduction

Globally, forests are responding to land-use and climate change. An increase in the frequency, duration and/or severity of droughts associated with global warming is reshaping ecosystems in the Mediterranean (Fao & Plan Bleu, 2013). Forest die back has been reported in some regions (Allen *et al.*, 2010; Carnicer *et al.*, 2011; Peñuelas *et al.*, 2017; Gómez-González *et al.*, 2018). In other regions, however, studies have reported increases in forest biomass linked with land-use changes and/or CO<sub>2</sub> fertilization. For instance, several remote sensing studies in Spain have reported that forests are greening (Peñuelas *et al.*, 2002; González-Alonso *et al.*, 2006; Alcaraz-Segura *et al.*, 2012; Vicente-Serrano *et al.*, 2014b), probably because successional processes following land abandonment are currently more influential than climate change in driving forest canopy dynamics (Vayreda *et al.*, 2013; Carnicer *et al.*, 2014; Martín-Alcón *et al.*, 2015). To our knowledge, nobody has yet attempted to disentangle the effects of forest succession and climate change on canopy greenness.

Quantifying, understanding, and enhancing the resilience of forests to climate change is a major area of interest (Nimmo et al., 2015; Oliver et al., 2015), especially in the Mediterranean area which is undergoing a warming that exceeds the global trend at present and in most projections (Guiot & Cramer, 2016b). In Spain, enhancing forest resilience to drought has become a major goal of protected area management, because the forests provide valuable ecosystem services including water regulation, timber and meat provision, regulation of climate and air quality, erosion control, as well as recreational and spiritual enjoyment (Scarascia-Mugnozza et al., 2000; Guiot & Cramer, 2016b; UNEP/MAP, 2016; de la Guerra et al., 2017). Strategies for climate change adaptation used and proposed include favouring mixed species stands, reducing tree density, eliminating species with high water demands and introducing resilient species (de la Guerra et al., 2017). Given, however, how recent these management plans are, no studies have evaluated their effectiveness on a national scale, with the exception of one (Alcaraz-Segura et al., 2008), which compared greening trends inside and outside protected areas. Instead, researchers have focused on other ecosystem functions and services. A study evaluating multifunctionality in European protected areas found that in Spain those areas were associated with lower timber production and climate regulation

functionality (van der Plas *et al.*, 2018). Another study found that land-use change in Europe's network of protected areas (i.e. Natura 2000), towards non-natural cover was greater than in non-protected areas, calling their effectiveness into question (Rodríguez-Rodríguez & Martínez-Vega, 2018). National-scale evaluation of the effectiveness of managing protected areas for climate resilience was however absent and is therefore needed.

Understanding differences in the resilience of different forest types is key to improving the resilience of forests to drought (Carnicer et al., 2011; Ruiz-Benito et al., 2013; Mochida et al., 2015; Martín-Alcón et al., 2015; Gavinet et al., 2016; Machar et al., 2017; Yin & Bauerle, 2017). Multispectral imagery collected by earth observation satellites provides information on the greenness of pixels, which is linked to total canopy cover, leaf biomass and photosynthetic activity of the forest stand (Tucker & Sellers, 1986; Asrar et al., 1989; Baret & Guyot, 1991; Cihlar et al., 1991; Carlson & Ripley, 1997; Zhang et al., 2003). Time series of remote sensing data have been used to detect forest mortality (Fraser & Latifovic, 2005; Coops et al., 2006; Garrity et al., 2013; Ogaya et al., 2015; Hart & Veblen, 2015) and also canopy-level responses to drought events. For instance, Gazol et al. (2018) estimated the responses of 11 tree species to four drought events in Spain, in terms of satellite-derived canopy greenness (normalized difference vegetation index (NDVI)) and stem growth derived from dendrochronology. They recorded the loss of greenness and growth during the drought events (i.e. sensitivity) and recovery following rain. The study found that recovery-to-sensitivity ratios varied greatly among the 11 species and along climate gradients: conifer-dominated woodlands in semi-arid regions were reported to be most sensitive to drought but recovered quickly while broadleafdominated woodlands in humid temperate regions were least sensitive to drought and recovered slowly. However, this study did not attempt to quantify long-term impacts, including the legacy of previous droughts (Anderegg et al., 2015; Peltier et al., 2016; Gazol et al., 2018).

Here, we evaluate one component of forest resilience to climate change - the ability of canopies to resist loss of leaves and/or quickly recover leaves – by looking at time-series of greenness alongside water availability. The analysis of such time-series of remote sensing data is now possible over large scales thanks to advances in cloud computing technology and offers the opportunity to evaluate forest responses to drought in new

detail. We analyse randomly sampled Spanish forests dominated by 10 species groups, inside and outside protected areas, to investigate canopy responses to strong drought events and also the more subtle accumulation of drought stress through time. We address the following questions: (i) to what extent is the greening trend observed in Spanish forests being modulated by drought and climate change? (ii) what environmental factors influence the response of canopy greenness to drought across Spain; (iii) how does drought resilience vary among forest types; and (iv) do protected areas increase forests resilience to drought? Finally, we tested whether long-term trends in NDVI observed from space relate to basal area trends measured in field inventories. A previous study from Spain found close agreement between ground- and remotely sensed estimates of NDVI when field estimates were made at the same spatial resolution as the remotely sensed pixel (Ogaya et al. (2015), and province-level averages of field and remotelysensed estimates of greenness were also in close agreement (González-Alonso, Merino-De-Miguel, Roldán-Zamarrón, García-Gigorro, & Cuevas, 2006). Here we extend this approach by comparing satellite imagery with the data collected by Spanish National Forest Inventory.

Given the above-mentioned increases in aridity during the past decade and the evidence of forest die-back as well as greenning in Spain, we expected to observe forest growth in some areas because of recent land abandonment and decline in areas that have recently become drier. In parallel, we expected that species dominating areas that have always been dry, i.e. south-east Spain, would be more resilient to drought than historically wetter areas. Concerning forest species' responses to drought, we envisaged that conifer canopies, specifically pine canopies, would be less resilient to drought compared to broadleaf canopies because of the reported succession advancement of oaks on pines in Mediterranean forests of Spain (Carnicer *et al.*, 2013); and that non-native fast-growing eucalypt would also be less resilient given their high water needs (Queirós *et al.*, 2020). Finally, given that protected areas are supposed to be managed for resilience, we expected them to respond differently to unprotected areas, while recognising that only 20 to 50 % are reported to have effective management (de la Guerra *et al.*, 2017).

# 2.2 Methods

### Site selection & pre-analysis

#### Data

•Land cover maps: CLC2000\_CLC1990\_V2018\_20 & CLC2006\_CLC2000\_V2018\_20 from CORINE Land Cover rasters.

# •Protected area status:

ENP (Espacios Naturales Protegidos) and rn2000 (Red natura 2000) shapefiles from the Spanish Ministry of Agriculture, Food and Environment.

#### Species data:

European forest species distribution map (Brus et al., 2012).

#### Methods

Stratified sampling used to sample 450 pixels randomly per forest type from areas that were over 60% forested inside and outside protected areas.
Samples which were nonforested according to the landcover maps were excluded from analysis.

#### Analysis

#### Data

•Satellite data: MODIS/006/MOD13Q1, MODIS/006/MYD13Q1 for NDVI 250 m resolution monthly averages from 2000 to end of 2017 & MODIS/006/MCD15A3H for LAI from the Moderate-resolution imaging spectroradiometer (MODIS) catalogue on Google Earth Engine: ~ 3,100 pixels

#### •Environmental data:

-Standard Precipitation Evapotranspiration Index (SPEI) from 2000 to end of 2017 from Vicente-Serrano et al. (2017). -Elevation Shuttle Radar Topography Mission (SRTM) digital elevation dataset, version 4 (Jarvis et al., 2008).

-Global Land Data Assimilation System 2.1 products: precipitation, solar radiation, maximum and minimum air temperature, and wind speed.

### Validation

#### **Data** •Ground data:

Basal Area from Spanish National Forest inventory permanent plots between the third (1997-2007) and fourth (1998-2008) survey but excluded plots measured before 2000.

#### •Satellite data:

Sentinel-2 level 1C images from May-August 2016.

#### Methods

- Spatial simultaneous autoregressive error estimation models were used to model basal area as function of NDVI and NDVI change as function of basal area change.

#### Methods

- Non-linear model was used to model NDVI as function of LAI. - Multivariate linear models were used to model long-term trends in NDVI, LAI and SPEI. - Linear models were used to model NDVI as function of SPEI and time. - Breakpoint regression analysis was used to compute resilience metrics. - Multivariate spatial simultaneous autoregressive error estimation models were used to model resilience metrics as a function of environmental factors, topographical factors, and species and protected area status.

Flowchart 1 Datasets used, and analyses performed in this study to quantify the resilience of Spanish forests to climate change and extreme droughts and determine its drivers.

# 2.2.1 Theory and definitions of resilience

Resilience to climate change has been defined in numerous ways and measured using many different approaches, making it hard to critically compare studies (e.g. Dakos, Carpenter, van Nes, & Scheffer, 2015; Hodgson, McDonald, & Hosken, 2015; Nimmo et al., 2015; Slette et al., 2019). Here we define resilience broadly as "the capacity of forest canopy to return to a state not qualitatively different from its pre-drought state by resisting and/or recovering" (Folke et al., 2010; Hodgson et al., 2015a). More specifically, we use the NDVI and LAI as greenness and leaf area indices and the standardized precipitation evapotranspiration index (SPEI) as water availability indicator (Vicente-Serrano et al., 2017). The simplest resilience concept is illustrated in Figure 2.1e - here we see vegetation's response to specific drought events—"resistance" is the capacity to withstand or tolerate drought, its inverse "sensitivity" is computed here as the absolute loss in greenness during a drought event; "recovery" and "adaptability" are both computed here as the absolute gain in greenness following a drought event. We use a segmentation approach to detect these drought related events (detailed in section 2.6). We also develop an approach to quantify short-term and long-term resilience to drought (Camarero *et al.*, 2018) based on measuring the correlation between greenness and water availability (Figure 2.1a-d) (detailed in section 2.5). Remote sensing approaches are unable (currently) to measure the recruitment of new species and the loss of others, which may influence resilience via adaptation processes, these recruitment processes and shift in species distributions are therefore not addressed in this work (Folke *et al.*, 2010).



# Figure 2.1 Conceptual diagram explaining studied resilience measures.

(a) A regression line (purple) is fitted to the SPEI<sub>x</sub> time-series (dark-red) representing long-term climate changes; (b) a regression line (blue) is fitted to the deseasonalised time-series of NDVI (dashed green) representing long-term change in greenness; (c) co-variation is estimated between detrended NDVI (green) and detrended SPEI<sub>x</sub> (red) from a linear model between the two; (d) deseasonalised time-series of potential greening (dotted green) and its corresponding trend (orange) are determined and the difference between potential and observed greening (shaded in red) corresponding to the long-term climate change influence on greenness; (e) deseasonalised NDVI is segmented (dashed purple line) and two biggest negative changes representing forest canopy sensitivity (i.e. NDVI loss) are detected followed by the recovery measures (i.e. NDVI gain) (solid purple segments).

# 2.2.2 Site selection

Spain has the largest forest cover of any country in the Mediterranean with more than a quarter of its territory dedicated to nature conservation, and over 1500 protected natural areas (de la Guerra et al., 2017; FAO & Plan Bleu, 2013). Stratified random sampling was used to select 4500 1-km<sup>2</sup> pixels representing 10 forest types and three protection statuses across Spain. Ten dominant species groups (forest types) were considered for the analysis identified from European forest species distribution maps (Figure 2.2b; Brus *et al.*, 2012). We sampled 450 pixels randomly per forest type from areas that were over 60% forested selecting 10 of the most abundant species groups (Figure S1.2) as computed from species distribution maps by Brus *et al.* (2012). The dominant forest species dataset used includes broad taxonomic categories, some of which span several bio-climatic regions, such as oaks and maritime pines (Figure 2.1b).

Previous land cover could influence plant-water relations within sites because former farmland is likely to be on deeper soils, and that in turn could influence the resilience of forests. To test its influence, the landcover type of each of our MODIS pixels was obtained by extracting data from the 1990 and 2000 CORINE Land Cover rasters (CLC2000\_CLC1990\_V2018\_20 and CLC2006\_CLC2000\_V2018\_20), and then downscaling from 100 m to 500 m resolution using a nearest neighbourhood method (Figure S1.3: Corine 1990 and 2000 classifications for our pixels). Out of 4500 pixels, 342 were classified as agricultural, irrigated, or non-vegetated lands in 1990 and 2000 years and were excluded because of inconsistencies with the map of Brus et al. (2012). Of the remainder, 304 (8.6%) were classified as "previously agricultural or irrigated land" in 1990 and had transitioned to 'forest' by 2000. We included previous landcover (i.e. agricultural vs forested in 1990) as a factor in our models.

Protected area maps were obtained from the Spanish Ministry of Agriculture, Food and Environment. We focussed on sampling locations categorised as Sites of Community Importance (SCI), Special Conservation Zones (ZEC) within the Natura 2000 network, contrasting these sites with those without legal protection (Figure 2.2a). These sites include private and public lands that are meant to be managed in an ecologically and economically sustainable way, including agricultural activities, hunting and tourism (Martínez-Fernández, Ruiz-Benito, & Zavala, 2015). ZEC are supposed to be wellmanaged multifunctional woodlands that provide different ecosystem services, however as mentioned in the introduction, ecologically functional goals are not always achieved because of a lack of proper management and funds. In 2017, 20-50% of Natura 2000 sites were SCI whose management plans were still under consideration for approval to become ZEC. Note that Nationally Designated Protected areas – which are concentrated in Catalonia and Andalusia - were omitted from the analyses, because these are more strictly managed, usually prohibiting all human activity. It would be interesting to differentiate between Natura 2000 and Nationally Designated Protected areas in a future study.





(a) Protected areas considered in this study taken from the Spanish Ministry of Agriculture, Food and Environment.; (b) dominant species of pixels extracted taken from Brus et al. (2012). Note that the "other broadleaves" category represents planted woodlands dominated by species such as almond, carob, elm, lemon, poplar, while "other conifers" represent species such as cedars and junipers.

# 2.2.3 Time series of greenness and drought severity

# 2.2.3.1 Datasets

Monthly estimates of forest greenness in the form of NDVI (for the period February 2000 to December 2017) were extracted from a NASA database (MODIS/006/MOD13Q1 & MODIS/006/MYD13Q1). NDVI was selected because it tracks seasonality more

accurately than the Enhanced Vegetation Index (EVI) and other indices (De Oliveira Silveira et al., 2008; Evrendilek & Gulbeyaz, 2008; Verbesselt et al., 2009), but most importantly because NDVI resilience measures were shown to correlate with tree-ring derived resilience measures (Gazol et al., 2018). The dataset comprises multispectral reflectance measurements recorded by MODIS Aqua and Terra satellites at a spatial resolution of 250 m (Didan, 2015a,b), from which 16-day composites were constructed. These data have been corrected for atmospheric and bi-directional surface reflectance effects, and water, clouds, heavy aerosols and cloud shadows have been masked out by NASA. We further masked time-series of NDVI following quality assurance information and aggregated it to monthly values at the resolution of 500 m. Leaf area index was also obtained from MODIS product MODIS/006/MCD15A3H for the year 2013 at 500 m resolution (Myneni et al., 2015) (Myneni et al., 2015) in order to relate losses and gains in greenness to actual biomass. The year 2013 was chosen because it was a relatively normal year in terms of wetness/dryness according to SPEI time-series. Summary data were exported for analysis in R. It is known that NDVI and leaf area index (LAI) are nonlinearly related, with NDVI saturating at high LAI (Figure S1.4), and this non-linearity is considered when interpreting results (Turner et al., 1999; le Maire et al., 2006). A nonlinear model was fitted to average NDVI for the year 2013 with average LAI, and the model was used to convert NDVI time-series into LAI time-series and interpret all results obtain from NDVI analysis in LAI terms as well (Table S1.1, M5, and Figure S1.4).

An absolute measure of yearly climatic water balance was computed for each site to evaluate the effect of the latitudinal climatic gradient on forest response to drought. It corresponds to monthly precipitation minus potential evapotranspiration averaged across the 18 years. Potential evapotranspiration was calculated using the "Penman" function in the *SPEI* package (Beguería & Vicente-Serrano, 2017), by inputting minimum and maximum temperature, mean daily external radiation, wind speed, and pixel latitude. All climatic variables were extracted from Global Land Data Assimilation System 2.1 products (Rodell *et al.*, 2004). In addition, time-series of monthly absolute water balance were also used to be compared with the relative water balance index, SPEI (used in this chapter to evaluate the intensity of drought).

Elevation data were obtained from the Shuttle Radar Topography Mission (SRTM) digital elevation dataset, version 4 (Jarvis *et al.*, 2008).

Time-series of SPEI, representing relative water availability, were extracted from a database available at 1.1 km resolution for the entirety of Spain from 1961-2017 and used as a climate change index (Vicente-Serrano et al., 2017). It is important to note that SPEI provides an index of temporal change in water availability within a site. It should not be used to make direct comparisons of absolute water availability among sites but can be used to compare the relative intensity of a dry or wet period. For example, in this paper, we are mostly interested in the severity of drought events relative to the severity of drought events experienced over time in a site and use this relative severity (i.e. SPEI) when comparing forest responses. SPEI is widely used as an alternative to SPI, which is based solely on precipitation (Vicente-Serrano et al., 2010; Azorin-Molina et al., 2014; Tejedor et al., 2016; Bottero et al., 2017; Gazol et al., 2018). SPEI is computed as follows: first, a monthly water balance is calculated for every month from 1961 to 2017, by subtracting weekly potential evapotranspiration from weekly precipitation. Secondly, because the impacts of drought can be cumulative, a sequence of alternative SPEI timeseries is created from SPEI values averaged over a different number (X) of months. In this study, SPEI is calculated for X ranging from 1 to 48 months. The cumulative water balance is calculated from the weighted average of a particular month and the X-1 previous months using a rectangular weighing function. The SPEIx is then obtained from normalizing water balance series into a three-parameter log-logistic distribution using non-biased Probabilistic Weighted Moments (PWMs) to calculate the parameters. The parameter estimation of the log-logistic probability distribution and detailed calculation procedure for SPEI index can be found in Vicente-Serrano et al. (2010). The result is a non-seasonal time-series of SPEI<sub>X</sub> values that represent the probability of a given month being relatively dry or wet compared to the reference period 1961-2014 (Mckee et al., 1993; Vicente-Serrano et al., 2010; Beguería et al., 2014). Given that the Spanish drought dataset consisted of four SPEI time steps per month (Vicente-Serrano et al., 2017), we averaged those four values to get time-series of monthly SPEI.

These datasets mentioned in this section, with the exception of SPEI, were all available through Google Earth Engine.

## 2.2.3.2 Greening and climate change trends

A particularly effective method of monitoring vegetation from space is detecting and understanding changes in time-series of greenness (Jamali *et al.*, 2015). These changes tend to fall under three categories: seasonal changes, gradual changes and abrupt changes (Verbesselt *et al.*, 2010). Recent methods of analysing these changes consist of decomposing the time-series into a non-linear 'trend' which captures the gradual changes caused by interannual climate and land-use variations as well as the abrupt changes caused by disturbances, a 'seasonality' which follows annual temperature and rainfall, and a 'residual/remainder' variations unexplained by the former factors (Verbesselt et al., 2010; Jamali et al., 2015). In this work, we focus only on gradual changes in NDVI and LAI trends, which are the type of changes that drought usually causes. In this first part, we decompose the NDVI time-series removing 'seasonality' and 'residuals', keeping only the non-linear trend in NDVI, in order to relate it to non-seasonal climate change index SPEI using the DBEST package in R (Jamali et al., 2015; Jamali & Tomov, 2017). The DBEST function detected abrupt changes in 20 of the 4158 pixels, which were excluded from subsequent analyses as they represent extreme events such as fire, clear-felling, and sensor-related artefacts which are beyond the scope of our study. A further 952 plots were eliminated because of missing NDVI or SPEI data-points leaving 3528 plots for further analysis. We used two linear models (equations 2.1 & 2.2, and Table S1.1, M1&M2) to determine the long-term trends in SPEI and greenness over the past 18 years. Linear models are commonly used to estimate long-term trends in vegetation and climatic data (Eslamian et al., 2011; Chu et al., 2019). Although they can be affected by start date and by temporal auto-correlation when the time-series are small (Bayazit & Önöz, 2007; Chu et al., 2019), the series evaluated here span a period of 215 months which minimizes these effects (see section S1.5 for more information on temporal autocorrelation).

$$SPEI_X(t) = \beta_C + \alpha_C \cdot t + \varepsilon_C(t), \qquad (2.1)$$

$$NDVI(t) = \beta_G + \alpha_G t + \varepsilon_G(t), \qquad (2.2)$$

where *t* is time (1 to 215 months) within the 18-year time series,  $\alpha$  and  $\beta$  are coefficients estimated by least-squares regression and  $\varepsilon$  are normally distributed residuals (in 2.2  $\varepsilon$  is the variation in the trend rather than the residual as that was eliminated with the seasonality). Subscripts in these models indicate C for climate and G for observed greenness.  $\beta$  is the predicted initial SPEI<sub>X</sub> or NDVI of a plot (i.e. on February 2000), and  $\alpha$  represents the long-term linear trend in climate (i.e. SPEI) or greenness of a plot, respectively.

Further linear models were used to evaluate how greening trends vary across Spain, testing whether they vary with elevation, average water balance, average greenness, forest type, and protection status (Table S1.1, model M10 - 11). Models were conducted using spatial simultaneous autoregressive error estimation (SSAEM), which account for the residual spatial structure within the neighbourhood of pixels (*spatialreg* package in R - Bivand & Piras, 2019). AIC and correlograms at varying neighbourhood distances were used to determine the best-supported model to account for spatial autocorrelation.

# 2.2.4 Determining the drought accumulation period across Spanish forests

To determine the drought accumulation period over which drought affects forest greenness, we recorded which SPEI<sub>X</sub> time-series correlated most closely with the forest greenness time-series at a site. We used a cross-correlation function with zero time lag (as the X scales of SPEI are already computed to account for time lags) correlating detrended SPEI<sub>x</sub> against detrended, deseasonalised NDVI for drought accumulation periods ranging from X = 1 to 48 months, and the value of X that gave rise to the highest correlation was noted: we refer to this as the drought accumulation period was used in all subsequent analyses. This allowed us to account for lags in forest response to drought and delayed mortality to which some species are susceptible, and for different water reservoirs that cause a delay in water deficit and surplus effects (Vicente-Serrano *et al.*, 2013).

# 2.2.5 Time-series analysis of forest response to drought

SPEIx and NDVI time-series were used to quantify two metrics for each pixel: shortterm covariance and long-term climate change influence (see Figure 2.1). A linear model (Table S1.1, M4) was fitted to the deseasonalized NDVI time-series using smoothed SPEIx time-series, where deseasonalisation was achieved using the DBEST package, and smoothing using locally weighted smoothing (theta = 0.1) in R, to eliminate noise and make SPEIx comparable to the NDVI trend:

$$NDVI(t) = \alpha_P \cdot t + \gamma_G SPEI_X(t) + \beta_P + \varepsilon_P(t), \qquad (2.3)$$

where t is time (1 to 215 months) within the 18-year time series,  $\alpha_P$ ,  $\beta_P$  and  $\gamma_G$  are coefficients estimated by least squares regression and  $\varepsilon_P$  is the residual. Subscripts in these models indicate, P for potential greenness, G for observed greenness.

Substituting equation 2.1 into equation 2.3 we get:

$$NDVI(t) = \alpha_P t + \gamma_G (\alpha_C t + \beta_C + \varepsilon_C(t)) + \beta_P + \varepsilon_P(t), \qquad (2.4)$$

where  $\alpha_P = \alpha_G - \gamma_G . \alpha_C$ ,  $\beta_P = \beta_G - \gamma_G . \beta_C$ , and  $\varepsilon_P = \varepsilon_G - \gamma_G . \varepsilon_C$ . Here  $\alpha_P$  is the potential greening trend; it is comprised of the observed greening trend  $\alpha_P$  and the influences of long-term changes in climate ( $\gamma_G . \alpha_C$ ) on greenness.  $\gamma_G$  provides an estimate of how strong the covariance between greenness and changes in water availability (CGW) is.  $\alpha_G - \alpha_P = \gamma_G . \alpha_C$  corresponds to estimated long-term climate change influence (CCI) on greenness.  $\varepsilon_G$  is the residual which contains the non-linear trend, and the noise (also normally distributed).

Regression modelling produces two new summary variables for each pixel: short-term CGW and long-term CCI. It is key to understand that CGW, represented by the coefficient ' $\gamma$ ' in Figure 2.1c which quantifies how greenness varies with drought index on a monthly basis, relates to both losses and gains and is not an indication of resilience alone. Large CGW values correspond with big losses and/or big gains. Strong and weak covariance could indicate different mechanisms to overcome droughts better known as drought avoidance and drought tolerance mechanisms respectively which relate to anisohydric and isohydric behaviours not just in terms of stomatal behaviour but also in terms of leaf shedding (Sade *et al.*, 2012; Roman *et al.*, 2015; Hwang *et al.*, 2017). CCI, on the other hand, represents the long-term climate change influence on greenness; it can be represented as the difference between the actual greenness and the potential greenness as demonstrated in Figure 2.1d if greenness in the long-term is affected to a similar degree to the short term by the coefficient ' $\gamma$ '.

Statistical modelling was used to evaluate how short-term covariance and long-term CCI varied across Spain, in relation to elevation, average water balance, and average greenness (Table S1.1, M14 - M21). Additional models included forest type and protection status as explanatory variables.

We evaluated whether field data confirmed remote sensing analyses at the national scale using the Spanish National Forest Inventory, albeit with plots that differed in resolution from the satellite data. The Spanish Forest Inventory is a systematic network of plots for each km of forested area in Spain (Villaescusa & Díaz, 1998; Villanueva, 2004). For basal area calculations, we used the permanent plots between the third (1997-2007) and fourth (1998-2008) survey but excluded plots measured before 2000. Each plot has a variable radius design, comprised of four concentric circular subplots of 5, 10, 15 and

25 m where adult trees of < 12.5 cm, < 22.5 cm, < 42.5 cm and  $\geq$  42.5 were measured, respectively. For each sampled tree it was recorded status (alive, death), height, d.b.h, and species identity. Basal area change was computed as the difference in stand basal area in m<sup>2</sup>/ha between the two surveys (Ruiz-Benito et al., 2013). Given the very different spatial resolution of the MODIS data (500 m) and the field plots (25 m) we restricted our analyses to pixels in which forest was relatively homogeneous. To do this, a cloud-free image of Spain was obtained (by mosaicking Sentinel-2 level 1C images from May-August 2016) and NDVI computed for pixels of 25m and 500m resolution centred on the plot locations. The year 2016 was chosen because it was relatively a normal year in terms of wetness/dryness (looking at SPEI) and the summer period was chosen to avoid the understory effects on the NDVI signal. Sites that had a difference in NDVI over 0.01 between the two resolutions were excluded from further analyses leaving 2150 out of 4649 pixels/plots to analyse. Modis NDVI data was extracted using the approach described in section 2.3.1 and the absolute NDVI trend (determined from the DBEST package) was computed between the dates of the third and fourth national forest inventory. Spatial autoregressive modelling was used to determine the relationship between the greenness and basal area change.

# 2.2.6 Break-point analysis approach to resilience estimation

Break point analyses were conducted to detect the greatest changes in NDVI and LAI within each time series, from which loss and gain indices were estimated. The time-series NDVI and LAI were decomposed into trend, seasonality, and remainder (see section 2.3.2), and the trend was segmented using the *DBEST* package in R (Jamali & Tomov, 2017). As illustrated in Figure 2.1e, loss and gain were estimated from the two most negative segments followed by a positive segment, respectively. Loss was estimated as the mean of the absolute negative changes in NDVI (i.e. NDVI<sub>peak</sub> - NDVI<sub>pre-event</sub>) and gain as the mean increase in NDVI following these negative changes (i.e. NDVI<sub>post-event</sub> - NDVI<sub>peak</sub>). Minimum water availability (minimum SPEI) as well as maximum water availability (maximum SPEI) were extracted over those two detected loss and gain periods respectively and their mean computed for each series, representing water deficit and water surplus events, respectively. Spain experienced major droughts in 2005, 2012 and 2017 (Figure 2.4a). Only the two biggest declining segments before March 2014 were used – allowing time for recovery – to estimate forest resilience components. We did not examine specific years or months because drought intensity varies over space and time.

Instead, we determined the water availability at times when major losses and gains in NDVI or LAI were detected in the time-series, therefore allowing droughts starting dates to vary. Nevertheless, drops in NDVI and LAI were mostly associated with the two drought years of 2005 and 2012 (Figure S1.5).

To determine the relationships between loss and gain, and to test whether it varied systematically among forest types and protection statuses, we used ordinary least-square regression. Loss and gain were log-transformed to improve residual normality (Table S1.1, model M5, Figures 2.10a and S1.6). Predictions were then back-transformed to an arithmetic scale with a correction factor (Figures 2.10a and S1.6) (Baskerville, 1972).

To help elucidate the drivers of resilience, losses and gains in greenness and leaf area, and their ratio estimates, were modelled as a function of elevation, average water balance, average greenness, relative water deficit (-minimum SPEI), water surplus (maximum SPEI), forest type, and protection status again using SSAEM (Table S1.1, M22 - M39).

# 2.3 Results

# 2.3.1 Water balance is the biggest determinant of forest greenness and leaf area

As expected, forests were greenest in the wetter regions of Spain (Figure 2.3d), with greenness (i.e. average NDVI) and canopy cover (average LAI) varying with the environment as follows:

Mean NDVI = 0.64 + 0.000054 [Water Balance]; standard error (SE)= 0.014 and 0.000014 respectively.

Mean LAI = 1.88 + 0.00022 [Water balance]; SE= 0.090 and 0.00008 respectively.



# Figure 2.3 Greenness and water availability landscape in Spain.

(a) Average NDVI over Spain for the wet year of 2013; (b) average leaf area index (LAI) over Spain for 2013; (c) average climatic water balance as computed from the difference between monthly precipitation and Thornthwaite potential evapotranspiration for 2013; (d) variation in average greenness and canopy cover with average yearly water balance (mm/yr). NDVI regression line in dark green and LAI regression line in bright green with uncertainty around these lines shaded in green.

# 2.3.2 Long-term trends in water availability and greenness

Over the past 18 years, 73% of Spanish land has become drier, with an average change in SPEI<sub>1</sub> of -0.24, which is almost a quarter of a standard deviation drier than the average for 1961 to 2014 (Figure 2.4). This corresponds to an increase in water deficit of about 2 mm/year as calculated from the linear relationship between SPEI<sub>1</sub> and water balance (Figure 2.4c). Of the forest pixels that we randomly sampled over Spain (Figure 2.2b), 35% showed a significant drying trend (linear modelling, p < .05), 37% did not change significantly and 27% got wetter (Figure 2.5a). The climate of the wetter regions changed least, whilst the drier regions became increasingly arid (i.e. Figure 2.4b,c).



#### Figure 2.4 Standard Precipitation-Evapotranspiration Index (SPEI) over Spain.

(a) SPEI<sub>1</sub> change over Spain for the period 2000-2017; with the inset showing the average SPEI<sub>1</sub> over Spain +/- standard deviation and linear trend in purple; (b) relationship between SPEI change and average water balance, computed from the Penman-Monteith equation (see S1.2:M6); (c) relationship between SPEI change and yearly water balance change over the past 18 years (see S1.2:M7).

Despite these strengthening water deficits, 75% of Spanish forest pixels became greener over time and only 12% became less green (Figure 2.5b). On average there was an 11% increase in LAI (from 1.7 to 1.9  $m^2/m^2$ ), and some variation with canopy density (i.e. average LAI): less green sites (lower quartile LAI = 1.36) accumulated 0.1  $m^2/m^2$  of

leaf area while the more green sites (upper quartile LAI=2.26) accumulated  $0.3 \text{ m}^2/\text{m}^2$  over 18 years.



**Figure 2.5 Changes in SPEI and greenness over the past 18 years in studied Spanish forests** (a) Relative frequency histogram of SPEI<sub>x</sub> change over forest plots with significant changes in red and non-significant changes in grey (linear modelling, p < .05); (b) relative frequency histogram of changes in greenness over forest plots with significant changes in pink and non-significant changes in grey (linear modelling, p < .05). Black lines indicate average of change in SPEI and NDVI.

Correlation of remote- and plot-based observations of forest change (see section 2.5 for details) showed a significant positive logarithmic relationship between basal area and average deseasonalised NDVI at the time of the third inventory, with a Nagelkerke R<sup>2</sup> of 0.22 (Figure 2.3a). A significant positive linear relationship was found between basal area change and NDVI trend change between the two inventories (Figure 2.6b) with a Nagelkerke R<sup>2</sup> of 0.12. These analyses build confidence that our remote sensing analyses of resilience correspond with changes observed on the ground.



#### Figure 2.6 Relationship between plot-based measurements of basal area and remotelysensed measurements of greenness.

(a) Basal area measured during the third Spanish national forest inventory as a function of average deseasonalised NDVI (as extracted from DBEST) for the same date; (b) greenness change as a function of basal area change between the third and fourth Spanish national forest inventory.

Examining individual time-series, we found a close covariance of greenness with climatic conditions: SPEI<sub>x</sub> explained 49% of the variation in canopy greenness (average R<sup>2</sup> of 3182 linear models fitted to paired SPEI-NDVI time-series). Only 19 % of the pixels responded immediately to water deficit (i.e. correlated best with a drought accumulation period X of only 1 month).

In the long-term, climate change influence (CCI) on greenness was significant in 58% of the plots (with 56% negative effects and 2% positive effects, p < .05) but changes were small in magnitude (Figure 2.7). The CCI on NDVI varied across Spain as follows (Figure 2.7a):

CCI<sub>[NDVI]</sub>= **-0.0016**+ **0.0023** [water balance] + **0.0010** [elevation], SE= 0.0005, 0.0004 and 0.0003 respectively.

To put this model in context, on average canopy greenness was observed to increase by 0.0274 over 18 years, assuming a linear relationship between NDVI and SPEI trends, our model predicts increase of 0.0284 if climate change had not occurred. The equation shows that climate change did have a stronger impact at dry sites and at low elevations (Figure 2.7a). Similarly, the climate change influence on LAI (Figure 2.7b) is given by: CCI<sub>[LAI]</sub>= -0.0015 + **0.0121** [water balance] + **0.0075** [mean LAI], SE=0.0038, 0.0031, and 0.0019 respectively.

CCI<sub>[LAI]</sub> increased from -0.020 at the driest sites to 0.017 at the wettest sites (i.e. from -1181.5 to -301.5 mm, these representing the 5<sup>th</sup> and 95<sup>th</sup> percentiles of observed distribution in annual water balance). It also increased with LAI from -0.013 at 0.88 to 0.011 at 2.93 (again the 5<sup>th</sup> and 95<sup>th</sup> percentiles of LAI). Again, this means that the CCI on greenness caused the LAI trend to be significantly smaller in drier or more dense sites (Figure 2.7b).



Figure 2.7 Climate change influence (CCI) on greenness (i.e. difference in greenness trend caused by long-term trends in climate), as a function of elevation (m), water balance (mm/year) and average LAI ( $m^2/m^2/year$ ).

(a) CCI as computed from modelling NDVI with SPEI as a function of environmental variables; (b) CCI as computed from modelling LAI with SPEI as a function of environmental variables. Uncertainty around regression lines is shaded in the environmental variable respective colour.

# 2.3.3 Water availability is the main driver of short-term changes in forest greenness

The short-term effect of relative water balance variation on canopy greenness (CGW, see section 2.5) varied across Spain as follows (Figure 2.8):

CGW<sub>[NDVI]</sub>= **0.0148 - 0.0041** [mean NDVI] **- 0.0034** [elevation], SE= 0.0008, 0.0003, and 0.0004 respectively.

The terms in square brackets are scaled environmental variables. The model demonstrates that the covariance was weaker in elevated areas. The covariance was also weaker in forests with high NDVI but once the result was converted to LAI, it translated into a stronger covariance for forests with denser canopies (i.e. large LAI):
CGW<sub>[LAI]</sub>= **0.0918 + 0.0262** [mean LAI] – **0.0222** [elevation], with SE=0.0052, 0.0018 and 0.0023 respectively.



Figure 2.8 Variation of short-term covariance between greenness and SPEI along forest density and elevation gradients.

(a) Covariance between NDVI and SPEI; (b) covariance between LAI and SPEI. Uncertainty around regression lines is shaded in the environmental variable respective colour.

Breakpoint analysis demonstrated that in the aftermath of a strong drought event, forests regained, on average, only 80% of their lost greenness during droughts. Given that forests accumulated leaf area over the 18-year study, they must have regained the remaining 20% of their leaves (and more) in subsequent years not captured by the analyses' characterisation of losses and gains. Losses and gains in LAI were greatest in dry regions (Figure 2.9(1)). The relative water deficit during a drought event (-minimum SPEI) and relative water surplus post-drought (maximum SPEI) both had a significant effect on all resilience components. The canopy greenness losses and gains were greater with an increase in water deficit (Figure 2.9a,b (2)). Furthermore, pixels hit by stronger drought were more resilient as deduced from the water deficit negative relationship to the gain-to-loss ratio (Figure 2.9c (2)). The NDVI gain, as well as gain-to-loss ratio, were equally affected by how wet the period that followed the drought was (Figure 2.9b,c (3)). Denser forests (i.e. forests with higher LAI) lost and gained more due to droughts (Figure 2.9(4)). Forests at higher elevations were more resistant to drought events (Figure 2.9a(5)).



#### Figure 2.9 Effects of environmental conditions resilience components.

(a) Loss during drought; (b) gain after drought; and (c) gain-to-loss ratio of LAI. The effect sizes shown are coefficients (mean  $\pm 99\%$  confidence intervals) estimated by spatial autoregressive modelling. Explanatory variables are scaled, so coefficients indicate the effect on these components of shifting to an environment that is +1 SD from the mean environment. The dashed lines indicate the average loss, gain, and gain/loss ratio for the mean environment.

#### 2.3.4 Influences of forest type on drought response

Forests exhibited a spectrum of responses to drought, with breakpoint analysis indicating that some forest types lost and re-gained little NDVI or LAI while others fluctuated greatly (Figure 2.10a). Gains and losses were correlated across forest types (r = 0.66 for NDVI and r = 0.48 for LAI; Figure 2.10a). Specifically, *Castanea* dominated forests had below-average losses and gains indicative of drought tolerance, while maritime pines had above-average losses and gains which can be indicative of the drought avoidance mechanism (Figure 2.10a). This range of responses was confirmed by the analyses of the entire time-series; there was a close correlation between the short-term covariance of greenness and SPEI, and the greenness gains and losses determined by breakpoint analysis within the different forest types (Figures S1.13 and S1.14). Species groups that lost and gained little after the drought had a lower short-term CGW while species groups that lost and gain a lot had higher short-term CGW (indicated by circle sizes in Figure 2.10a; short-term covariance is correlated to loss (r = 0.87 for NDVI and r=0.48 for LAI) and gain (r = 0.44 and r=0.32 for LAI, p < .05 in both cases).

We found that the non-native *Eucalyptus* had low gain-to-loss ratios following droughts (Figure 2.9b), which explains the decline in leaf area in 26% of examined *Eucalyptus* plots, a significantly higher percentage than the average of 12% (Table S1.2). Looking at the long-term CCI, we found that growth in most Spanish forests is similarly impacted by SPEI trends (Figure 2.10c). Only two groups, *P. pinaster* associated with xeric sites, as well as *Q. robur and Q. petraea*, were more severally pressured by climate change (Figure 2.10c). Combining this with previous findings, we conclude that the overall greening of Spain is possible in part because of species that are resilient to drought while

the decline in many *Eucalyptus* plantations (26%) is mostly caused by their low short-term resilience.



## Figure 2.10 Summary coefficients for the forest types of the spatial autoregressive model performed to evaluate resilience components.

(a) Relationship between the loss, gain and the short-term response to drought of forest types; (b) gain-to-loss ratio (log scale); (c) long-term climate change influence on greenness. Value for forest type indicates the mean response for forests outside of protected areas. Overall mean for forest outside protected areas indicated by the black dot in (a) and the dashed lines in (b) and (c), and the error bars represents 99% confidence intervals. Note losses and gains were logtransformed to improve normality of residuals since both measurements are right-skewed, and because gains tend to be smaller when losses are large.

# 2.3.5 Resistance of protected areas to climate change and effect of previous land-cover

Canopy greenness and leaf area inside protected areas were more stable over the 18 year time-series (Figure 2.11c). Looking at the covariance between SPEI and canopy greenness results, protected forests were significantly less sensitive to drought than unprotected forests (i.e. lost and gained less greenness during droughts) (Figure 2.11b). On the other hand, the equivalent response in leaf area change was not significant indicating that the leaf area did not change much in these forests (Figure 2.11c). No significant difference was found in the gain-to-loss ratio in the most extreme droughts yet, since, as mentioned previously, Spanish forest canopy greenness was found to be typically resilient (Figure 2.11a).



**Figure 2.11 Leaf area losses and gain in the short-term across different protection statuses.** (a) LAI losses and gains to sever droughts with fitted line back transformed from the log-log relationship between the two; (b) summary coefficients for the protected areas of the spatial autoregressive model performed to evaluate short-term covariance between SPEI and NDVI; and (c) summary coefficients for the protected areas of the spatial autoregressive model performed to evaluate short-term covariance between SPEI and LAI. Values in (b) and (c) are for all forest types. Averages for non-protected areas are indicated by the dashed lines and the error bars represents 99% confidence intervals.

#### 2.4 Discussion

#### 2.4.1 Long-term and short-term climate change influence on forest canopy.

The regression and breakpoint analyses of NDVI time series over the past 18 years shed light on why Spanish forest canopies are so remarkably resilient to climate change, on average greening despite the drying trends in the region. The NDVI time-series covaried closely with relative water availability ( $R^2 = 0.49$ ) which agrees with previous findings (Gouveia et al., 2012). In the short-term this covariance caused significant variation in canopy greenness and leaf area in response to drought events, with average losses in LAI during strong droughts amounting to  $0.32 \text{ m}^2/\text{m}^2$ , however, in the longterm, this covariance had a much smaller influence on greening trends with predicted changes to LAI amounting on average to  $0.0002 \text{ m}^2/\text{m}^2/\text{yr}$  with a standard deviation of 0.004. Drought effects on vegetation are commonly defined as a multi-scalar phenomenon, progressing from stomatal closure, and/or leaf abscission to embolism and hydraulic failure in response to water deficit (Mckee et al., 1993; Vicente-Serrano et al., 2010), but few studies on forest resilience have dealt with this temporal aspect of trees response to drought (Schwalm et al., 2017; Camarero et al., 2018). The use of SPEI at different accumulation periods X allowed us to account for lags in forest response to drought and to better capture the effect of water deficit on vegetation. Recent analyses of Spanish forests indicate that drought was responsible for 50% of damage to forest canopies ("damage" defined as >25% defoliation of the canopy), followed by insects and

pathogens that were responsible for 24% of damage (IDF España, 2017). However, these analyses focus on the sensitivity of woodlands, not recovery. On average, 80% of losses in greenness were recovered in the 18 months following a drought event, while the remaining 20% were recovered in subsequent years to give the long-term greening trend we observe (Figures 2.10b, 2.10a and S1.7). These results suggest that forests in Spain mostly undergo defoliation that is easily recoverable in the wet period following a drought, while 20% of the damages that can be more permanent are outgrown in the next couple of years before another drought happens. Water availability in the period after the severe drought is important for forest recovery (Jiang et al., 2019), as we indeed found that greater water availability (maximum SPEI) led to greater recovery while minimum SPEI was associated with bigger losses in greenness and leaf area.

Surprisingly, forests exposed to the strongest droughts had the highest gain-to-loss ratios (Figure 2.10b). This phenomenon was observed in several other studies on the effect of drought on forest canopy and basal area (Delissio & Primack, 2003; Dorman, Perevolotsky, Sarris, & Svoray, 2015; Gazol et al., 2018 (see supplementary material); Schwartz, Budsock, & Uriarte, 2019; Serra-Maluquer, Mencuccini, & Martínez-Vilalta, 2018; Slik, 2004), but remains poorly understood. Perhaps intense droughts have a thinning effect on forests as they are associated with greater losses in leaf area (Figure 2.9a). These losses in leaf area which represent an increase in forest litterfall as well as canopy openings could reduce stand transpiration, interception of precipitation and competition for light and water resources (Delissio & Primack, 2003; Sohn et al., 2016; Navarro-Cerrillo et al., 2019; Schwartz et al., 2019). In turn, the reduction of competition above and below ground can boost the recruitment of more resilient trees and the productivity of the surviving trees during the wet period following an intense drought (Slik, 2004; Schwartz et al., 2019). It is possible however that observed increases in remotely sensed short-term resilience is not related to the detected increases in basal area increment (Dorman et al., 2015; Gazol et al., 2018), but instead to the increase of understory photosynthetic activity (Breshears et al., 2005; McDowell et al., 2008; Schwartz et al., 2019).

#### 2.4.2 Spain is greening despite increased aridity

The impacts of climate change on forest health is a highly topical issue (Allen *et al.*, 2010). Temperatures in the region have increased by 1.3°C, compared to 0.85°C

worldwide, since the end of the 19th century, and rainfall has decreased by 20% in some regions but has increased in others (Barbeta *et al.*, 2013; Guiot & Cramer, 2016a; UNEP/MAP, 2016; Zhu *et al.*, 2016). We found an average decrease in the water balance of 1.9 mm/year over our pixels for the period 2000-2017, which follows decreases in precipitation by 1.9 mm/year and increases in temperature by 0.03 °C/year for the period 1961-2011 (Vicente-Serrano *et al.*, 2014a). Indeed, several studies have reported localised dieback associated with extreme drought events in Spain (Lloret *et al.*, 2004; Ogaya *et al.*, 2015; Guada *et al.*, 2016; Lloret & García, 2016; Molina-Venegas *et al.*, 2018).

However, the narrative of declining forest health associated with global warming contrasts with observations made by multispectral sensors, which indicate that Spain is greening (Peñuelas *et al.*, 2002; González-Alonso *et al.*, 2004, 2006; Alcaraz-Segura *et al.*, 2008; Hill *et al.*, 2008; Khorchani *et al.*, 2018). We found that 75% of Spanish forested pixels analysed had become greener over the past 18 years (+0.03 NDVI and +0.18 m<sup>2</sup>/m<sup>2</sup>/yr LAI). Suggested causes of these trends include increased radiation (Khorchani *et al.*, 2018), land-use change (García-Ruiz & Lana-Renault, 2011; Khorchani *et al.*, 2018), partly due to abandonment of grazing lands in the last few decades (Hill *et al.*, 2008; Carnicer *et al.*, 2014) and increased basal area of woodlands that are no longer used for timber or charcoal (Otero *et al.*, 2015). Spain joins many other regions of the world that are greening despite climate change (Eastman *et al.*, 2013; Zhu *et al.*, 2016): these global studies have suggested nitrogen fertiliser application and deposition, CO<sub>2</sub> fertilization and more favourable climate conditions all contribute to the trend (Mao *et al.*, 2013; Los, 2013; Eastman *et al.*, 2013; Zhu *et al.*, 2016).

#### 2.4.3 Dense canopies are most sensitive to drought

Changes in satellite-detected greenness are known to be correlated to leaf biomass change and photosynthetic activity (Tucker & Sellers, 1986; Asrar *et al.*, 1989; Baret & Guyot, 1991; Cihlar *et al.*, 1991; Carlson & Ripley, 1997; Zhang *et al.*, 2003), and many studies have used this information to estimate forest biomass from satellite (le Maire *et al.*, 2011; Galidaki *et al.*, 2017). Examining the relation between the Spanish national forest inventory basal area and greenness we found a significant positive relationship that supports these studies. Consequently, our results indicate that in Spain higher canopy density increases competition and transpiration leading to increased sensitivity to drought (i.e. losses in LAI) which agrees with previous studies on forest density effects (Raz-Yaseef *et al.*, 2012; Bottero *et al.*, 2017; Navarro-Cerrillo *et al.*, 2019). We found that forests that have denser canopies, i.e. have a high average NDVI or LAI, are more sensitive to changes in SPEI. The effect of forest density becomes however insignificant when looking at the gain-to-loss ratio to extreme drought (short-term CGW), meaning that density-caused losses in greenness or leaf area are always followed by similar NDVI or LAI gains. We believe that the lack of forest-density effect on short-term greenness resilience is mostly due to the overall resilience of the forests and that stronger droughts will cause this effect to be significantly negative.

#### 2.4.4 Differential response of forest types and protected areas

Spanish forests are currently dominated by pines, which occupy 67% of forested lands, including *P. pinaster* and *P. sylvestris* in big proportions (Figure S1.2) (Brus *et al.*, 2012). The second most dominant species groups are oaks (22% including Q. robur and Q. petraea), secondary successional species, which are favoured by managers and are reported to be advancing on pines (Pausas et al., 2004; Brus et al., 2012; Doblas-Miranda et al., 2014; Martín-Alcón et al., 2015). Understanding the resilience to drought of these two groups is therefore paramount for Spanish ecosystems. Here, forest types differed in response to droughts, indicating differences in the drought resilience behaviours of species that dominate these forest types (Hwang et al. 2017). We found that *Castanea* lost little greenness during drought, consistent with anisohydric species that keep their stomata open and continue photosynthesising for longer when droughts occur (Martínez-Sancho et al., 2017; Mota et al., 2018). This "tolerance behaviour" results in their leaf water potential becoming increasingly negative during drought periods, which can push anisohydric trees beyond their limited hydraulic safety margins, leading susceptible species to hydraulic failure, that can be temporary or permanent (Martínez-Sancho et al., 2017; Kannenberg *et al.*, 2019a). At the other end of the spectrum, *P. pinaster* lost many leaves in response to drought. Isohydric species, like P. pinaster, tend to close their stomata to preserve hydraulic conductivity and then drop leaves as the drought continues (Galiano et al., 2011). Species with an "avoidance behaviour" can die during prolonged droughts as a result of hydraulic failure. Some studies also suggest that carbon starvation can occur (Galiano et al., 2011; Sevanto et al., 2014; Savi et al., 2019), but other researchers remain unconvinced that this mechanism is important (Muller *et al.*, 2011; Körner, 2014). In short, because stomatal closure was considered to be the first response to drought in isohydric species, there was a long-standing assumption that this was the

limiting factor to gas exchange, stopping photosynthesis and tissue formation, and leading to carbon starvation (Körner, 2013). This assumption was challenged time and time again with data proving that turgor loss which happens during drought affects conductivity and carbohydrate use before carbon balance deficit occurs. No consensus is reached on the subject as both seem to be interlinked and can happen at the same time (Sevanto *et al.*, 2014).

Plantations of *Eucalyptus* responded differently to other forest types, recovering slowly from drought (Figure 2.10a) and in a number of cases (26%), higher than other species (12%), failing to recover (Table S1.2). There are reports of *Eucalyptus* declining in response to drought in the Mediterranean regions of their native Australia (Matusick *et al.*, 2012, 2018; Brouwers *et al.*, 2013). In Spain, *Eucalyptus* is planted in wetter regions that have not become drier over the past 18 years, and most reports discuss *Eucalypt* in the context of timber production, pests and diseases (Cadahía *et al.*, 2011; IDF España, 2017) rather than their response to drought (Peñuelas *et al.*, 2001; Barradas *et al.*, 2018).

The study provides no evidence of the widespread permanent hydraulic failure of either isohydric or anisohydric species, as most forest canopies we investigated recovered in greenness following drought events. With the exception of *Eucalyptus* plantations, there were no significant differences in the gain-to-loss ratio of forest types, which might indicate that these contrasting behaviours were similarly effective in terms of canopy resilience. These findings need to be treated with caution, given that few of the forest types were comprised of single species. For instance, P. sylvestris is recognised as an isohydric species (Galiano et al., 2011), but forests classified as dominated by this species did not respond to drought in the way expected of an isohydric species - they lost about average canopy greenness during drought (Figure 2.11a) - so we suspect that other woody species contributed to the greenness signal. Additionally, stands with mediumlow canopy cover that leaves exposed understory and shrub or herbaceous which can contribute to the greenness. Focusing analyses on stands with known species composition will help clarify the responses of species and communities to drought (e.g. Hwang et al., 2017). Furthermore, studies that link canopy greenness trends with detailed physiological measurements are needed to understand the mechanistic explanations behind resilience.

Our regression analyses demonstrate that the management of woodlands in protected

areas has made their canopy greenness, i.e. NDVI, more resilient to drought because their short-term responsiveness to water availability is relatively low (Figure 2.11b). When looking at LAI, however, the response to water availability was not significantly different in protected areas, contradicting the NDVI results (Figure 2.11c). To extract more information on the matter, we decided to look at the number of declining LAI pixels instead of the effect on all pixels; it was significantly smaller in Natura 2000 forests and the decline was also significantly less pronounced (Table S1.2). These results indicate that Natura 2000 forest might have a more positive effect on the forest canopy resilience. Field studies in the region have demonstrated that thinning can improve resilience (Navarro-Cerrillo et al., 2019) but thinning can also decrease leaf area. This is the first study to determine the effect of these protective measures on forest canopy resilience to climate change at the national scale from satellite imagery. More studies are needed to determine which measures in these protected areas are actually enhancing forest resilience. As mentioned in section 2.2, the management of Natura 2000 sites varies greatly depending on the responsible administration, the funds available, the biogeographic region and whether or not the site is a Nationally Designated Protected area, therefore, future studies can take these factors into account to uncover more information on management effectiveness. Finally, gain-to-loss ratios obtained by breakpoint analysis, as well as LAI response, could be failing to show that protected forests are more resilient to drought mainly because of the overall resilience of Spanish forest canopy greenness to past changes in water availability. Alternatively, given that the short-term NDVI responsiveness to drought was not very strong, it could be that protected areas have failed to make a difference in forest resilience thus far; more data are needed to evaluate this. As mentioned in van der Plas et al. (2018), many protected areas have been established recently, thus there has been insufficient time for the implementation of their transformative management actions. In addition, many have been created to protect and restore degraded and abandoned lands which require extra time to recover (van der Plas *et al.*, 2018). Although we found no effect of the land cover change from 1990 to 2000 on the resilience of forest canopies, we did not evaluate the effect of past forest management, which would also be interesting to study.

#### 2.4.5 Research and management implications

Returning to the questions posed at the beginning of this study, it is now possible to state that canopy greenness of Spanish forests have been remarkably resilient to droughts in the 2000-2017 period: these secondary forests are continuing to accumulate biomass and becoming greener despite climate change making this region hotter and drier. Unlike our expectations, most forest types, regardless of their drought resistance behaviour and management, recovered from losses incurred by extreme drought events. Finally, we demonstrate that the protection and management of these forested lands have the potential to be effective in alleviating the effects of climate change on canopies by increasing the forest capacity to resist during a drought.

Breakpoint and regression approaches provide complementary insights into resilience and its components. Short-term covariance between water availability and NDVI or LAI were highly correlated with sensitivity and to a lesser extent recovery measures and could be used to assess the stability of a forest in face climate variation, as well as provide insights into the prevailing drought resistance mechanism of a species. The long-term climate change influence, on the other hand, can be used to estimate drought pressure on these forests. Finally, break-point analysis, which allows losses and recovery of canopy greenness due to drought events to be determined, could be used alongside forest die-off information to determine the tipping point of forests.

Our study has focused on the resilience of forest canopies to drought but shifts in species distribution and changing disturbance regimes will also influence resilience as the climate warms. Several studies have already analysed past shifts in species distribution as well as modelled and predicted future changes in plant communities and their distributions using ground data (Lines, 2012; Ruiz-Labourdette *et al.*, 2012; García-Valdés *et al.*, 2013; Rabasa *et al.*, 2013; Lloret *et al.*, 2013; Valladares *et al.*, 2014). Most of these studies mentioned a decrease in the climatic suitability in the future for most species and predicted altitudinal shifts. A few mentioned an increase in habitat for broadleaves at the expense of pines while one study predicted an increase in the range of low altitude pines.

Furthermore, extreme drought events increase the risks of fires and insect outbreaks (Allen *et al.*, 2010). Our methodology can be applied to such secondary events if data such as fire occurrence, insect distribution and physiology, and geology is available; and it

would be the next natural step to identify management options that would maximize the resilience of forests to different extreme biotic and abiotic events. For instance, fire occurrence data can be tracked from satellite (Justice *et al.*, 2002; Turco *et al.*, 2019), and pathogen damage can be detected from hyperspectral data, LiDAR data or both (Stereńczak *et al.*, 2019; Lin *et al.*, 2019). Furthermore, species composition and stand development information are becoming more and more accessible thanks to hyperspectral imagery and repeat LiDAR scans (Simonson *et al.*, 2012, 2016; Coomes *et al.*, 2017; Nunes *et al.*, 2017; Jucker *et al.*, 2018a). Future work could also explore whether stand height, age, soil type, and species composition influence resilience; and include field data at the same resolution to gain a better understanding of the linkages between remotely sensed greenness and forest change.

Chapter 3 Mapping Mediterranean tree species: airborne hyperspectral vs spaceborne multispectral approaches

#### Abstract

Multispectral sensors on Earth Observation (EO) satellites are proving invaluable for monitoring the resilience of forests to climate change. Knowledge of the species composition of these forests is needed to interpret differences in resilience but this has been challenging to map remotely. However, increases in spatial and spectral resolution of EO data open new opportunities to map species. In this study, we first use airborne hyperspectral imagery to classify two oak and two pine species over 42.2 km<sup>2</sup> in Spain. Random Forest classification of the 2 m hyperspectral imagery delivered accuracies over > 0.9% when classifying individual tree crowns as belonging to one of the four species, and an average adjusted R<sup>2</sup> of 0.78 when predicting percent cover within the 900 m<sup>2</sup> inventory plots. We then use these maps as "plane truth" data to evaluate the accuracy of classification using a Sentinel-2 image classified in Google Earth Engine (GEE). Looking at a 250 m pixels size (equivalent to the smallest MODIS pixel) the agreement between the airborne and spaceborne classification was 64% on average (range: 0-100%). Spaceborne-derived random forest models were better at predicting the total area of pine canopies than oak canopies, average R<sup>2</sup> of 0.64 vs. 0.43, which is probably due to differences in tree heights between the two taxa at an early successional stage. The inclusion of topographical data with Sentinel 2 multispectral data did not improve the classification accuracy of the random forest algorithm in GEE.

#### **3.1 Introduction**

The composition of plant species is a major contributing factor to whether an ecosystem will transition from one state to another following disturbance or perturbation (Oliver *et al.*, 2015). Estimating the resilience of tree species and forest ecosystems to climate-driven risks is increasingly important given climate-change effects on forests globally (Klein & Hartmann, 2018; Anderegg *et al.*, 2020). That is why suggested ways to enhance the resilience of forests include admixing tree species in a bid to diversify their response to biotic and abiotic stress (Bolte *et al.*, 2009; Messier, Puettmann & Coates, 2013; Fares *et al.*, 2015). While studies on tree species interactions can reveal a lot about complementarity and competition in specific ecosystems and under specific environmental conditions, they are costly and their results are not generalisable. Complementarity can turn into competition under different environmental conditions, at different locations, or at different stages in the lifetime of trees (Forrester *et al.*, 2016; Jucker *et al.*, 2020). Approaches to evaluating diversity effects on trees' resilience to climate-driven risks at a larger spatial scale and under a variety of environmental conditions are therefore needed.

High-revisit frequency satellites such as MODIS generate detailed time-series which can be analysed to determine ecosystem resilience to disturbances and climatic changes at long time-scales (Khoury & Coomes, 2020), and detect phenological changes (Zhang *et al.*, 2003; Liu *et al.*, 2015). Long time-series of vegetation indices are used to uncover long-term inter- and intra-annual information on the ecosystems being studied (Verbesselt *et al.*, 2010; Uyeda *et al.*, 2017; Jung *et al.*, 2019) but studies using them often assume homogenous cover or accept the heterogeneity of the land being surveyed. It is quite difficult to link low spatial resolution satellite data to small scale inventory data (Figure 2.6) (Khoury & Coomes, 2020) and rare to be able to survey a whole pixel (Lambert *et al.*, 2013). Furthermore, the homogeneity assumption over large pixels (>250 m), apart from being a limitation in most studies, hinders the discovery of species-specific thresholds or the determination of the effect of species mixing without access to very costly ground-data. While we used time-series of MODIS data to look at dominant species differences in Chapter 2, these time-series analyses are yet to be used to determine the resilience of specific species combinations. Species mapping offers a solution to determine the species

composition of coarse satellite pixels, however hyperspectral and LiDAR data surveys used for such solutions are not necessarily affordable.

Forest tree species mapping is consistently relying on advances in remote-sensing technologies and analysis algorithms to provide scientists, forest managers, and conservationists with valuable information about the distribution of species over landscapes and ecosystems. Whether being used as inputs to species-specific models of growth/biomass or as stand-alone products, species maps are becoming indispensable, numerous studies focus on optimizing the accuracy of classification for specific locations but the number of studies focusing on their pitfalls or application remains limited (Fassnacht *et al.*, 2016). Sentinel 2 multispectral imagery is increasingly used in combination with machine learning algorithms to map land covers, species distributions and functional traits over landscapes (Ma *et al.*, 2019; Vasilakos *et al.*, 2020; Aguirre-Gutiérrez *et al.*, 2021). These developments have great potential to complement the use of low-resolution satellites for ecosystem monitoring, yet the number of studies exploring Sentinel 2 capacity in mapping species over landscape remains small.

Previously, scientists have attempted to overcome the gap between the low ground resolution of MODIS and the low temporal resolution of Landsat by fusing the two datasets together (Wu *et al.*, 2012; Chen *et al.*, 2015; Gao *et al.*, 2015; Wang *et al.*, 2021). Many different algorithms are proposed for the fusion and the processing of such data is no easy task. Ignoring issues such as the geolocation errors, and the differences in sensor systems (Wu *et al.*, 2012), the main limitation in such datasets is the assumption of no land cover change over the period of the fusion (Jamshidi *et al.*, 2019; Filgueiras *et al.*, 2020; Wang *et al.*, 2021). Such limitation is detrimental in time-series analysis looking to detect change and transitions in monitored ecosystems. Here we propose a different approach to bridging that gap and we ask whether high spatial resolution Sentinel 2 imagery can be used to map species composition over high temporal resolution MODIS pixels. This has a huge potential in allowing researchers to drop the assumption of the homogeneous landscape at such large scales (250 to 1000 m) and instead know to a 10 m precision what they are monitoring.

In pursuing this aim we map four dominant species over a Mediterranean landscape in central Spain which will allow the use of the mapped species data in studies looking at determining diversity effects over the region from long time-series of satellite imagery (**Chapter 4**). We classify a Sentinel-2 mosaic following two approaches, one which uses species maps derived from an airborne classification and one which uses our knowledge of the area and high-resolution imagery to train the classifier by eye. The first training method is used because it is validated against field-collected ground data; while the second training method is used to determine the effectiveness of a quick 'eye-trained' classification that could be done by anyone following the popularity of 'citizen science'. We report the results of the first method below and the result of the second method in the supplementary information. We use the hyperspectral classified as the true map when validating the Sentinel 2 results: 'plane truth'. We address three main questions: (i) using hyperspectral imagery which classification algorithm results in the greatest accuracy between linear discriminant analysis, partial least square discriminant analysis, and random forest classification? (ii) how does classification (2 x 2 m pixel) in a 250 x 250 m window? (iii) of the bands used for classification, which are most influential in the classification and what do they say about the species?

Airborne

Digital Surface Model derived from

LiDAR data collected in July and

at least  $0.5/m^2$ ) under the 'Plan

August of 2010 (point density was

Nacional de Ortofotografía Aérea'

#### 3.2 Methods

#### Ground

#### Data

-Basal area and height of all trees within 36 (30 x 30 m) plots in Alto Tajo collected in 2011 and collected again in 2017. -Tree crown measurements

collected on all trees in the 36 plots in 2011.

-Geolocation of 80 trees within 10 plots in Alto-Tajo collected in 2017.

### Method to compute canopy area

- Linear mixed model was used to model canopy areas as function of basal area, heights with species combination in the plot and plot identity as random effects.

Validation Method

- Linear model used to

model species canopy

area data as function of

hyperspectral-derived

species cover.

cover from ground canopy

#### •Hyperspectral data

Data

•Point clouds:

project in Spain.

Atmospherically corrected and filtered hyperspectral data: 253 bands with spectral resolution of 5.13 nm in the range 385 – 981 nm and 11.25 nm in the range 992 -2479 nm collected by Aisa Fenix imager (380–2500 nm) in July 2017 under a Natural Environment Research Council Airborne Research Facility (NERC) award. •Digital Photography Phase One iXU-RS 1000 (0.48, 0.56 and 0.66 nm).

### Methods to create species distribution map

 Digital surface model (DSM) was created using LAStools from LiDAR point cloud.
 Radiometric calibration was

performed on hyperspectral imagery by NERC ARSF. - Airborne processing library by

NERC ARSF in Jasmin (supercomputer) was used to filter, resample, and register hyperspectral imagery unto the DSM.

ATCOR 4 was used to atmospherically correct hyperspectral imagery.
Digital photography and DSM were used to help delineate

crowns in QGIS. - Vegetation indices were added as bands onto the hyperspectral

imagery.

- Three machine learning algorithms (LDA, PLSDA, random forest) were used to map the four species of interest over the hyperspectral imagery collected.

Airborne-derived species distribution map→ airbornederived species cover

#### **Spaceborne**

#### Data

•Satellite data: Sentinel-2 level 2A: 12 cloud-free images collected in June - August 2017, 12 bands used.

#### Topographical data:

Digital elevation from Shuttle Radar Topography Mission (SRTM) version 4 (Jarvis et al., 2008).

### Methods to create species distribution map

- LightGMB was used to filterout cloudy satellite imagery in Google Earth Engine (GEE) - Median and Mosaic images were created from satellite imagery with vegetation indices computed and added as bands. - Training and validation samples were create based on the knowledge of the area for the 'by-eye' classification method and using hyperspectral derived map for the 'plane-truth' method. - The random forest algorithm in GEE was used to map the four species of interest over the landscape.

#### **Validation Methods**

Logistic regression used to model spacebornederived species cover as function of airbornederived species cover.
Pearson correlation used to compare species composition from airborne- and spacebornederived cover maps.
Confusion matrix used to evaluate the accuracy of spaceborne-derived map against 'plane truth' map.

Flowchart 2 Datasets and processing steps to map forest tree species over Alto-Tajo.

#### 3.2.1 Data

#### 3.2.1.1 Site information and field plots

The study site is in central Spain, in Alto-Tajo (approx. lat.: 40.72°; long.:2.17°, 1200m a.s.l.). The climate is Mediterranean with a mean annual temperature over the region is 10.2 °C, and mean annual precipitation is 499 mm yr<sup>-1</sup> (Jucker *et al.*, 2014). In the summer of 2017, hyperspectral data and RGB imagery were collected over an area containing permanent forest inventory plots established in 2011 as part of a study into the effect of species diversity on ecosystem functioning (Baeten et al., 2013; Jucker et al., 2014a). A total of 36 plots were established in Alto Tajo, varying in diversity from 1-4 species. The species pool includes two pines *Pinus nigra* and *P. sylvestris*, one deciduous oak *Quercus* faginea, and one evergreen oak Q. ilex, including 12 possible combinations. Each permanent plot consisted of an area of  $30 \times 30$  m in which all stems  $\geq 7.5$  cm in diameter were identified and permanently marked (3216 stems in total). During the first census, in 2011, basal area, heights, as well as other productivity and diversity measures were collected and remeasured in the 2<sup>nd</sup> census in 2017. Tree cores were also collected and allowed for the construction of a productivity history over the plots which will be explored in detail in the next chapter. Eight monoculture plots and two mixed plots were re-visited in 2017 (Figure 3.2a), 5 and 20 trees respectively were randomly selected and georeferenced with differential GPS (SXBlue II system, Geneq, Montreal, Quebec, Canada) and data concerning canopy composition were collected and studied in Chapter 5.

#### 3.2.1.2 Predicting crown cover from inventory plot data

We generated species specific allometric equations to estimate crown area from basal area and height measurements taken in the first census. The functions were later used to predict the crown area in the second census. Crown areas, basal areas and heights were all log-transformed to normalise the residuals. Linear mixed models fitted the log-transformed data better than non-linear models, suggesting that the allometries followed power laws. (Jucker *et al.*, 2014b). We used the 'step' and the 'lmer' functions in R to select the mixed model with the smallest AIC (see Table S2.1). The best model allowed the height intercepts and slopes to vary with the species combination and plot identity, i.e. random effects specified as 'log H | Species Combination/Plot ID'. Crown area was predicted from basal area and heights with an *RMSE* of 5.66 m<sup>2</sup> and an adjusted R<sup>2</sup> of 85% (Figure 3.1).





a) Species crown area as function of tree basal area; b) crown area as function of tree height; c) crown area predicted by the model below vs. observed crown area.

The best-supported model was  $\log_e(CA \ (m^2)) = 0.75 \log_e BA \ (m^2) + 0.41 \log_e H \ (m) + 4.36$ , with BA: basal area , and H: height. Height intercept and slope varied significantly between plot species combinations which are expected given that different combinations of oaks and pines allow for different canopy vertical structures as a result of competition for light. This competition, in turn, influences productivity and ultimately canopy size (Jucker *et al.*, 2014a).

#### 3.2.1.3 High-resolution hyperspectral data

Hyperspectral and RGB imagery was collected over Alto-Tajo on the 19-21 June 2017 by the (former) Airborne Research and Survey Facility of the Natural Environment Research Council (ES17/126). The hyperspectral data were collected with an Aisa Fenix imager (380–2500 nm) and photographs were taken by a Phase One iXU-RS 1000 (0.48, 0.56 and 0.66 nm), flown at an average altitude of 2145 m a.s.l. (Figure 3.2c). The resulting spectral resolution was 5.13 nm in the range 385 – 981 nm and 11.25 nm in the range 992 - 2479 nm; there was a total of 253 bands. LiDAR data acquired by the Plan Nacional de Ortofotografía Aérea project in July and August of 2010 (point density was at least  $0.5/m^2$ ) were processed with LAStools to create a digital surface model. The hyperspectral data were registered onto the LiDAR-derived data digital surface model (Figure 3.2b) at a ground resolution of 2 m and filtered and binned using NERC ARSF Python tools in JASMIN (see Bongalov et al. 2019). Further calibration and filtering were conducted: the ATCOR4 software was used to make atmospheric corrections, using the rugged terrain model (see Bongalov *et al.* 2019); pixels with illumination angle >  $60^{\circ}$ were filtered out. The analysed imagery spanned a total area of 42.2 km<sup>2</sup> excluding flightline edges.



#### Figure 3.2 Maps of a study region in Alto Tajo Natural Park, Spain.

a) Location of the Park and forest inventory plots; b) the LiDAR-derived Digital Surface Model; c) high-resolution RGB mosaic; d) close-up of one inventory plot with tree crowns and ground section used in the training and validation of classification algorithms delineated in orange. The white grid represents 250-m pixels of MODIS multispectral data which will be used (in Chapter 4) to track long-term vegetational changes in the park. The yellow points represent the position of forest inventory plots.

#### 3.2.1.4 High-resolution multispectral satellite data

A cloud-free Sentinel-2 level 2A mosaic was created in GEE from 12 images collected in June - August 2017. Using Sentinel Hub's cloud probability layer in GEE based on LightGBM (<u>https://github.com/microsoft/LightGBM</u>, Barbier *et al.*, 2016; Ke *et al.*, 2017; Zhang *et al.*, 2017), pixels that had a >30% probability of being clouds or cloud shadows were filtered out. Satellite swath edges were also masked out by screening and masking the images of extreme reflectance values. The remaining pixels were reduced to a 12band cloudless mosaic by taking the median across the images.

#### 3.2.2 Classification

#### 3.2.2.1 Tree-crown classification using hyperspectral imagery

Three methods for classifying individual tree crowns were evaluated: linear discriminant analysis (LDA), partial-least-squares discriminant analysis (PLS-DA), and random forest (RF). Polygons were created in QGIS (version 3.8 Zanzibar, http://gis.org/) to delineate individual tree crowns and non-forested background by locating the georeferenced trees (section 2.1.1) on the RGB imagery and the LiDARderived digital surface model. Atmospherically corrected hyperspectral data was then extracted in R from the tree crown and background polygons. Tree crown pixels with NDVI < 0.65 and background pixels with NDVI > 0.65 were masked. Brightness normalization consisting of spectral averaging, i.e. dividing each pixel spectra value by mean spectra of the pixel, was applied before the addition of spectral indices (Chan et al., 2020). Spectral indices were taken from Chan et al., (2020) with extra indices added from the Index DataBase (Henrich et al., 2009) to make use of the full spectra of our data and improve the estimation (added indices are reported in Table S2.2). They were then used to train and validate three classifiers, using 'MASS' package (Ripley et al., 2013) for the LDA, 'caret' package (Kuhn, 2008) for PLSDA, and 'randomForest' package (Liaw & Wiener, 2012) for RF classification. The training involved 70 % of crown pixels and validation of the remaining 30%. We tested whether dark pixel filtering improves accuracies by eliminating pixels with maximal reflectance values falling below 25% of mean maximal reflectance over any given flight-line. There were also overlapping flight lines allowing the collection of more data for some of the crowns. We tested whether averaging the overlapping data would make a difference to the predictions. Accuracies of individual-tree-crown models were assessed by reporting the overall, user and producer accuracies of the confusion matrix using the 'confusionMatrix' function from 'caret'. Accuracies of the best two algorithms were further evaluated at the forest plot level, by comparing the canopy cover of each species (i.e. the sum of the individual crown areas) with the canopy cover predicted by the model, relative to total canopy area or to total plot area (900 m<sup>2</sup>).

#### 3.2.2.2 Mapping species using Sentinel-2 multispectral imagery

We classified Sentinel-2 imagery using hyperspectral-derived species classification map as plane-truth data. To create a calibration/validation dataset we first resampled the

2-m hyperspectral-derived map to 10m (the size of Sentinel-2 pixels) using the 'mode' algorithm in GDAL (http://gdal.osgeo.org/). We created a calibration/validation dataset comprised of 600 pixels -120 samples for each of the four species classes and 120 for the background class. Finally, we trained a random forest classifier in GEE. A total of 99 vegetation indices were computed from Index DataBase and used in the classification (Henrich *et al.*, 2009) (see Table S2.3). Knowing that the species differ in their distribution along elevational gradients (Martín-Alcón, 2015), the elevation, slope and aspect, as computed from the Shuttle Radar Topography Mission (SRTM) digital elevation dataset, version 4 (Jarvis *et al.*, 2008), were also added as variables in the classifier in one of the random forest algorithm runs to test whether topographical parameters improved the accuracy of the classifier (Table 3.3).

#### 3.2.2.3 Classifier variable importance

Variables' importance was checked for the random forest algorithms using the available 'explain' function in GEE and 'importance' function from the 'randomForest' package in R. The computation of the importance was based on the total decrease in node impurities (computed as Gini index) from splitting on the variables.

#### 3.2.3 Predicted composition of 250m pixels

We compared predicted species composition from high-resolution hyperspectral and Sentinel-2 imagery at a 250-m scale (i.e. equivalent to the smallest MODIS pixel resolution). First, a MODIS image was obtained over the area at 250-m resolution and vectorized using the "spex" package in R to obtain the MODIS product grid with a total of 892 pixels fully covered by the hyperspectral data. By overlaying the MODIS grid on the hyperspectral and Sentinel 2 species maps, we counted the number of pixels occupied by the four species of interest within each grid cell. We then evaluated the degree of agreement between the two species maps by comparing the pixel counts. Logistic regression with a binomial error structure was used to predict species-specific canopy cover derived from Sentinel-2 as a function of species-specific canopy cover derived from hyperspectral imagery and other variables (see Figure 3.3). Another method computing accuracy from contingency matrix for each grid cell, i.e. takes into account the position of species within the grid cell, was also tested and its results reported in the supplementary information Section S2.4.



## Figure 3.3 Prediction of the species composition within 250-m pixels (i.e. MODIS pixels) from higher resolution imagery.

a) Species classification derived from airborne hyperspectral imagery at 2-m resolution (plane truth), b) Sentinel-2 multispectral imagery at 10-m resolution; c) donut graphs representing class proportional cover for a sampled pixel (highlighted orange and purple in a and b) from the airborne and spaceborne imagery and their position on a bivariate plot (dotted line showing a 1:1 relationship).

#### 3.3 Results

#### 3.3.1 Predicting composition using airborne hyperspectral imagery

The highest classification accuracy of tree crowns was achieved by PLS-DA with an overall accuracy of 92% (Table 3.1) followed by RF with 0.83% average accuracy. Training the classifiers with all the data instead of averaging over the overlapping flight-lines resulted in better accuracies (accuracies reported in Table S2.1). Eliminating darker pixels within each flight-line did not result in a better result.

#### Table 3.1 Classification accuracy achieved by three different algorithms.

LDA: linear discriminant analysis; PLS-DA: partial least squares discriminant analysis; RF: random forest. To the right classification accuracy (%) at the pixel level and to the left classification accuracy (%) at the crown level (i.e. the most frequent classification for each crown).

Method	Pixel level			Crown level				
	Overall Average accuracy user's		Average producer's	Overall accuracy	Average user's	Average producer's		
		accuracy	accuracy		accuracy	accuracy		
LDA	0.77	0.76	0.77	0.81	0.82	0.82		
RF	0.83	0.83	0.85	0.90	0.89	0.93		
PLS-DA	0.92	0.90	0.90	0.95	0.96	0.96		

Table 3.2 Confusio	n matrix	obtained	from	the	RF	species	classification	model	showing
predicted and actu	al species	s IDs.							

Bck. Background including bare ground and shrub; Pn: *P. nigra*; Ps: *P. sylvestris;* Qf: *Q. faginea;* Qi: *Q. ilex;* PA: Producer's Accuracy (%).

		Pixel level Prediction							Crown level Prediction					
-	_	Bck.	Pn	Ps	Qf	Qi	PA (%)	Bck.	Pn	Ps	Qf	Qi	PA (%)	
е	Bck.	17	0	0	0	0	1	6	0	0	0	0	1	
inc	Pn	1	15	2	1	4	0.65	0	4	1	1	0	0.67	
ere	Ps	1	1	16	0	0	0.89	0	0	2	0	0	1	
lefe	Qf	0	0	0	7	1	0.88	0	0	0	4	0	1	
В	Qi	1	0	2	1	14	0.82	0	0	0	0	3	1	
Use	r's													
accı	iracy	0.94	0.84	0.76	0.78	0.74		1	1	0.67	0.8	1		
(%)														

The predicted percentage canopy covers of the four species were more closely correlated with the field estimate when looking at canopy cover relative to total canopy area ( $R^2 = 0.78$  and RMSE = 15.51) (Figure 3.4a) than when looking at canopy cover relative to plot area ( $R^2 = 0.66$  and RMSE = 20) (Figure 3.4b). Examining the species-specific canopy areas relative to the total canopy area inside of plots, there was a small negative bias for *P. nigra* and *Q. faginea* and a small positive bias for *P. sylvestris* and *Q. ilex* (Figure 3.4a). The tendency for pines, especially *P. nigra*, to be underpredicted is likely underpinned by their bigger and denser canopies, which often led to >100% canopy cover relative to the ground area (Figure 3.4b). Overall, the RF-derived map described plot-level canopy cover composition much better than the PLS-DA derived map, by predicting the species-specific cover relative to total cover more closely for most species except *P. sylvestris*. For this reason, the RF-derived map was chosen to be the 'plane truth' when compared against Sentinel 2 derived species map.



## Figure 3.4 Abundance of four species as an estimate from 30 x 30 m forest inventory data and from hyperspectral imagery classification map.

a) Abundance of four species with field data expressed as a percentage of total canopy area. b) Abundance of four species as a percentage of ground area. Linear regression lines are shown for each species and adjusted R<sup>2</sup>, RMSE and bias statistics are provided.

#### 3.3.2 Classification of Sentinel 2 imagery

We mapped our four species of interest using freely available Sentinel 2 data in GEE. We found a very high accuracy (93%) when validating the model on eye-trained data in GEE (Table S2.5) and using the least cloudy pixel composited product. The maximum accuracy when trained and validated on the airborne-derived species map was 0.5 % as obtained from the summer median Sentinel-2 mosaic (Table 3.3). Adding ancillary data related to elevation did not improve the average accuracy of the model, however, interestingly, these variables were the most important when included in the model (Figure S2.4).

he airborne-derived map. Background class results not shown.										
Training Data	Overall accuracy	User's Accura	icy (%)			Producer's Accuracy (%)				
		Pn	Ps	Qf	Qi	Pn	Ps	Qf	Qi	
Sentinel 2 Sentinel 2	0.49	0.46	0.70	0.62	0.21	0.48	0.48	0.59	0.33	
+ Elevation	0.49	0.47	0.59	0.59	0.28	0.46	0.67	0.53	0.44	

**Table 3.3 Accuracy of classifications of Sentinel-2 data using random forest modelling.** Summer median with vs. without ancillary elevation data trained over 70% stratified sample of the airborne-derived map. Background class results not shown.

#### 3.3.3 Accuracy of Sentinel-based maps at the 250-m scale

A central aim of this study was to test whether Sentinel-2 imagery can help to predict the species composition at the 250 x 250 m scale of MODIS pixels. Modelling MODIS pixel tree composition derived from Sentinel 2 with the composition derived from airborne hyperspectral data led to good results when looking at species cover proportional to land area in all species except *Q. ilex* which was much better modelled in proportion to total tree cover (Table S2.4). In all cases except for *Q. faginea*, including map derived information about the number of species or diversity of species in a pixel improved the predictions (Table 3.4). The models estimating pines proportion were better than those estimating oak proportions over the Alto-Tajo landscape. Looking at the predictions together the correlation between the compositions of a MODIS pixel was on average 58% according to Kendall's tau (Figure 3.6) with most pixels correlating (r=0.67).

Table 3.4 Logistic regression of species cover predicted from Sentinel-2 imagery vs 250-m pixels as a function of species covered airborne-derived pixel composition and summary metrics.

 $\Delta$ AIC column reports the difference in AIC between the simple model and a backwards-selected model with multiple explanatory variables. X = sqrt(hyperspectral-derived tree cover); Y = total tree cover;

Species	Model	ΔΑΙC	<b>R</b> <sup>2</sup>
P. nigra	- 3.58 + 8.64 X	0	0.61
	- 2.70 + 9.42 X - 2.21 Y- 0.50 Z + 0.71 W	-26.6	0.65
Р.	- 3.54 + 12.82 X	0	0.60
sylvestris			
	- 4.58 + 18.31 X + 2.69 Y+ 0.46 W- 18.4233 X:Y	-27.6	0.63
Q. faginea	- 3.29 + 11.32 X	0	0.48
	- 3.46 + 10.92 X + 0.42 W	1.2	0.50
Q. ilex	- 1.77 + 5.09 X	0	0.23
	- 0.99 + 5.80 X - 2.98 Y- 0.33 Z + 0.86 W	-77.54	0.35

Z = Number of Species; W=oaks or pines (0) or both (1)



Figure 3.5 Relationship between airborne hyperspectral-derived species cover (2x2 m) and spaceborne multispectral-derived species cover (10 x 10 m) over MODIS pixels in the area for the four species of interest.

The curves are fitted using logistic regressions.



**Figure 3.6 Histogram of the correlation (Kendall's tau) between the four species abundances estimated by the two approaches over MODIS pixels.** The dashed line represents the mean correlation coefficient.

# 3.3.4 Spaceborne multispectral vs. airborne hyperspectral mapping of species.

Exploring variable importance in classifying a pixel as one of the four species of interest, elevation, aspect and slope came out as three of the most important variables (Figure S2.3a). This was interesting as removing them from the training set did not significantly decrease the accuracies obtained from the Sentinel 2 classification in GEE (Table 3.3). *P. sylvestris* covered higher altitudes than the other three species (Figure 3.7a), while growing on relatively flatter slopes (Figure 3.7b). *Q. faginea* had a significantly limited range in terms of elevation compared to the other species (Figure 3.7a). On average there were no significant differences between preferred terrain aspects for each species, however, the tolerance towards more extreme aspect values was clear in pines as opposed to oaks (Figure 3.7c).



Figure 3.7 Three important variables in determining species composition were elevation (m) (a), slope (radians) (b), and aspect (radians) (c).

Box edges correspond to the first and third quartiles (the 25th and 75th percentiles), whiskers are 1.5 \* IQR (where IQR is the inter-quartile range); capital letters indicate significant differences (p < .05) in groups' mean following Welch's ANOVA and Games Howell Post-hoc tests; lowercase letters indicate significant differences (p < .05) in groups' variance following Levene's, ANOVA and Tukey Post-hoc tests.

#### 3.4 Discussion

#### 3.4.1 Mapping algorithms

We evaluated three algorithms to map four tree species over Alto Tajo. The advantages and disadvantages of these mapping classifiers are revised in Chan *et al.* (2020). We find first that PLS-DA is the best at identifying the different classes at the pixel and crown levels. Following a second validation with plot-level data we find that the random forest algorithm surpassed PLS-DA in predicting the composition of FunDivEurope plots, despite the non-perfect alignment of the coordinates. The difference between the two algorithms was mostly due to oaks being better predicted by the random forest algorithm. Given the small number of trees in the training dataset, 5 trees per plot and a total of 80 crowns delineated, these results are very accurate and demonstrate the power of using machine learning algorithms to classify hyperspectral data.

#### 3.4.2 Airborne vs spaceborne species mapping

Sentinel 2 map consistently overestimated tree cover in the Alto Tajo region, we believe that this is due to the difference in resolution between airborne and spaceborne imagery which was used for the classification. Effectively, 10 m pixels recognized as oaks or pines are inevitably covered by some background as most tree crowns are less than 50 m<sup>2</sup> (Figure 3.1) and the tree density in these Mediterranean forests is highly variable, from 24% cover in oak forests up to 189% cover in mixed forests. Looking at the species user accuracies from Sentinel 2, we find that *P. sylvestris* (Table 3.3) had comparable user accuracy to another study mapping the species over a natural reserve in Sweden (Persson et al., 2018). In that study, however, researchers set a threshold of 70% canopy cover for pixels to be included in the classification which we did not do in our study, and we believe is the major contributing factor to the lower accuracies we find. The forest landscape over Alto-Tajo has low canopy cover, most of our plots had canopy cover below 50% (Figure 3.4b), and therefore such filtering will leave very few areas to be classified. Another study mapping genus instead of species in the large mountainous area in Poland, found higher accuracies for pines and oaks using Sentinel 2 but also found that accuracy was dependent on forest cover with low cover areas being classified much less efficiently (Grabska et al., 2020). A study in a Mediterranean ecosystem found also better accuracy but looked at mixed species groups and including seasonal metrics when training the classifier (Puletti et al., 2018).

The compositions of the MODIS pixels derived from the two maps correlated with an average of 58%, reaching up to 100% in some cases. The agreement between the two maps as determined by the contingency table method was on average 64% (Section S2.4). Given that the quality of the training data is essential for obtaining high classification accuracies (Congalton *et al.*, 2014) and that we used the airborne-derived map as truth for training and classification this might suggest that the airborne derived map aggregated at 10 m has lost some of its accuracy. It would be hard to determine with certainty which map is the more correct one, thus we decided to select pixels with a high

similarity score and correlation for analysis in the next chapter to ensure that the composition of the chosen pixels is a little contested.

#### 3.4.3 Variable importance

We tested the random forest algorithm in GEE on Sentinel 2 data and its derived indices vs. a training dataset that would also include topographical information. Given that topography is known to affect canopy composition (Jucker *et al.*, 2018b), several studies include topographical information in their training dataset to assist the algorithm in defining the acceptable boundaries for each species and avoid outliers (Dorren *et al.*, 2003; Zhu & Liu, 2014; Grabska *et al.*, 2020). Although topographical variables were classified as the most important in the classifier that did include them (Figure S2.4a), they did not significantly improve the accuracy of the algorithm unlike what Grabska *et al.* (2020) found. A close examination of the topographical variables' distribution showed that there were indeed significant differences between the species groups (Figure 3.7). While elevation and slope were different in both the variance and the means between certain groups (Figure 3.7c). These results suggest that Sentinel-2 bands and the derived indices can indirectly capture topographical information about the Alto-Tajo landscape.

#### 3.4.4 Implications

The high revisit frequency of EO satellites allows us to monitor closely changes in forest canopy at a low cost, as well as analyse their response to climate change and disturbances. Understanding forests' response, however, requires a more detailed picture of the ecosystem being studied. From environmental conditions to species composition, some of these details can be provided by satellites and weather stations, while others are highly dependent on ground measurements. One such detail is the species composition of the forests in question which usually depends on costly ground observations and species distribution mapping or modelling. In this work, we classified the landscape of Alto-Tajo in an effort to determine the species composition in MODIS pixels before using the information in the following chapter for time-series analysis. We achieved high classification accuracy with AISA hyperspectral data (> 90%) in determining plot composition and moderate accuracy with the Sentinel 2 multispectral

data in determining the composition of MODIS pixels with the agreement between airborne and spaceborne classification being on average 64%.

Chapter 4 Different species, same droughts: Do treerings and canopies tell the same story?

#### Abstract

Managing forests to increase resilience to drought is important as the climate warms. The resilience of aboveground wood production (AWP) to drought is known to depend on the species composition and diversity of woodlands, but it is unclear whether the same is true for the resilience of the leaf area index (used as a proxy for forest cover). We analysed annual time-series of LAI and AWP from woodlands dominated by combinations of two oak and two pine species in central Spain, which had been subjected to major droughts in the past 20 years. We expected that (i) there would be upward trends in LAI and AWP because the forests are successional; (ii) the stability of AWP and LAI would be negatively affected by species richness, based on previous studies in these woodlands; (iii) species composition and species richness would impact forest resilience to drought, because of functional differences between the four species dominating this landscape; (iv) AWP would be more sensitive than LAI to droughts because of resource allocation priorities within trees, but still, covary with LAI; (v) annual wood production would be driven by LAI and by water balance, reflecting that primary productivity is influenced by stomatal conductance as well as canopy area.

We worked with two datasets: annual AWP calculated from increment cores extracted from trees in 36 inventory plots with known species composition and mean yearly LAI measurements estimated from satellite imagery (MODIS) for 398 pixels within which species composition was derived from airborne hyperspectral imagery collected in 2017. For 28 of the 36 sites, we had 336 pixels with a matching composition which we used to compare annual LAI and AWPdirectly. Using maximum likelihood estimation, we explored whether canopy area (a proxy for stand development stage), species richness and species composition influenced LAI and AWP and their resilience to drought. Changes in water balance over time characterised by the standardised precipitation and evaporation index (SPEI) were used in the time-series analysis and to identify drought periods.

The analyses partly support our predictions: (i) LAI trends were mostly positive over the landscape and related to higher wood productivity; (ii) AWP became less stable with the increase in canopy area while LAI became more stable but they did not vary with species richness; (iii) the evergreen oak, *Quercus ilex*, increased forest canopy sensitivity significantly probably due to leaf shedding in response to extreme droughts but also decreased resilience; (iv) AWP was indeed more sensitive to drought than LAI; (v) AWP was driven by both LAI and SPEI (models explained ~50% the AWP variation); the AWP of oak-dominated forests was strongly influenced by LAI while the AWP of pine-dominated forests was strongly influenced by SPEI.

We show the combination of species mapping with hyperspectral imagery and LAI tracking with MODIS imagery provides novel insights into the effects of species composition of LAI resilience, and the knock-on implications for wood production, a significant component of carbon sequestration.

#### 4.1 Introduction

There is substantial evidence that more diverse forests have greater net primary productivity than less diverse ones (Ammer, 2019), but whether the link can be detected by remote sensing is still unknown.-While some studies account for species proportion and look at their interactions, others have found an increase in productivity being directly caused by an increase in stand density, sometimes even decided upon by managers instead of occurring naturally (Pretzsch & Biber, 2016). In Mediterranean forests, species diversity has been associated with higher wood production and greater canopy packing (Vilà *et al.*, 2007; Jucker *et al.*, 2014a,b, 2015). The question that remains open is whether an increase in productivity due to density or due to increasing canopy complexity can be detected by looking at canopy metrics from space using vegetation indices such as NDVI and EVI. Such studies are rare because usually remotely sensed time-series of vegetation assume a homogenous forest cover instead of a mixed one unless being used to map out species diversity at a smaller time- and spatial-scales.

A second reported benefit of diversity is the higher resilience or higher stability in face of climate-change, due to asynchronies and distinct species responses to biotic stress and disturbances (Steckel *et al.*, 2020). However, this effect is far from universal and was found to be highly dependent on the species mixture being studied, as well as on the level of biotic stress to which the forests was subjected (Grossiord, 2019; Pardos *et al.*, 2021). Looking at wood production and its resilience, a recent study on European forests across biomes found that when species mixing did offer an increased resilience to drought it was often a mixing between conifers and broadleaves, which offer contrasting responses to drought events (Pardos *et al.*, 2021). They also suggested that the ability to predict future mixing effects will rely on understanding long-term trends in time-series in response to biotic stress (Pardos *et al.*, 2021). In Mediterranean mixed forests, complementary effects in mixed forest that lead to high wood production in relatively wet year switch to competition for water when conditions are dry, making wood production unstable in the long term (Jucker *et al.*, 2014a). Whether this negative effect on forest stability can be observed from satellites remains unknown.

Multiple studies have investigated the association between time-series of tree-ring width or its derivatives or proxies (e.g. maximum latewood density, wood productivity) and time-series of NDVI, with results ranging from 'strongly positive' relationship
between the two variables to no relationship at all (D'Arrigo et al., 2000; Beck & Goetz, 2011; Beck et al., 2013; Bunn et al., 2013; Pasho & Alla, 2015; Vicente-Serrano et al., 2016a, 2020; Decuyper et al., 2016; Babst et al., 2018). Putative physiological explanations for weak relationships include temporal decoupling between wood production and canopy production and maintenance (Litton et al., 2007; Vicente-Serrano et al., 2016b), differential wood production with a decoupling between wood density and tree-ring width (Beck et al., 2013), and competing growth patterns between reproductive and vegetative (Ryan et al., 2018). For instance, a study in Alaskan forests found no relationship between tree rings width and NDVI and a significant relationship between NDVI and maximum latewood density suggesting it was related to site-level differences affecting growth and a low canopy cover (Beck et al., 2013). However, a recent study in Spain did find a relationship between tree-ring growth and NDVI aggregated at different time-scales suggesting that the coupling between wood production and canopy greenness is not instantaneous but not spanning more than a year for Mediterranean forests (Vicente-Serrano et al., 2020). Furthermore, the link between tree-ring increments and NDVI seems to be species-dependent (Vicente-Serrano et al., 2020). In this study, we evaluate whether knowing the specific species composition of remotely sensed pixels can help us improve the relationship between remotely sensed canopy metrics and wood production metrics and uncover more about the physiology of the species in question.

Looking at a landscape in central Spain where mixed pine-oak forests were found to be more productive than monocultures, with on average 48% more above-ground woody production (AWP) each year (Jucker *et al.*, 2014a), we attempt to detect the mechanism modulating the productivity-diversity effect by looking at canopy area LAI change under drought. We analyse 16 years of remote sensing-derived estimates of LAI and 25 years of tree-ring-derived wood productivity to determine whether responses to drought are modulated by three main factors: canopy area, species composition and diversity. We investigated four questions: (i) what are the temporal patterns of leaf area and mean wood productivity over this Spanish landscape and are these trends impacted by species composition, species richness and canopy area? (ii) how stable are LAI and AWP and is this stability affected by these three factors? (iii) how resilient are LAI and AWP to extreme droughts and is this resilience different between species? (iv) to what extent is AWP controlled by water availability and LAI (rather than either one of these variables) and is this relationship dependent on the three factors?

### 4.2 Methods

### Wood Production

### **Ground Data**

•Tree-ring data:

-453 wood cores collected for the FunDivEUROPE project in 2011(first census) and 2017 (second census),

#### •Plot data:

-36 (30 x 30 m in size) permanent plots in Alto Tajo, Spain.

-Plots were monocultures of Pinus nigra, P. sylvestris, Quercus ilex and Q. faginea or a combination of the species.

-Diameter, height, basal area of every tree with DBH > 7.5 cm in the 36 plots were collected in the first and second census.

-Crown illumination index class was collected for every tree in the first census.

#### **Canopy Health/Growth**

#### Airborne-derived and satellite data

Species cover from hyperspectral-derived species distribution map (Chapter 3).
MODIS/006/MOD13Q1, MODIS/006/MYD13Q1 for NDVI 250 m resolution from 2000 to end of 2017 from the Moderate-resolution imaging spectroradiometer (MODIS) catalogue on Google Earth Engine: 398 MODIS pixels (each 250 m x 250 m in size.

#### Water availability data

Standard Precipitation Evapotranspiration Index (SPEI) from 2000 to end of 2017 from Vicente-Serrano et al. (2017).

- Total canopy area of plot (CA<sub>j</sub>)
- Species proportions in plot: *Ppn, Pps, Pqf,* and *Pqi*
- Effective species richness in plot
- Time-series of Above-ground Wood Productivity from 1992-2017

### Computation of long-term stability and short-term resilience metrics

- AWP stability:

 $S_{AWP} = AWP_{\mu} / AWP_{\sigma}$ 

where  $AWP_{\mu}$  is the temporal mean and  $AWP_{\sigma}$  is the temporal standard deviation of AWP

- AWP mean=  $AWP_{\mu}$
- AWP trend derived from linear model
- AWP sensitivity = AWP<sub>drought</sub>-AWP<sub>pre-drought</sub>
- AWP recovery = AWP<sub>post-drought</sub>-AWP<sub>drought</sub>
- AWP resilience = AWP recovery/AWP sensitivity

- Species proportions in pixel: *Ppn, Pps, Pqf,* and *Pqi*
- Effective species richness in pixel
- Time-series of Leaf Area Index from 2000-2017

Total canopy area of MODIS pixel  $(CA_k)$ 

### Computation of long-term stability and short-term resilience metrics

LAI stability:

 $S_{LAI} = LAI_{\mu}/LAI_{\sigma d}$ , where  $LAI_{\mu}$  is the temporal mean and  $LAI_{\sigma d}$  is the detrended variation of LAI<sub>k</sub> over pixel k.

- LAI mean=  $LAI_{\mu}$
- LAI trend derived from linear model
- LAI sensitivity =  $LAI_{drought}$ - $LAI_{pre-drought}$
- LAI recovery= LAI<sub>drought</sub>-LAI<sub>pre-drought</sub>
- LAI resilience = LAI recovery/ LAI sensitivity

#### Analyses

- Linear regression models linking time-series of AWP, LAI, and SPEI (See table 4.1).
- Maximum likelihood estimation of canopy area, species composition and richness effects:

$$y = CA^{a} \cdot (b_{1}Ppn + b_{2}Pps + b_{3}Pqf + b_{4}Pqi) \cdot (1 + c SRe) + \varepsilon_{1} + \varepsilon_{2}CA, \qquad (4.4)$$

where y is the response variable and CA is canopy area (% plot area for field plots or % of pixel area for MODIS pixels), *Ppn*, *Pps*, *Pqf*, and *Pqi* are the proportions of CA that are *P*. *nigra*, *P*. *sylvestris*, *Q*. *faginea* and *Q*. *ilex* respectively, and SRe is the effective species richness, while a,  $b_1$ ,  $b_2$ ,  $b_3$ ,  $b_4$ , c,  $\varepsilon_1 + \varepsilon_2$  are parameters estimated using maximum likelihood methods.  $\varepsilon_1 + \varepsilon_2$  are normally distributed parameters, centred on zero, which account for the residual variation.

Flowchart 3 Datasets used, and analyses performed to quantify wood production and canopy resilience to droughts and understand how they relate to each other and to water availability.

### 4.2.1 Study site

The study site is located in the Alto Tajo Natural Park, in the Guadalajara province of central Spain (40.9°N, 1.9°W). This work builds upon the data collected by the FunDivEUROPE project that established 36 (30 x 30 m in size) permanent plots in that area (see Baeten et al., 2013) and the collected hyperspectral data for species mapping in 2017 (Chapter 3). The mean annual temperature is 10.2 °C, and the mean annual precipitation is 499 mm year<sup>-1</sup>. Forested areas are populated by four focal species *Pinus nigra*, *P. sylvestris*, *Quercus ilex* and *Q. faginea* (Jucker *et al.*, 2014a). The permanent plots were selected to have varying diversity levels from monocultures to fully mixed plots but with little variation in topography and environmental condition. The functional composition (FC) of the plots was one of conifer, deciduous, evergreen and all possible combinations of the three.

Time-series of the standard precipitation evapotranspiration index (SPEI), representing relative water availability, were extracted from a database available at 1.1 km resolution over the site area in central Spain for the period 1992-2017, and used both for the time-series analysis predicting AWP and for the determination of the drought years (Vicente-Serrano *et al.*, 2017). The study region despite being not very dry in absolute terms relative to the rest of Spain and not having dried up extensively in the past 18 years (Figure S3.5a), was affected by two relatively extreme droughts in 2005 and 2012 with SPEI reaching below -2 (Figure S3.5b).

### 4.2.2 Selection of MODIS pixels for leaf area analysis

A total of 398 MODIS pixels (each 250 m x 250 m in size) were used to examine temporal variation in canopy greenness of the four species of interest. All these pixels lay within the region in which species composition had been mapped by airborne hyperspectral sensing, and pixels varied from monocultures to four-way mixtures (see Chapter 3 for information on species mapping over Alto Tajo). They were selected was based on the confidence we had in the species composition predicted from remote sensing: the selected pixels had high correlations between species compositions estimates made by airborne hyperspectral and spaceborne imagery (i.e. Kendal correlation coefficients > 0.6) and similarity scores > 55% (see Chapter 3 for details on Kendal and similarity score computation).

# 4.2.3 Canopy area in AWP and LAI datasets and datasets matching for AWP prediction

### 4.2.3.1 Canopy area and species proportions in the two datasets

The total canopy area of each plot *j* (CA<sub>*j*</sub>) was computed by adding species canopy areas in each plot as estimated in Section 3.2.1.2 and converting it to % of total plot area which is equal to 900 m<sup>2</sup>. The total canopy area (CA<sub>*k*</sub>) in each MODIS pixel *k* was determined from the hyperspectral-derived map by counting the number of mapped 2 m tree pixels in each MODIS pixel and multiplying it by hyperspectral pixel area (4 m<sup>2</sup>) then converting it to % of total MODIS pixel area which was equal to 47310 m<sup>2</sup>.

Species proportions *Ppn*, *Pps*, *Pqf*, and *Pqi* of *P. nigra*, *P. sylvestris*, *Q. faginea* and *Q. ilex* respectively, were computed as function of CA<sub>j</sub> and CA<sub>k</sub> by simply taking species specific canopy area in each plot and pixel and converting it to % of CA<sub>j</sub> and CA<sub>k</sub>.

### 4.2.3.2 Matching pixel canopy composition with plot canopy composition

A significant difficulty in relating LAI and AWP time-series is the spatial mismatch between NDVI pixels and ground plots from which a number of tree-ring data are created (Ivanova *et al.*, 2021). The relationship improves with smaller NDVI pixel size which allows minimizing landscape heterogeneity contained within a pixel (Bhuyan *et al.*, 2017). We adopted a different approach to deal with this issue, that of comparing wood to canopy productivities by using matching plot/pixel composition instead of averaging tree-ring observation over greenness pixels or assuming that the pixel is representative of these tree-rings which is what is most commonly done.

A third dataset was created, in which each MODIS pixel is associated with field plots with similar species composition. To create the dataset, we correlated the set of *Ppn*, *Pps*, *Pqf*, and *Pqi* in each MODIS pixel to the set of *Ppn*, *Pps*, *Pqf*, and *Pqi* of each inventory plot. We then kept the best correlation for each pixel and filtered the dataset to keep only correlations above 0.9 (Figure 4.1). We obtained a dataset of 336 MODIS plots with species composition very similar to 28 of the original 36 inventory plots. We use this combined dataset to estimate AWP from LAI on yearly basis.



**Figure 4.1 Matching the composition of pixels and ground plot canopy compositions.** Every MODIS plot gets assigned the closest field plot in terms of canopy composition as determined from Pearson correlation. The result was filtered to keep only correlations > 0.9. Black dots represent the rest of the plots.

### 4.2.4 Above-ground Wood Production time-series

### 4.2.4.1 Ground data

A total of 453 wood cores collected for the FunDivEUROPE project in 2011 and 2017 were used in this study to predict above-ground wood production in every plot. Initially 12 cores were collected from each monoculture plot and 6 cores per species in each of the mixed plots. A size-stratified sampling approach was followed for selecting random trees in each plot for coring (Jucker *et al.*, 2014a). This means that tree diameters of all trees within a plot were first measured and classified in 6 size classes before the random selection of at least one tree in each class to ensure the correct representation of growth stages present in each plot. Diameter, height, basal area of all trees with DBH > 7.5 cm in the 36 plots were collected in the first and second census. Trees were also characterized in the first census as belonging to one of 5 crown illumination index (CI) classes (see for index description). Given that CI was not specified for each tree in the second census we estimated it for newly recruited trees (i.e. trees that were < 7.5 cm in the first census) after evaluating four linear mixed effect models (Table S3.1) based on AIC and assumed that the CI did not change considerably in the span on 5 years.

### 4.2.4.2 AWP computation

Wood production time-series were constructed from tree-rings following Jucker *et al.* (2014a,b) with an additional five years of data added, resulting from new tree cores collected in 2017. Briefly, time-series of yearly tree-ring increments (mm year<sup>-1</sup>) were first constructed from tree cores that were collected in 2012 and 2017, cross-dated, and measured using CDendro software suite (Cybis Elektronik & Data, Saltsjöbaden, Sweden).

Second, the equation taken from Jucker *et al.* (2014b) was modified to use FC instead of species richness used in the original equation based on AIC results comparing four

different equation for biomass growth estimation (see Table S3.2) to convert tree ring increment to yearly species-specific biomass growth models:

$$log(G_i) = \alpha_{j[i]} + \beta_1 \cdot log(D_i) + \beta_2 \cdot CI + \beta_3 \cdot FC_j + \varepsilon_i,$$

$$(4.1)$$

where  $G_i$ ,  $D_i$ , and  $FC_i$  are biomass growth, stem diameter and crown illumination index, respectively, of tree *i* growing in plot *j* with functional composition  $FC_j$ .  $\alpha_j$  (the intercept) is the intrinsic growth rate of a tree species growing in plot *j*;  $\beta_{1-3}$  (the coefficients) represent the species growth response to diameter size, light availability and functional diversity; and  $\varepsilon_i$  is the residual error. The parameters in equation 4.1 were first estimated using decadal averaged data for cored trees over a reference time period 2001-2011 from Jucker *et al.* (2014b).

Third, equation 4.1 was applied to all trees in the second census data to predict biomass of all focal stem in the 36 plots for the period 1992 - 2017.

Finally, the biomass of all focal trees in a plot was summed to construct *AWP<sub>j</sub>* timeseries over each plot *j*. Trees marked as dead, cut or with a dry top in the second census were excluded from AWP computation (< 5% of cored trees and < 2% of all trees), and non-focal trees were also excluded (< 2% of all trees).

### 4.2.5 Leaf area index time-series

Three vegetation indices, Normalized Difference Vegetation Index (NDVI), Enhanced Normalized Difference Vegetation Index (EVI) and Normalized Difference Water Index (NDWI), were computed over and extracted from 398 MODIS pixels (250 m) in GEE from the 'MOD13Q1' and 'MYD13Q1' collections (version 6, Didan, 2015a,b). The relative merits of these indices to predict inter-annual variation in AWP (in MgC ha<sup>-1</sup> yr<sup>-1</sup>) was evaluated by looking at their capacity to predict annual values of AWP, and from these analyses, NDVI was selected for further analysis (see Section S3.1 for comparison between the indices).

Time-series of vegetation indices were decomposed to remove seasonality and noise using 'DBEST' (DBEST R package, Jamali *et al.*, 2015; Tomov, 2016; Jamali & Tomov, 2017). Vegetation index trends were aggregated from monthly values to yearly values and regressed model alongside Time (in years) against the time-series of annual AWP from matching plot compositions (see Section 4.2.2 for the matching method). Predicted R<sup>2</sup> was then computed for each set of time-series to determine how well the different vegetation indices predict changes in AWP. We found little difference between NDVI and EVI, while NDWI performed worse than the others (Figure S3.1). We used NDVI since it is the most commonly used vegetation index (Vicente-Serrano *et al.*, 2016b) and transformed it to LAI using the relationship established in Chapter 2 (see Section S1.3).

### 4.2.6 Statistical analyses

Statistical analyses were performed on the three datasets available: the 36 inventory plots within which AWP was calculated annually over 25 years, the 398 MODIS pixels within which LAI was estimated annually over 18 years, and the dataset of 28 plots with 336 matched pixels within with LAI and AWP were tracked over time.

### 4.2.6.1 Computing effective species richness.

Effective species richness was used as a diversity measure in the study. To estimate it for the two datasets we first determined the total canopy cover in each plot and pixel. We first computed the Shannon index for the canopy proportion in the inventory plots and MODIS pixels, using the "vegan" package (Oksanen, 2020). We then transformed the Shannon index to a measure of effective species richness (SRe) ranging from 1 to 4 using the following formula *SRe=exp(Shannon index)* (Jost, 2006).

### 4.2.6.2 Computing trends and stability

To determine the long-term trends in the LAI and AWP datasets, we simply regressed the yearly time-series of AWP and LAI against time (in years since 1992 and 2000 respectively) and extracted the linear trend coefficients.

To evaluate the temporal stability, i.e. the stability of the whole time-series, of the two datasets we computed stability following Jucker *et al.*, (2014) for AWP:

$$S_{AWP} = AWP_{\mu} / AWP_{\sigma}, \tag{4.2}$$

where  $AWP_{\mu}$  is the temporal mean and  $AWP_{\sigma}$  is the temporal standard deviation of  $AWP_{j}$ .

LAI time-series had strong positive linear trends in most pixels and the variance had to be computed around that trend to be comparable to the variance in *S*<sub>AWP</sub>. LAI stability was computed as suggested by Tilman *et al.* (2006) following the formula:

$$S_{LAI} = LAI_{\mu}/LAI_{\sigma d}, \tag{4.3}$$

where  $LAI_{\mu}$  is the temporal mean and  $LAI_{\sigma d}$  is the detrended variation of  $LAI_k$  over pixel k.

### 4.2.6.3 Computing resilience metrics

We computed resilience metrics (following Khoury & Coomes, 2020) to test whether resilience patterns to extreme droughts are similar for canopy and wood growthTemporal stability computed in the previous section is related to resistance (which is the inverse of sensitivity) (Lehman & Tilman, 2000; Lloret *et al.*, 2011), however, given that it is computed from the whole time-series and normalized by using the time-series mean in its computation, it does not allow the determination of resilience to extreme events. We, therefore, computed sensitivity, recovery, and resilience to better understand the response of the forests to extreme drought events.

To measure resilience, we segmented using the 'DBEST' package in R the yearly timeseries of LAI and AWP spanning the same period (2000-2016) and extracted resilience metrics as described in Khoury and Coomes (2020). Simply, following the segmentation of the annual time-series, the two biggest losses, and the gains following them, were averaged for each plot<sub>*j*</sub> and pixel<sub>*k*</sub> representing a measure of sensitivity and recovery from drought. Resilience was computed as the ratio of recovery/sensitivity.

The more traditional method of computing sensitivity and recovery for a set timeperiod pre- and post- drought was computed for comparison using a period of 1 year around the droughts of 2005 and 2012 (See section S3.8 for these results).

# 4.2.6.4 Understanding how wood productivity relate to leaf area and predicting AWP from LAI and SPEI

Given the expected asynchronies between the two datasets in questions (Wagner *et al.*, 2013), studies often attempt to maximize the correlation between the two by identifying NDVI-derived phenological metrics (e.g. NDVI aggregated at different time-scales, maximum greenness) instead of using raw NDVI values and/or applying statistical algorithms (e.g. principle component analysis) (Vicente-Serrano *et al.*, 2016a, 2020; Ivanova *et al.*, 2021). In their work, Vicente-Serrano *et al.* (2016a, 2020) found that in Spain tree-rings relate to NDVI phenological metrics at a small time-scale, never beyond one year, while in other regions of the globe much longer timescales needed to be taken into account to explain yearly tree-ring growth.

Building on the knowledge from previous studies (Vicente-Serrano *et al.*, 2016a, 2020), we expect annual NDVI values and by extension annual LAI values to be associated with annual AWP in Spain. We decided to follow a simpler approach, monthly NDVI values were first converted to LAI values as described in section 4.2.5. Monthly LAI time-series were then decomposed using 'DBEST' package to eliminate the seasonal and noise components of the time-series leaving us with a non-linear LAI trend. Non-linear LAI trend values were then averaged over each year to obtain time-series of annual LAI.

Monthly SPEI<sub>8</sub> time-series were aggregated from bi-monthly time-series to annual time-series also by taking the average for each year. All SPEI scales (1-48) were first aggregated to yearly values and correlated (Pearson's correlation) to the different AWP time-series. The scale correlating the most with AWP time-series was used later for AWP prediction. That scale was determined to be 8 months.

We fitted 4 different regressions to understand how AWP, LAI, and SPEI relate to each other (Table 4.1).

#	Model	Years	Frequency	SPEI scale
M1	LAI ~SPEI+TIME	16	Monthly	1-48
M2	AWP~SPEI+TIME	25	Yearly	8
М3	AWP~LAI +TIME	16	Yearly	8
M4	AWP~SPEI+LAI+TIME	16	Yearly	8

### Table 4.1 Linear regression models linking time-series of AWP, LAI, and SPEI.

## 4.2.6.5 Maximum likelihood estimation of canopy area, species composition and richness effects

To address the overarching question of how canopy area, species composition and diversity affect wood production and leaf area and their response to drought, we modelled all AWP and LAI metrics: average, trend, stability, sensitivity, resilience, as well as the coupling between them (i.e. R<sup>2</sup> from model M3) and the difference in the R<sup>2</sup> between M4 and M3, using maximum likelihood estimation for the following equation:

$$y = CA^{a} \cdot (b_{1} Ppn + b_{2} Pps + b_{3} Pqf + b_{4} Pqi) \cdot (1 + c SRe) + \varepsilon_{1} + \varepsilon_{2} CA, \qquad (4.4)$$

where y is the response variable and CA is canopy area (% plot area for field plots or % of pixel area for MODIS pixels), *Ppn*, *Pps*, *Pqf*, and *Pqi* are the proportions of CA that are *P. nigra*, *P. sylvestris*, *Q. faginea* and *Q. ilex* respectively, and SRe is the effective species richness, while *a*, *b*<sub>1</sub>, *b*<sub>2</sub>, *b*<sub>3</sub>, *b*<sub>4</sub>, *c*,  $\varepsilon_1 + \varepsilon_2$  are parameters estimated using maximum likelihood methods.  $\varepsilon_1 + \varepsilon_2$  are normally distributed parameters, centred on zero, which account for the residual variation; the second of these parameters was included because the variance of residuals was observed to increase with canopy area in some cases (depending on the response variable). For an easier interpretation of the parameter estimated we scaled SRe by subtracting 1 so that a value of 0 corresponded to monocultures and a value of 3 corresponds to fully mixed. Maximum likelihood models were fitted using the package "bbmle" in R (Bolker, 2013). To determine the significance of the fixed variables, we compared the models in Table S3.2 computing the second-order Akaike information criterion (AICc) using the "ICtab" function in "bbmle". Confidence intervals and prediction intervals were computed following the delta-method (Beyene & Moineddin, 2005).

### 4.3 Results

Several summary and resilience metrics were derived from the AWP and LAI timeseries and modelled with canopy area, species proportion in the canopy, and species diversity to determine the impact of these three variables on wood production and leaf area. We could not detect any effect beyond the relationship to canopy area for any of the AWP metrics (Table 4.1). We found strong canopy proportion effects on the LAI metrics and summary metrics of the relationship between AWP and LAI. All these results are revisited in more detail below, where we plot the best fitting model for each metric. Diversity effects on LAI were also not statistically significant in this study, we did however note that diversity effects were significant before the incorporation of species proportions in our model, which means that collinearities between species proportions and SRe did influence this result. In every instance, the model containing species proportions was always more informative than the model containing diversity effects instead, which means that observed diversity effects are simply a function of species proportions and that there were no interaction effects between the species.

# Table 4.2 Maximum likelihood analysis of the effect of species richness, species proportions and canopy area on wood production (AWP) and leaf area (LAI) responses to extreme droughts.

Numbers and signs in bold indicate significance. Numbers in red are marked for significant differences between the different species. CA ranges between 0-2 with 2 being equivalent to 200 % of plot or pixel area, species proportions vary between 0-100 % of CA, and SRe varies between 0-3 with zero representing plots with 1 species and 3 plots will all 4.

									Predicted
Variable	Data	CA <sup>a</sup>	b₁ Ppn	b₂ Pps	b₃ Pqf	b₄ Pqi	c SRe	Var	R <sup>2</sup>
AWP mean	Field	0.4096	0.0058	0.0079	0.0066	0.0037	0.0967	+	0.62
AWP trend	Field	0.8589	2.1403	2.3410	-1.9466	0.8589	2.1403	-	0.40
AWP stability	Field	-0.1693	0.0517	0.0534	0.0612	0.0504	-0.0421	-	0.12
AWP sensitivity	Field	0.4843	0.0025	0.0035	0.0028	0.0013	0.0930	+	0.53
AWP resilience	Field	0.0690	0.0091	0.0079	0.0082	0.0148	-0.0742	-	0.36
LAI mean	RS	0.1904	0.0206	0.0235	0.0131	0.0157	0.0048	-	0.46
LAI trend	RS	0.5785	0.0026	0.0030	0.0016	-0.0025	0.5228	+	0.40
LAI stability	RS	0.0681	0.4032	0.4772	0.3265	0.2514	-0.0024	-	0.23
LAI sensitivity	RS	0.0964	0.0009	0.0007	0.0008	0.0018	-0.0289	+	0.20
LAI resilience	RS	0.1014	0.0129	0.0141	0.0119	0.0064	-0.0307	-	0.09
M3 R <sup>2</sup>	RS	0.1579	0.0033	0.0036	0.0076	0.008	-0.1311	+	0.19
M4 R <sup>2</sup>	RS	0.0401	0.0070	0.0037	0.0081	0.0055	-0.0745	+	0.29
$M4 R^2 - M3 R^2$	RS	-0.1275	0.0028	0.0005	0.0010	-0.0005	0.1482	+	0.67

# 4.3.1 What are the trends in terms of leaf area and wood productivity over this Spanish landscape?

On average wood production in plots was 0.6 MgC ha<sup>-1</sup> yr<sup>-1</sup>, while LAI over the landscape was on average 1.53. AWP and LAI both increased with a higher canopy area (Figure 4.2a and b). Species richness did not affect this relationship in both cases, but species proportions in the canopy did affect the relationship between LAI and canopy area (Figure 4.2b and Table 4.2b). Many forest stands were observed to increase in LAI over the past two decades of observations as trees colonised open sites following agricultural land abandonment (Figure 4.2b) but species richness had no effect on LAI trend (Table 4.2). Pines which had higher leaf area (Figure 4.2b) also contributed the most to the increase in leaf area over time (Figure 4.2d), while stands containing a large proportion of *Q. ilex* had lower positive LAI trends. About 20% of pixels declined in LAI (Figure 4.2d), which were on average mostly dominated by *P. nigra* and *Q. ilex*. AWP was observed to increase with higher proportions of *Q. ilex* in the canopy (Figure 4.2c) however the  $\Delta$ AICc of this specific model was not much smaller than the null model and therefore we cannot really draw conclusions on it.



### Figure 4.2 Maximum likelihood predictions for some of the equations in table 4.1 looking at AWP and LAI averages and trends over sites in central east Spain.

a) Relationship between average AWP and canopy area. b) Relationship between average LAI, canopy area, and species proportion. c) Relationship between AWP trend over the past 35 years, canopy area and species proportions. d) LAI trend over the past 16 years as a function of canopy area and species composition. Black line represents pixels with equal species cover proportions. Solid lines represent predicted relationships from maximum likelihood parameter estimates when pixels are covered by one species only (does not happen in the MODIS dataset but does happen in the field dataset). Dark faded bands represent 95% confidence intervals and light faded bands represent prediction intervals (1 standard deviation). In b) confidence intervals overlap with prediction intervals.

# 4.3.2 How stable are LAI and AWP and is this stability affected by canopy area, species composition and species diversity?

Data from field plots suggests that AWP temporal stability decreases with an increase in canopy area (Figure 4.3a), while remotely sensed LAI suggests that LAI stability increases with canopy area and differs between pixels covered by different species proportions (Figure 4.3b). Forests dominated by pines were more stable than forests dominated by oaks in terms of leaf area (Figure 4.3b). Species richness did not have an effect on the temporal stability of AWP or LAI (Table 4.1).



### Figure 4.3 Relationships between stability and canopy area, estimate using maximum likelihood methods.

Stability of aboveground wood production a) and leaf area index b) over the past 16 years as a function of canopy area and species composition. Solid lines represent predicted relationship from maximum likelihood parameter estimates (see Table 4.2), dark faded bands represent confidence interval (95%) and light faded bands represent prediction intervals (1 standard deviation). Black solid line in b) represent the estimated relationship for a pixel with equal species cover proportions.

# 4.3.3 How do canopy area, species proportions and species richness AWP and LAI affect forest resilience to extreme droughts?

AWP and LAI were both reduced in drought years but to different extents. On average AWP was reduced by 42% (Figure 4.4a), while LAI only dropped by 6% (Figure 4.4b) following extreme droughts. AWP sensitivity to drought was greater in stands with higher canopy area (Figure 4.4a) while LAI sensitivity was not significantly affected by canopy area (Table 4.1) (Figure 4.4b). Species richness had no effect on the respective sensitivities of AWP and LAI, species proportion, on the other hand, demonstrated that forests dominated by *Q. ilex* were particularly sensitive to drought in terms of LAI (Table 4.2). *Q. ilex* dominated forests lost twice the leaf area compared to forests dominated by pines and/or the deciduous *Q. faginea* (Figure 4.4b). Sensitivity and recovery were positively related with plots recovering 77% (i.e. average AWP resilience ratio of 0.77) of their wood production rate in the two years following extreme droughts (Figure 4.3c) and pixels recovering 90% (i.e. average LAI resilience ratio of 0.9) of their LAI values in that time (Figure 4.3c), and a weak positive relationship between LAI resilience

and canopy area (Figure 4.3d) (Table 4.1). Surprisingly, *Q. ilex* dominated forests were also half as resilient as other forests (Figure 4.3d).



### Figure 4.4 Relationships between sensitivity (and resilience ratio) and canopy area and species proportions.

a), b) Relationship between AWP and LAI sensitivity to extreme droughts. c), and d) Relationship between AWP and LAI resilience to extreme droughts. Solid lines represent predicted relationships from maximum likelihood parameter estimates (see Table 4.2), dark faded bands represent confidence interval (95%) and light faded bands represent prediction intervals (1 standard deviation). Black solid lines in b), and d) represent the estimated relationship for a pixel with equal species cover proportions.

### 4.3.4 To what extent is AWP controlled by water availability and changes in

### LAI?

SPEI predicted LAI variation much better than AWP variation suggesting that forest leaf area mirrors more closely the trends in waters availability at a site albeit to a much smaller magnitude than AWP response to water scarcity (Figure 4.5a and 4.5b). Regression models that attempted to explain AWP with LAI or SPEI alone had only moderate success with an average R<sup>2</sup> of 0.31 (Figure 4.5b and c). The coupling between LAI and AWP varied with species proportions in the canopy. Forests that were dominated by oaks had on average a much higher coupling between LAI and AWP (Table 4.1 and Figure 4.6a). Regression models that combined SPEI<sub>8</sub>, LAI, and time predicted 50% of the variation in yearly AWP on average reaching up to 85% (Figure 4.5d). Adding SPEI to the model in Figure 4.5c greatly improved the prediction for forests dominated by *P. nigra* suggesting that *P. nigra* wood production is much more strongly affected by water availability than its canopy (Figure 4.6b). Adding SPEI also improved the AWP prediction for forests dominated by *P. sylvestris* and *Q. faginea* but to a much lesser extent than *P. nigra*, while it seems to have slightly worsened the prediction for forests dominated by *Q. ilex* (Figure 4.6b).



Figure 4.5 Histograms of R<sup>2</sup> values of regressions models relating time-series of AWP, LAI and SPEI.

Regression is over 25 years for AWP alone, and for 17 years when the regression includes LAI. SPEI<sub>X</sub>: all SPEI scales (1 - 48) were used to determine the best fitting drought model. SPEI<sub>8</sub>: SPEI aggregate every 8 months was used in modelling AWP. Time<sub>m</sub>: Time in months from 2000 to 2017. Time<sub>y</sub>: Time in years from 1992 for b) and from 2000 in c) and d). a) Relating annual AWP to yearly LAI values, solid line is average 0.31; b) relating yearly AWP to yearly SPEI, solid line is average 0.31; c) relating AWP to both yearly LAI trend and SPEI, solid line is average 0.50; d) relating monthly LAI to monthly SPEIX, solid line is average of 0.53.



**Figure 4.6 AWP-LAI coupling as a function of species composition and canopy area.** a) Goodness of fit of the coupling between AWP and LAI calculated without including SPEI in the model; (R<sup>2</sup>). b) Difference between a model which includes SPEI and a model with only LAI and time. Note time is included in the regressions to remove long-term trends. Solid lines represent predicted relationships from maximum likelihood parameter estimates, dark faded bands represent confidence interval (95%). Black solid lines represent the estimated relationship for a pixel with equal species cover proportions.

### 4.4 Discussion

### 4.4.1 Wood production and leaf area trends.

LAI trends over the past 16 years in the study area were mostly positive which is in agreement with previous research on forest greening and densification in Spain (Peñuelas et al., 2002; Khorchani et al., 2018; Khoury & Coomes, 2020). LAI trends varied with canopy area and species proportions with denser canopies growing the most which agree without finding from Chapter 2 (Figure 4.2d). Furthermore, LAI trends were positively related to average AWP (Figure S3.4). Wood productivity and leaf area both increased significantly with canopy area in Mediterranean montane forests dominated by oaks and pines (Figure 4.1a and b). The relationship between AWP and canopy area is unsurprising as canopy area increase is related to basal area increase (Figure S3.3b) and therefore biomass. NDVI and LAI are known to be related to each other and to green biomass over landscapes (Heiskanen, 2006; Potithep et al., 2010; Du et al., 2014), often non-linearly (le Maire et al., 2006), it is however always advised to validate these vegetation indices against ground data if possible (Chakroun et al., 2014). While the canopy area used in this study to model LAI is derived from airborne hyperspectral mapping, the latter was validated against ground canopy cover (see Figure 3.4 in Chapter 3). Our results, therefore, indicate that MODIS-derived LAI can capture differences in canopy density over this Spanish landscape without reaching saturation.

# 4.4.2 Changes in wood production and leaf area stability with stand development.

AWP became less stable with denser canopies, while LAI became more stable. Jucker *et al.* (2014b) suggested that Spanish forests are different from other European forests when it comes to the effect of diversity on the stability of wood production because their drought-prone summers turned complementary interactions into competitive ones when water resources were in short supply. While we did not find that species richness destabilised AWP, canopy area did which could be indirectly accounting for a change in species richness as mentioned at the beginning of the results. The increase in canopy area is also related to an increase in basal area (Figure 3.2b) and agrees with other studies on the density effect on wood production in semi-arid environments (Bottero *et al.*, 2017). A recent systematic review suggests that the positive effects of diversity on productivity and other ecosystem services are far from being the rule (Grossiord, 2019). The fact that

mean annual LAI became more stable with higher canopy areas disagrees with our results from Chapter 2 indicating that greener or denser forests, considering the whole of Spain, are more sensitive to drought. We believe that this difference is due to the different special scales of the study. Forests studied in this Chapter had a maximum LAI of 2.2 (Figure 4.2b) while the earlier study covering the whole of Spain had LAI values reaching up to 5 (see Figure 2.3b) which is bound to have a much stronger effect on LAI stability. Instead, the increased stability found here is perhaps linked to an increase in the climate buffering effect induced by a larger shaded area (De Frenne *et al.*, 2019).

### 4.4.3 No species richness effects on AWP and LAI.

Previous studies working within the same forest inventory plots as ours have found a positive effect of diversity on productivity (Jucker et al. 2014a,b, 2016; also replicated by us in Figure S3.2a). These findings agree with other studies exploring the effects of species richness and packing density on productivity (Ruiz-Benito et al., 2014; Pretzsch et al., 2015; Jucker et al., 2020). However, we examined the effect of diversity on both wood and remotely sensed leaf area through a different lens to other previous studies, working with the canopy areas of different species instead of basal areas used in many previous studies (Jucker et al., 2014a,b) or even species composition classes (Pardos et al., 2021). When using canopy area in our analyses, the relationship between species richness on wood productivity was non-significant (Table 4.2). We expected that previously observed positive effects on wood productivity by diversity are actually indirectly caused by an increase in canopy packing (Jucker et al., 2015) and expected to observe a relationship between SRe and canopy area that would explain these results (i.e. we expect collinearity effects between canopy area and SRe are causing diversity to be non-significant). We however did not find results supporting our predictions, with the effect of diversity being non-significant on canopy area (Figure S3.2b) in the ground dataset.

We did find, however, that collinearities between diversity and species proportions in the remotely sensed dataset caused SRe to have a non-significant effect on LAI metrics. Species proportions were for instance were consistently better at predicting LAI metrics than SRe. It is however important to keep in mind that canopy area in this study is a measure of horizontal canopy and therefore does not capture vertical or density changes in canopies which is also suggested to increase with diversity (Jucker *et al.*, 2015). This could be a reason why our measure of canopy area itself did not vary with SRe, and why our diversity measure which is based on this canopy area might not be capturing the full diversity effect on canopy structure which in turn can impact productivity (Hardiman *et al.*, 2011). In their study, Hardiman *et al.* (2011) found that wood productivity is primarily impacted by canopy structural complexity and not canopy diversity. In this light, it is important to keep in mind that the results discussed in this study about diversity effects are those which extend beyond the diversity effects on canopy horizontal packing.

### 4.4.4 AWP is more sensitive to extreme drought than leaf area

We found that AWP is much more sensitive to extreme droughts than LAI, which may reflect resource allocation strategies in trees. As reviewed by Litton *et al.* (2007), trees partition carbon to foliage in a very conservative manner, while the portion allocated to wood production is highly dependent on nutrient availability and environmental conditions. Consistent with these findings, in very dry years, AWP response to drought was 12-fold greater than the LAI response in the driest years, with average losses in AWP amounting to 41 % (Figure 4.4a) while average losses in LAI were only 3.5% (Figure 4.4b), broadly in agreement with previous studies (Gazol *et al.*, 2018).

Forests dominated by pines did not lose more LAI during droughts because they had the most resistant canopy, while *Q. ilex* dominated forests lost more leaf area. These results are due to the different responses of *P. nigra* and *Q. ilex* to drought (Figure 4.6). *Q. ilex* was previously found to respond to drought with reduced flushing of new leaves and by shedding old leaves, which explains the strong LAI losses (Camarero *et al.*, 2015). *P. nigra*, on the other hand, an isohydric species, possessing strong stomatal regulation, only sheds its needle in large quantities once stomatal regulation is insufficient to maintain internal water balance during prolonged or extreme droughts (González de Andrés & Camarero, 2020).

Despite this region being affected by extreme droughts in 2005 and 2012 (Figure S3.5) and despite the considerable reduction in wood productivity, the losses in leaf area were very small compared to losses in LAI in other parts of Spain (see Chapter 2), even for forests dominated by same studied species (e.g. *P. sylvestris*). It is important to keep in mind that other factors such as topography, soil conditions, tree age and size, and forest density can have a moderating or exacerbating influence on the species resilience to drought (Merlin *et al.*, 2015; Khoury & Coomes, 2020). We already observed such an

effect here with canopy area increasing LAI stability in these forests and can hence suggest that other factors may have come into play to confer a higher LAI resilience in pines and avoid drought-induced needle shedding in the study area. In another study, for instance, in south-east Spain, the pine species incurred significant losses in leaf area, even mortality, due to drought events (Guada *et al.*, 2016).

### 4.4.5 Relating wood production to remotely sensed canopy variations

Combining SPEI with LAI improved AWP predictions by 22% which indicate a level of decoupling between leaf area and wood production which reflects different drought response mechanism and perhaps different resource partitioning in the forest tree species. The level to which adding SPEI improved yearly AWP prediction did indeed vary significantly between forests dominated by different species. The improvement was most apparent for *P. nigra* (Figure 4.6a), which points to a strong response of AWP in black pine-dominated forests to relative water availability, consistent with the previously mentioned isohydricity of *P. nigra*. Assuming that the difference between M4 and M3 does tell us something about resource partition to canopy and wood production, the results that this does not vary with canopy area is also in agreement with finding by Litton *et al.* (2007), indicating that tree density does not affect carbon partitioning in trees.

LAI alone explained 31% of the variation in AWP over this Spanish landscape. Despite the simpler approach, our result is comparable to the correlations found in Vicente-Serrano *et al.* (2016) for NDVI and tree-ring increments in which they found an average correlation between best NDVI aggregation level and tree-ring increment to be equal to 0.5. Our results are also consistent with their observed pattern for the four species, although the relationship in pines was significantly weaker in our study (Figure 4.6a). Wood production and leaf area in oak-dominated forests were significantly more related than in pine-dominated forests reaching up to 50% on average for *Q. ilex* dominated forests (R<sup>2</sup> in Figure 4.6a).

### 4.4.6 Implications

Relating AWP to LAI we found that wood production in oaks, even the evergreen oaks, is much more related to their leaf area, than in pines which regulate their production by stomatal closure instead of the shedding of leaves. The divergent pattern in pines is indicative of different resource allocation priorities under drought, as well as a demonstration of their isohydric behaviour. While increases in wood productivity and LAI were linked to higher canopy area, we found no evidence of diversity effects beyond that of the impact of the individual species proportion. These results suggest that looking at leaf area or greenness resilience patterns from space and relating them to AWP resilience can reveal interesting phenological and resource partitioning properties for different tree species.

# Chapter 5 Effects of Mediterranean woodland diversity on leaf functional traits

### Abstract

Within the context of rapid climate change in the Mediterranean region, identifying how tree species interact with each other and their environment is key to creating resilient ecosystems. While several studies emphasise the positive role that biodiversity has on ecosystem functioning, others focused on Mediterranean systems find counter examples in which increasing diversity is destabilizing and diminishes resilience. We analysed the leaf traits of monocultures and mixed forests in Alto Tajo, central Spain, dominated by two pines (*Pinus nigra* and *P. sylvestris*) and two oaks (*Quercus ilex* and *Q. faginea*). Out of 14 leaf traits measured, we found strong differences in stable isotope ratios (carbon and nitrogen) of pines and strong differences in photosynthetic traits in oaks between trees growing in monocultures and mixed forests. We found that *P. nigra* and *P. sylvestris* had greater water use efficiency when grown in more diverse forests and that *Q. faginea* benefited from diversity by having higher leaf relative water content and maximum fluorescence in mixed plots.

### 5.1 Introduction

The effects of land-use change on forests in the Iberian Peninsula, precipitated by socioeconomic trends in the 20<sup>th</sup> century, are more apparent than any effects of global warming (Lasanta *et al.*, 2009; Vayreda *et al.*, 2012; Gazol *et al.*, 2018). The decreasing anthropogenic pressure on forests and the widespread land abandonment, caused by the conversion to fossil fuel and urbanization, have resulted in forest densification and succession from conifer to late-successional angiosperms (Puerta-Piñero et al., 2012; Vayreda et al., 2013; Martín-Alcón et al., 2015). Relatively shade-tolerant oaks, naturally dispersed by animals (birds, rodents and wild boars) into pine forests, are favoured by forest managers because they fulfil diversification goals initially aimed at restoring Mediterranean forests landscapes to what they were before the widespread deforestation mid-19th century (Gil & Aránzazu Prada, 1993; Pausas et al., 2004; González-Moreno et al., 2011; Sheffer, 2012; García et al., 2017). Around 90% of the reforestation in Spain was done with pines because of their pioneering ability, i.e. the ability to grow on degraded and barren soils, while diverse forest populated by native oaks was the final goal (Pausas et al., 2004). Oaks are also recommended for re-sprouting abilities, which confer higher resilience to fire disturbances in the Mediterranean (Pausas et al., 2004; Puerta-Piñero et al., 2012). When it comes to woodland responses to climate change, however, there are conflicting results, suggesting that the resiliencies of these diverse, successional forests are highly dependent on their local ecosystem characteristics, such as climate, fire frequency, understory and others (Pausas et al., 2004; Carnicer et al., 2013; Grossiord et al., 2014). Hence, management decisions that aim to encourage diversification of monocultures across Mediterranean landscapes must take into consideration how diversity affects the resilience of local species to disturbance as well as climate change.

Leaf traits reveal important information about plant functioning and allow us to monitor changes in canopy chemical composition which are associated with nutrient cycling and resource use within plants communities (Reich, 2012, 2014). Mixed woodlands in Spain have been shown to have different foliar isotope compositions in pines and oaks, and isotope compositions are affected by the identity of neighbouring species (Grossiord *et al.*, 2015; Forner *et al.*, 2018). These differences were linked to different rooting systems and water management mechanisms. Pines had a stronger reaction to water depletion with greater change in water use efficiency and sap flow as compared to neighbouring oaks (Forner *et al.*, 2018). *Quercus faginea*, on the other hand, has a considerably lower water use efficiency when surrounded by pines as opposed to other oaks (Grossiord *et al.*, 2015). However, in wet years, when water is not a limiting factor, pines have been shown to have a bigger increase in wood productivity than oaks, due to a decrease in light competition, while in dry years all those benefits are lost and the effect of diversity reversed (Jucker *et al.*, 2014a). These findings suggest that species mixing might be more beneficial to oaks than pines, especially in dry years. However, few studies have considered the responses of canopy traits to diversity in these species.

Canopy properties can be used to understand the responses of individual trees in a stand to a range of stressors, that can act over a variety of timescales. In the short term, variation in the abundance of foliar stable isotopes can reveal important information about the physiological activity, such as the rates of photosynthesis and water transport within trees. Carbon isotope discrimination ( $\delta^{13}$ C) is commonly used as a proxy for water use efficiency, which is the amount of water spent during transpiration to obtain a unit of CO<sub>2</sub> (Bazzaz, 1979). Nitrogen isotope discrimination ( $\delta^{15}$ N) is related to nitrogen access and assimilation, as well as nitrogen fractionation in the plants which can reveal important information about nitrogen cycling mechanisms. Foliar nitrogen content is known to be positively correlated to photosynthetic activity, as a large portion of the nitrogen is invested in the photosynthetic apparatus (around 80%) and variation in foliar nitrogen reflects the abundance of photosynthetic proteins (Evans & Seemann, 1989; Hikosaka, 2004). A reduced foliar nitrogen content suggests that a tree is experiencing nitrogen limitation over a more prolonged timescale. Cellulose, hemicellulose and lignin foliar contents are structural traits accumulated over the life cycle of a leaf or needle, tied to toughness, longevity and defence (Hikosaka, 2004; Nunes et al., 2017). Leaf water content can be used to assess the water status of plants, with fresh water content (FWC) reflecting water status at the time of measurement and relative water content (RWC) indicating the water quantity relative to the maximum capacity of a leaf to store water. FWC, also known as live fuel moisture content, varies with seasonal changes of dry mass and can be measured remotely from spectral data (Zhang & Zhou, 2019), while RWC is strongly linked to leaf balance of water supply and transpiration rate, and can only be measure manually (Anithakumari et al., 2012). Photosynthetic traits such as chlorophyll content, photosynthetic capacity and maximum fluorescence reflect carbon capture

capacity (Sperlich *et al.*, 2015). Finally, specific leaf area (SLA) and leaf dry matter content (LDMC), are important indicators of species position on the plant economic spectrum (Grime, 1977; Lambers & Poorter, 1992; Reich, 2014). Variation in biotic and abiotic stress can cause plants to vary the traits described, as a form of adaptation, or a result of limitation. Measuring these traits across species and communities can therefore provide insight into the responses of forests to changing stresses and environments.

In this study, we ask how the foliar traits of four common Mediterranean tree species are affected by stand diversity. We also examine if measured traits reflect differences in species phonologies given that they are measured during a dry Spanish summer. To do this, we analyse 14 foliar traits related to photosynthesis, nutrient cycling and structure in four Mediterranean species growing in mixed plots and monocultures in Alto Tajo Natural Park, Spain.

### 5.2 Methods

### 5.2.1 Field site and study design

The study was conducted in the Mediterranean mixed forests of the Alto Tajo Natural Park, located in the Guadalajara province of central Spain (40.9°N, 1.9°W). Leaves and needles were sampled in 10 permanent plots established by the FunDivEUROPE project (see Baeten et al., 2013), which were designed to test the effects of diversity on ecosystem functioning by selecting woodlands that varied in diversity but had minimal variation in soil type, topography and climate. All plots had calcic cambisol soils (FAO classification) and were situated at altitudes between 960 and 1390 m.a.s.l. The mean annual temperature is 10.2 °C, and the mean annual precipitation is 499 mm year<sup>-1</sup>. Forested areas are primarily composed of *Pinus nigra*, *P. sylvestris*, *Q. ilex* and *Q. faginea* (Jucker *et al.*, 2014a). Ten forest plots (30 x 30 m in size) were selected for the study, 8 of which were monocultures and 2 of which were mixtures of all four species. Five individuals of each target species were sampled in each plot for subsequent functional trait analysis, with each species-diversity combination replicated twice.

### 5.2.2 Function trait collection and analysis

Fourteen functional traits were measured on sunlit leaves from 80 individual trees, all of which were> 10 cm diameter at breast height. Measurements were taken in June 2017, during a period of high temperatures. Leaf biochemistry determination and traits extraction were carried out in accordance with previous trait campaigns, as developed

and described by Carnegie Airborne Observatory (see http://spectranomics.ciw.edu). Briefly, for water content and leaf mass/area traits, leaves and needles amounting to approximately 1 gram were collected, weighed and wetted overnight in a plastic bag between two pieces of wet paper towels. They were then weighed at turgor, oven-dried at 60°C for 72 hours, and then reweighed for the dry weight. These leaves were also scanned in RGB at 300 dpi, and their area estimates with the 'leafareavision' python package (Paine *et al.*, 2019). Fresh water content (%) was computed as shown in equation 5.1, relative water content (%) was computed as shown in equation 5.2 (Saura-Mas & Lloret, 2007), SLA (cm<sup>2</sup>.g<sup>-1</sup>) was computed as shown in equation 5.3 and leaf dry matter (%) content was computed using equation 5.4 (Saura-Mas & Lloret, 2007).

$$fresh water \ content = 100 \times \frac{leaf \ fresh \ weight \ (g) - leaf \ dry \ weight \ (g)}{leaf \ fresh \ weight \ (g)}$$
(5.1)

$$relative water \ content = 100 \times \frac{leaf \ fresh \ weight \ (g) - leaf \ dry \ weight \ (g)}{leaf \ weight \ at \ turgor \ (g) - leaf \ dry \ weight \ (g)}$$
(5.2)

$$SLA = \frac{\text{total leaf area } (cm^2)}{\text{leaf dry weight } (g)}$$
(5.3)

$$leaf dry matter = 100 \times \frac{leaf dry weight (g)}{leaf weight at turgor (g)}$$
(5.4)

For carbon and nitrogen concentrations and their stable isotope ratios, a Finnigan MAT 253 (Thermo Fisher Scientific) mass spectrometer was used on samples that were powdered with a ball mill. For the structural traits, a carbon fraction analysis was performed using an Ankom fibre analyser (Ankom Technology) which sequentially digested ground samples, with increasing acidity, allowing the concentration of hemicellulose, cellulose, lignin and recalcitrants (e.g. soluble carbon such as carbohydrates, lipids, pectin and soluble proteins) to be determined, in that order (Van Soest, 1994). To assess potential photosynthetic activity, the amount of chlorophyll was measured using a CCM-200 chlorophyll content meter (Opti-Sciences, ADC BioScientific Ltd.), and is reported as the chlorophyll index, which is computed as the ratio of percent transmission at 931 nm to 653 nm (Richardson *et al.*, 2002). Photosynthetic yield and fluorescence yield were measured with a portable chlorophyll fluorometer, the MINI-PAM (Waltz) equipped with leaf clip after the samples were dark-adapted for 30 min.

Statistical analyses were performed within the R statistics framework (R Core Team 2019). We used the 'nlme' R package to compute linear mixed-effects model of changes

in each trait (y) related to the fixed effects of species and diversity level and their interaction. Plot identity was specified as a random effect. The 'effects' package in R was used to compute confidence intervals for estimated coefficients from the mixed effect models. R<sup>2</sup> was determined using the 'rsquared' function from the 'piecewiseSEM' package.

### 5.3. Results

### 5.3.1 Canopy carbon and nitrogen

Differences in carbon and nitrogen content were significant between species but not between mixed forests and monocultures. Carbon content was significantly lower in both oak species compared to the two pines (Figure 5.1a), while nitrogen content was significantly higher in the deciduous *Q. faginea* compared to the three evergreen species (Figure 5.1b) which is often related to the higher photosynthetic capacity of deciduous (Escarré *et al.*, 1999).  $\delta C^{13}$  was significantly higher *P. sylvestris* growing in mixed plots than in monocultures, while no effect of species or diversity was observed in the three other species (Figure 5.1c).  $\delta N^{15}$  was higher in conifers situated in mixed plots while no effect of diversity was observed on stable nitrogen ratio in oaks.  $\delta N^{15}$  was also considerably higher in *Q. faginea* compared to three other species (Figure 5.1d).



**Figure 5.1 Linear mixed effect model results for the variation of canopy carbon and nitrogen traits between species and two diversity levels.** 

Error bars represent 95% confidence intervals around the average and R<sup>2</sup> are from conditional mixed-effect models. a) Canopy carbon content (%); b) canopy nitrogen content (%); c) canopy  $\delta C^{13}$  ratio (‰); d) canopy  $\delta N^{15}$  ratio (‰).

### 5.3.2 Photosynthesis

The chlorophyll content of *Q. ilex* was significantly higher when in a mixed forest than in a monospecific stand (Figure 5.2a), however, this difference does not translate into a difference in photosynthetic activity (Figure 5.2b and 5.2c). Maximum fluorescence was significantly greater in oaks than in pines, when both species grew in a mixture, but was similar across all species living in monoculture There was a positive relationship between chlorophyll content and maximum fluorescence in oaks (Figure 5.2d). We found a positive association between foliar nitrogen content and photosynthetic yield in the two pines (Figure 5.2e), indicating that the increase in nitrogen is associated with an investment in the photosynthetic apparatus. However, the relationship was stronger between foliar nitrogen content and maximum fluorescence yield in all species which is in turn tied to fluorescent proteins (Figure 5.2f).



### Figure 5.2 Photosynthetic traits.

a) Chlorophyll content index; b) Photosynthetic yield a.k.a. maximum potential efficiency of PSII ( $\phi$ PSII); c) maximal fluorescence (Fm); d) relationship between maximal fluorescence yield and chlorophyll content index for *Q. faginea* and *Q. ilex*; e) relationship between photosynthetic yield and nitrogen content; f) relationship between maximum fluorescence yield and nitrogen content in all four species. \* Chlorophyll content measurements performed on pine needles are not reliable due to the needles not covering the full area of the CCM-200 sensor. Error bars represent 95% confidence intervals around the average and R<sup>2</sup> are from conditional mixed-effect models.

### 5.3.3 Water content

Canopy fresh water content varied significantly between species, as did relative water content (Figure 5.3). In both cases, pine species have a higher water content than both oak species, with the exception of *Q. faginea* growing in mixed species plots, indicating naturally higher water content in pine needles than oaks leaves. The deciduous oak had a relative canopy water content comparable to pines in mixed forests but not when in monocultures, suggesting that they might be having a more similar water-storing strategy to pines than to the evergreen oak.



### Figure 5.3 Linear mixed effect model results for the variation of canopy water content between species and two diversity levels.

Error bars represent 95% confidence intervals around the average and R<sup>2</sup> are from conditional mixed-effect models. a) Canopy fresh water content (%); b) canopy relative water content (%).

### 5.3.4 Structural traits

Differences in hemicellulose and cellulose were found between species but not between monospecific and mixed stands, whist lignin content showed no significant variation across all treatments (Figure 5.4). Both SLA and LDMC varied significantly between species (Figure 5.5) with pines having a lower LDMC than oaks. LDMC mirrored patterns in SLA for *P sylverstris*, *P. nigra*, and *Q. faginea*, but they were only weakly correlated at the leaf level (r=0.23). *Q. ilex* was found to have a very high LDMC whilst having a low SLA, meaning that its leaves were very dense. No significant effect of stand diversity was found on any structural traits (p > 0.1).





a) Hemicellulose and bound proteins content (%), b) cellulose content (%), c) lignin and recalcitrants content (%). Error bars represent 95% confidence intervals around the average and  $R^2$  are from conditional mixed-effect models.



### Figure 5.5 Leaf structural traits.

a) Specific leaf area  $(mm^2/g)$ , b) Lead dry matter content (%). Error bars represent 95% confidence intervals around the average and R2 are from conditional mixed-effect models.

### 5.4 Discussion

The leaf traits of pines and oaks differed between mixed forests and monocultures. Pines differed primarily in nutrient processing, while oaks differed in leaf structural properties and chlorophyll content.

### 5.4.1 Water use efficiency

High  $\delta^{13}$ C, is often used as an indicator of water use efficiency and water availability to trees (Jucker *et al.*, 2017). The differences we found in  $\delta^{13}$ C between pines and oaks agree with previous findings from Alto Tajo Natural Park (Forner et al., 2018). They found that *P. nigra* had the highest water use efficiency as well as the biggest change in this efficiency when analysing drought effects through time. However, pines growing in monocultures did not demonstrate a greater water use efficiency when compared to oaks growing in either the mixed or monoculture plots. On the contrary, *P. sylvestris* had the lowest  $\delta^{13}$ C value, suggesting lower instantaneous water use efficiency, while others other species had non-significantly different  $\delta^{13}$ C values (Figure 5.1c). This could be due to *P. sylvestris*, which is a shallow rooter, having a faster and stronger response to drought in the area. Given that our plots were chosen to have similar topographical and environmental conditions, the observable difference in the water use efficiency in pines is probably due to the increased diversity levels in mixed plots which ultimately impacts resource sharing. Pines are drought-avoiding species that react rapidly to high temperatures and low water availability by closing their stomata to avoid water loss and hydraulic failure (Poyatos et al., 2008; Forner et al., 2014). This regulation inevitably affects photosynthesis and the water use efficiency of needles, causing an increase in both  $\delta^{13}$ C

and  $\delta^{15}N$  (Serret *et al.*, 2018). We took measurements following a relatively dry period in the summer (see the standard precipitation evapotranspiration index for June and July 2017 in Figure S1), we reason that the pines growing in mixed plot have a reduced access to water resources because of their competition with oaks and had already initiated their water-saving mechanism at the time of our sampling, while pines growing in monocultures had not yet experienced a severe decrease in water availability. Oaks, on the other hand, are more drought-tolerant species, meaning that they are able to maintain productivity and photosynthesis as drought develops (Forner *et al.*, 2014). Additionally, they have deeper roots which allow them to access other water resources as compared to shallower roots pines such as *P. sylvestris*; which is probably why the latter has the biggest difference in  $\delta^{13}C$  between diversity levels.

A study looking at species interaction in a mixed plot based on species neighbourhood only found a significant difference in *P. nigra* surrounded by *P. sylvestris* and in *Q. faginea* surrounded by conspecifics (Grossiord et al., 2015). Unlike them, we found that P. sylvestris has the biggest difference in carbon isotope discrimination between monocultures and mixed plots, while there was no significant change in water use efficiency for *Q. faginea*. This difference could be due to the experiment design being different given that we are looking at trees in a plot that had been monocultured or mixed for years, while they were looking at tree neighbourhoods in mixed plots. Also, their isotope measurements were related to pine needles collected from two different years which is a contributing factor as isotope composition may change in that period of time. Our results agree however with their findings about sap flow density reduction in *P*. sylvestris, which was more pronounced when in mixed neighbourhoods. The fact that the *P. sylvestris* showed more  $\delta^{13}$ C difference is probably due to its shallower roots compared to P. nigra (Peñuelas et al., 2002; Corcuera & Camarero, Jesús Julio Eustaquio, 2004; Montserrat-Martí et al., 2009). Despite the fact that P. sylvestris individuals are considerably older in mixed forest (see Figure S4.2c), that shouldn't have an impact on their water use efficiency; the increased light availability, on the other hand, due to shorter neighbouring oak species could have an impact. Indeed, Brienen *et al.* (2017) found a positive but weak relationship between crown illumination index and the intrinsic water use efficiency of these pines, and no relationship to age or height.

### 5.4.2 Photosynthesis

Oaks had differences in their photosynthetic traits and their water management strategy in the case of *Q. faginea*. These changes cannot be disentangled however from the canopy closure effect caused by the fact that oaks are usually sitting below pine canopies in mixed forests. Oaks are shade-tolerant species that are usually shorter than pines in early successional forests (see Figure S4.2b). The higher fluorescence capacity in oaks (Figure 5.2c), which is accompanied by a significantly higher chlorophyll content in *Q. ilex* when in mixed forest (Figure 5.2a), can be a mechanism by which oaks adapt to a lower light interception area and period, a classic case of acclimation to shading (Lambers et al., 1998; Sabaté et al., 1999). These adaptations allow oaks to have a similar photosynthetic yield to trees at the top of the canopy (Figure 5.2b). It could also be that the partially shaded leaves of oaks growing in mixed forest are protected against photoinhibition which is why they have higher fluorescence capacity. Additionally, Q. faginea leaves had higher relative water content when in mixed plots, which is an indication of higher water availability at the time of sampling (Figure 5.3b). This deciduous oak is actually recognized for being relatively a water-spending species compared with other oaks and for having deeper roots (Castro-Díez & Navarro, 2007). These properties, accompanied by the fact that they are rather shaded from the sun in mixed plots, causes a decrease in water loss by transpiration and better access to water sources when not competing with conspecifics which allows for higher water content in its seasonal leaves. Jucker, Bouriaud, Avacaritei, & Coomes (2014) discussed possible benefit for *Q. faginea* growth rates when growing in mixed plots. These growth benefits are however less significant during drought, but others such as delayed and weaker response to decreases in water availability are activated (Grossiord et al., 2015). Actually, Grossiord et al. (2015) started observing a decline in oak sap-flow due to summer drought after their second sample collection in late July, while our sampling was in early July, which could be why isotope discrimination difference in oaks was not yet significant. Even though we didn't observe any difference in isotope composition for *Q. faginea*, our results support previous studies suggesting an increased benefit to oaks when mixed with other species (Jucker et al., 2014a; Grossiord et al., 2015).

### 5.5 Conclusion

We found that *P. nigra* and *P. sylvestris* were very similar in their traits and temporal measurements would be needed to be able to differentiate their responses to environmental factors. Oaks, on the other hand, were different in most traits, likely due to the fact that one of them is evergreen and the other deciduous. Both oaks showed fewer signs of water stress than pines when growing in mixed forest. Whilst the water use efficiency of pines increased significantly in mixtures, *Q. faginea* growing in mixed plots had higher leaf water contents than those growing in monoculture. These results suggest that monitoring these forests under extreme drought would be useful in identifying which species mixtures will be more resilient to climate change in the future.
## Chapter 6 General Discussion

#### 6.1 Wider context

Forests represent the most promising natural-based solution to climate change, uptaking close to 30% of human carbon emissions each year (Anderegg et al., 2020). The potential of this natural-based solution is however modulated by climate change itself, particularly by droughts. Droughts are typically multi-timescale events that trigger a multitude of different responses in trees (Beguería & Vicente-Serrano, 2017; Zang et al., 2019); and cause considerable fluctuations in global gross primary productivity, explaining at least 47% of its variation in the past 30 years (Zscheischler et al., 2014; Anderegg *et al.*, 2020). Besides topographical factors and severity of the climatic events which are often less controllable by humans, an important factor in determining the extent to which forests respond to droughts, i.e. the extent of forest resilience or stability to droughts and climate change, is forest species composition and forest management actions (Seidl, 2014; Gren & Zeleke, 2016; Gazol et al., 2018; Khoury & Coomes, 2020). Two third of the forests worldwide are populated by at least two species naturally or by choice (FAO, 2016; Grossiord, 2019; Pardos et al., 2021), making tree species composition and diversity effects on drought resilience one of the most important research topics. Being able to study these mixed forests on much larger scales using a combination of remote sensing and machine learning algorithms will soon allow us to answer ever more complex ecological questions about species interactions and response to climate change.

One year after Reyes and Kneeshaw (2014) asked whether ecological resilience is ready for operationalisation in forest management and concluded that it was not, the journal *Trends in Ecology and Evolution* published an issue about resilience (Hodgson et al., 2015a) and 5 years later an editorial about its operationalisation (Chambers et al., 2020). What hindered and still hinders the use of resilience concepts by managers is the elusiveness of tipping points and disagreements between scientists on the nature of resilience. It is hard to achieve consensus on a concept that is evolving; even if scientists end up agreeing on a specific wholistic definition for 'resilience to event', agreeing on a specific method will probably be impossible or be very limiting. Researchers are still trying to uncover the mechanisms behind the response of ecosystems, forests, and trees to disturbances and perturbations, and new analysis techniques, bigger data collections, and higher data resolution can open new doors when it comes to quantification of resilience and identification of any tipping points. In this thesis, we combined machine

learning classification with time-series and breakpoint analysis to quantify the resilience to drought of tree species in Spain. The use of these analysis tools allowed us to respond with ever more precision to several ecological questions surrounding the resilience of forests, but also to uncover wider implications related to the use of resilience concepts in ecology which will be discussed in section 6.3.2.

#### 6.2 Contributions

In **Chapter 2** of this thesis, detecting non-abrupt changes in greenness, and then associating them to drought allowed us to resolve two limitations in drought resilience estimation: (1) capturing sensitivity, recovery, and recovery time fully without the assumption of a regular response and (2) allowing drought start-date, length, and accumulation rate to vary freely, which reflects drought occurrence more realistically. Furthermore, in estimating the long-term changes and monthly variance of NDVI first (Figure 2.1 a - d), we indirectly evaluated the concept of increased variance for ecosystem shift detection (Carpenter & Brock, 2006) against the short-term estimation of resilience components (Figure 2.1 e) (Lloret et al., 2011). We found that variance of NDVI expressed as a function of SPEI variance (or  $\gamma_G$ .  $\varepsilon_C$ , see Figure 2.1 c), does vary linearly with NDVI sensitivity (Figure 2.10 a), which suggests that the concept of increasing variance before a transition can be as informative as these resilience components about the closeness of a system to a transition. How operational these two resilience concepts are to estimating 'tipping points' remains to be seen (see also Section 6.3.2). It is important to note that we treated each time-series as representative of the ecosystem in that pixel averaging the response of the two largest droughts and looking at the variance of the whole time-series (18 years) instead of evaluating the variance with a moving window. This approach is justified by our interest in understanding what factors drive differences in resilience at larger spatial scales, but also by the fact that separating the data obtained from the two different perturbations detected did not offer any additional information.

Published studies have attempted to detect the increase in ecosystem variance or decrease in ecosystem resistance and recovery over time (Carpenter & Brock, 2006; Seekell *et al.*, 2012; de Oliveira Roque *et al.*, 2018). We, however, did not find any evidence to support that there were such changes over the past 18 years in Spain except for a few declining sites (12% of over 3000 sites). Using data on such a large scale allowed us to detect the drivers of drought resilience, but also to determine which forest proportion

and what species in Spain are declining because of climate change. This paints a clearer image of the trends at that scale than systematic reviews of local studies, which are often incomparable.

In **Chapter 3**, we examined how well freely available Sentinel 2 data mapped four tree species over a regenerating forest landscape in central-east Spain. Evaluating three classification algorithms, we obtained the greatest accuracy from 'random forest'. Interestingly, 'random forest' outperformed PLS-DA when it comes to canopy detection on the plot level, although it did not have the highest accuracy at the crown level. Furthermore, we found that the temporal aggregate summer median image of Sentinel 2 imagery is more accurate in classifying the forest than a least cloudy yearly composite. We also found that a rapid by-eye classification training on the median Sentinel 2 image led to classification accuracy which was only 4% less accurate than the dataset trained by the plane-truth map, but both results had smaller accuracy compared to the validation done on the by-eye dataset. This suggests that imprecisely trained machine learning algorithms might report very high accuracy in relation to non-accurate image-based training datasets which do not reflect the reality of the landscape. Scientists should therefore be very careful if opting to train machine learning algorithms by labelling high-quality imagery by eye instead of careful identification of canopies in the field.

In **Chapters 4** and **5**, we studied the effect of species composition and increasing species diversity on species responses to drought in forests in central-east Spain, and we found contrasting responses of wood production, leaf-level traits and remotely sensed leaf area. The differences between wood production and canopy properties are relevant to monitoring carbon sequestration from space and to answering stress and disturbance response in tree species. Relating remotely sensed vegetation changes to carbon storage in wood form, beyond estimates of total biomass in a landscape, is still in its infancy (Vicente-Serrano *et al.*, 2016a, 2020). Most of the difficulties in linking wood production to canopy greenness observations stem not from our lack of understanding of tree phenology but because of our lack of understanding of tree response to stress and disturbance. We know that trees prioritise the maintenance of their canopies, including reproductive tissues, and roots, before allocating resources to wood growth (Litton *et al.*, 2007). We know that wood growth season length can vary greatly between species (Cannell, 1989; Cherubini *et al.*, 2003). We even know the kinetics involved in wood

production which can help cold climate trees maximize their wood production daily (Rossi *et al.*, 2006). Furthermore, beyond fixed environmental drivers, wood growth varies greatly between species, with tree age, and tree size (Jucker *et al.*, 2014a; Wang & Hamzah, 2019). However, perturbations and disturbances greatly affect these growth patterns, and it is these effects that make it difficult to predict wood productivity from environmental and canopy observations.

In **Chapter 4**, we explored how relating remotely sensed leaf area and drought index time-series to wood production time-series can help us identify divergent response mechanisms in forest tree species. Methodologically, it is interesting to note that while wood production derived from tree-ring increments is already a yearly series, MODIS-derived NDVI or LAI is a monthly series that needed to be aggregated to a yearly series. While aggregating LAI to yearly time-series would provide one possible approach, we found that decomposing the LAI time-series, eliminating the temporally auto-correlated residuals and the seasonality, and then averaging the non-linear trend led to a better AWP prediction when it comes to relating the two datasets. We also found that converting NDVI values to LAI values improved the prediction. Just as in the break-point analysis in **Chapter 2**, keeping the seasonality and the noise dilutes the climate-sensitive signal of the vegetation.

#### 6.3 Future directions

#### 6.3.1 Other disturbances and perturbations.

In **Chapter 2**, we demonstrated how time-series and change point detection analysis can be used to quantify the resilience of forest ecosystems to extreme drought perturbations. Climate change is predicted to make water scarcity more frequent and more severe, but drought is only one of the abiotic perturbations that forest ecosystems are subjected to. These predictions also apply to many other abiotic disturbances such as fires, floods, cyclones, among others (Seidl *et al.*, 2017; Anderegg *et al.*, 2020). Biotic disturbances (e.g. insect and pest outbreaks) and anthropogenic intervention (deforestation for other land uses, depletion of water resources, fires) also play a big part in degrading forest ecosystems (Funk *et al.*, 2019), even surpassing the negative effects of climate change (Danneyrolles *et al.*, 2019). All of these disturbances and perturbations would have effects on forests that can be examined remotely to determine their effects on forest functioning. Unlike the case for drought, most other abiotic disturbances would

be classified as severe events which usually have a clear start- and end-dates. This can facilitate the detection of the immediate forest response, although the long-term legacy effects of such events would need to be disentangled from other strong drivers of vegetation cover such as changing water availability.

#### 6.3.2 Tipping lines or response mechanism?

Examining the patterns of response to drought, we find that most Spanish forests are resilient to extreme droughts, as previously reported. Although our findings do not forecast the resilience of an ecosystem or species to future droughts, they provide a valuable picture of the trends observed in the region.

First, we found that Eucalyptus forests are significantly less resilient than the native species in Spain, a result that can be used to sound the alarm on planting more *Eucalyptus* in the region. The number of declining *Eucalyptus* forests was 14% higher than the average; the next species which needs close attention is *P. nigra*, whose declining greenness was 8% higher than the average of 12% for all species. Although the number of *P. nigra* pixels that were losing greenness was not significantly higher than the average, the negative climate change influence on the long-term trends of the species and the very high sensitivities and recoveries suggests it might be close to a tipping point.

Second, we determined the drought response time of the forest canopy. Many resilience studies focus on estimating the recovery rate. While estimating the recovery rate and decline rate for our dataset in **Chapter 2** did not offer extra information, the return period itself was valuable, as it allows to determine the period in which the occurrence of another drought would hinder the recovery and cause serious long-term damages to the forests. This period, which was on average equal to a year and a half, did not vary significantly between species groups. If it did vary, then it would indicate which species group is going to be more sensitive to an increase in drought frequency. Furthermore, evaluating differences in the two largest droughts in the past 18 years, we did not find any proof that the duration separating those events had any effect on forest response, which is explained by the rapid recovery of greenness (1.5 years on average) compared to the average duration between the two events (5.5 years).

Concerning tipping points, while such a concept could prove useful for forest management, we did not find any proof that it exists for forest ecosystems. Pixels that failed to recover after drought events were present anywhere in the decline zone shaded in red below the curve in Figure 6 (see Figure S1.7 for data). We found that relationships fitted separately for each species group after accounting for the environmental factors are usually logarithmic functions where the deviation from the 1:1 line, coined "line of full resilience" by Schwarz et al. (2020), indicate a loss of resilience (Figure 6). We found that certain species groups characterised by small sensitivity and recovery values had a smaller slope coefficient for the logarithmic function, while groups with high sensitivity and recovery had a higher slope coefficient. We suggested that these differences can be indicative of different drought response mechanisms (Chapter 2). However, upon analysing the resilience of wood production in a local study in Spain (Chapter 4), we found that changes in greenness had contrasting patterns to changes in wood production which has implications for this theory. Unlike our previous prediction, isohydric pines did not lose and gain more leaf area than oaks, instead, pixels dominated by the evergreen oak lost more leaf area and less wood productivity. The idea of discerning different forest response mechanisms made more sense when looking at the resilience of wood production instead of greenness. Isohydric pines responded strongly to droughts by slowing their wood production drastically (Figure 4.6b), while tolerant oaks reduced their wood production to a much smaller extent. What does this say about resilience patterns in LAI? Are they actually indicative of the opposite drought response mechanisms?

We suggest that the difference is due to the spatial scales of the study. In **Chapter 2** we were looking at the whole of Spain which allowed us to capture the whole spectrum of species response to drought; pixels responses were normally distributed along the 'line of full resilience' for each species and diverging at high sensitivity values (i.e. NDVI losses varied between 0.03 and 0.07, 1<sup>st</sup> and 3<sup>rd</sup> quantile respectively). While in chapter 4 the measured greenness response was relatively extremely small (before being converted to LAI, NDVI losses varied between 0.01 and 0.02, 1<sup>st</sup> and 3<sup>rd</sup> quantile respectively, being smaller than the 1<sup>st</sup> quantile sensitivity value in **Chapter 2**). This difference is due to the fact that Alto-Tajo despite having had droughts in the past 30 years is not considered a very dry region and had not observed an extreme increase in relative dryness over the past 18 years as observed from the map in Figure S3.5a. As previously discussed in **Chapter 4**, this means that the combination of factors presents in those sites contributed to high resilience in black pine which did not shed their needles. The question of whether high sensitivity and recovery values in canopy or wood production are indicative of

specific drought response mechanisms and compartmentalization in trees remains open and needs further investigation. We suggest that future studies should attempt to combine AWP and LAI datasets at larger scales to see how the coupling between the two varies along topographical and environmental gradients.



**Figure 6 Diagrams demonstrating the concepts of 'tipping lines' and 'lines of full resilience'.** Tipping lines imply the existence of a threshold that once crossed the system transitions into another stable state. The threshold is dynamic in nature because it depends on several factors but is also hard to detect which is why the dashed tipping line is surrounded by a zone of uncertainty shaded in grey. The dotted line and the double dotted line represent two forest systems the first dominated by drought-tolerant species and the second by drought avoidant species. The red lines in (a) represent two perturbations, the dotted purple line represent the 'line of full resilience', the solid black line in (b) represents the deviation from the 'line of full resilience' and in (c) the slope line of all potential lines of full resilience.

#### 6.3.3 Monitoring changes in canopy composition

Findings in **Chapter 5** suggest that tree diversity caused differences at the level of canopy leaf traits. Although we did not reach a conclusive explanation as to why we did not detect these differences when looking at remotely sensed greenness in **Chapter 4**, studies that map canopy traits from remotely sensed data have shown promising results that could be explored to detect and analyse diversity effect (Bongalov *et al.*; Asner & Martin, 2009a; Dotzler *et al.*, 2015; Swinfield *et al.*, 2019; Aguirre-Gutiérrez *et al.*, 2021). For instance, a study over logged old-growth tropical forests mapped canopy phosphorus and nitrogen concertation at a large scale (400m<sup>2</sup>) detecting patterns associated to topography that would have gone unnoticed in a traditional field study (Swinfield *et al.*, 2019). There is a potential for exploring whether more detailed spectral information would reveal more about the canopy status than time-series of simple vegetation indices, and would help us identify other coupling effects between AWP and canopy traits.

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## Supplementary information 1



## S1.1 Workflow

## Figure S1 Determining forest resilience to drought workflow.

## S1.2 Species groups and land cover sampled over Spain.

In this work, we sampled 10 of the most frequent species groups in Spain from the species distribution map by (Brus *et al.*, 2012).



**Figure S1.2** Species groups' distribution over Spain (taken from Brus *et al.*, 2012) mapped in (a) and their relative frequency plotted in (b).

Land cover map was extracted over our plots to determine land cover change between 1990 and 2000 and to eliminate pixels falling in non-natural classes. As demonstrated in Table S1.1, land cover change did not have a significant effect on our models and was not included in the manuscript.



**Figure S1.3** Corine land cover of sampled forest pixels over Spain in 1990 (a) and 2000 (b).

## S1.3 Relationship between NDVI and LAI.

To interpret changes in remotely sensed canopy greenness (i.e. NDVI) correctly, it is essential to consider its relationship to actual forest characteristics such as leaf area index (LAI). NDVI has an exponential relationship with LAI meaning that at higher NDVI observed changes translate to much bigger changes in LAI on the ground.





**Figure S1.4** Relationship between average NDVI and average LAI from MODIS for year 2013.

## S1.4 Detection of the biggest drought events.

Drought events detected with DBEST package in R, corresponding to the peak dates observed in the SPEI time-series (Figure 2.5) and dates reported in the literature. The first one was in 2005 and the second one in 2012 (Figure S1.2).



**Figure S1.5.** Frequency distribution of the dates of the biggest NDVI losses detected in 18-year time-series.

## S1.5 Statistical modelling

To test how canopy greenness varies with water availability using remotely sensed NDVI, we developed regression models aiming at explaining forest response to drought in the short- and the long-term among different forest types inside and outside protected areas (Table S1.1).

#### **Temporal auto-correlation:**

The NDVI series analysed do not have an auto-correlated residual (only the non-linear trend was used). *SPEI*<sup>1</sup> time-series have independent values with little temporal auto-correlation because each value is computed relative to the same month in the reference period instead of being related to other months in the same year, at higher scales, however (X > 1) temporal auto-correlation increases as per the computation of the index which aggregates X months together. Differencing the time-series or attempting to eliminate the auto-correlation in these time-series would make the trend estimation from SPEI incomparable to that of NDVI, and eliminate the effect that we are looking to quantify (i.e. level of water deficit accumulation needed for the forest to respond to drought). Given that whitening of time-series prior to trend analysis is still being debated (see (Bayazit & Önöz, 2007; Razavi & Vogel, 2018), we decide to not pre-whiten and proceed with a simple linear trend analysis which would be comparable to the NDVI trend.

#### Spatial auto-correlation:

Moran's I on distance classes was computed for all the linear models' residuals done on time-series derived metrics using the *"pgirmess"* package in R (Giraudoux *et al.*, 2018). Plotting Moran's I allowed us to visualise the patterns of spatial auto-correlation in the residual of our models. Buffer distances in which to construct the weighting matrix to be used in the spatial regression model were tested between 15 km and 50 km with 5 km increments; models minimizing AIC the most were reported in the results. Pixels/plots within the buffer area were assigned an equal weight equivalent when computing their errors in the regression model, while error of pixels/plots lying outside the buffer distance would have a weight of zero. Functions "dnearneigh", "nbdists", "nb2listw", "errorsarlm" from the packages *"spdep"* and *"spatialreg"* were used in sequence to run spatial regression models (Bivand *et al.*, 2015; Bivand & Piras, 2019).

#### Table S1.1 Regression models used to evaluate changes in greenness with drought.

Model structure follows lm, nls and errorsarlm formula syntax in R. Model fit corresponds to adjusted R<sup>2</sup> for linear models and Nagelkerke pseudo-R<sup>2</sup> in spatial autoregressive models. Model

fit and for linear models M1-M5 correspond to the average taken from 3182 models. Models in *italics* included "previous landcover" as a factor; they were not reported for lack of significant difference in the AIC with the previous model.

Model	Structure	Model fit	Model AIC	SSAEM AIC
Linear	regression models applied on the individual time-seri	ies		
M1	SPEI ~ Time	0.08	-	-
M2	NDVI ~ Time	0.3	-	-
M3	LAI ~ Time	0.3	-	
M4	NDVI ~ Time + SPEI	0.49	-	-
M5	log(gain)~ log(loss)	0.32	-	-
Non-lin	ear multiple regression model			
M6	NDVI ~ $a(1 - exp(-b(LAI - c)))$	-	-	-
Spatial	simultaneous autoregressive error estimation model	s (SSAEM	1s)	
M7	$\Delta$ SPEI x 215 ~ Water balance	0.86	-2033	-7977
M7	$\Delta$ SPEI x 215 ~ $\Delta$ Water balance x 215	0.86	-1476	-8006
M8	NDVIm ~ scale(Water balance) + scale(Elevation) +	0.60	-6702.2	-7979
	<pre>scale(NDVIm) + Forest type + Protection status</pre>			
		0.40	( <b>-</b> 00)	
M9	NDVIm $\sim$ scale(Water balance) + scale(Elevation) +	0.60	-6700.4	7977.2
	scale(NDVIm) + Forest type + Protection status+			
M10	ANDVLy 215 coole(Water balance) + coole(Elevation)	0.10	11407	11676
MIU	$\Delta NDVI X 215 \sim \text{Scale}(\text{Water Datafice}) + \text{Scale}(\text{Elevation})$ + scale(NDVIm) + Forest type + Protection status	0.10	-11407	-11070
M11	ANDVI x 215 $\sim$ scale(Water balance) + scale(Flevation)	0.10	-11405	-11674
	+ scale(NDVIm) + Forest type + Protection status+	0.10	11100	1107 1
	Protection status			
M12	NDVIm ~ water balance	0.57	-6262.1	-7800.1
M13	LAIm $\sim$ water balance	0.54	5158	3873.2
M14	CCI[NDVI]~ scale(Water balance) + scale(elevation)	0.35	-22522	-23776
M15	CCI[LAI]~ scale(Water balance) + scale(LAIm)	0.24	-8218	-9818
M16	CGW[NDVI]~ scale(NDVIm) + scale(elevation)	0.33	-18879	-19846
M17	CGW[LAI]~ scale(LAIm) + scale(elevation)	0.36	-7124.6	-8052.2
M18	CCI[NDVI]~ scale(Water balance) + scale(elevation) +	0.35	-20701	-21539
	Forest type + Protection status			
M19	$CCI[LAI] \sim scale(Water balance) + scale(LAIm) + Forest$	0.23	-7579.3	-7976
MOO	type + Protection status	0.22	101(4	100(2
MZU	$CGW[NDVI] \sim Scale(NDVIIII) + Scale(elevation) + Foresttype + Protection status$	0.33	-19104	-19862
M21	$CGW[LAI] \sim scale(LAIm) + scale(elevation) + Forest$	0.37	-7398.6	-8070.6
	type + Protection status	0107		007010
M22	log(NDVI Loss) ~ scale(Water balance) + scale(-SPEI	0.32	4106.6	3745.5
	min) + scale(SPEI max) + scale(elevation) +			
	scale(NDVIm)			
M23	log(LAI Loss) ~ scale(Water balance) + scale(-SPEI	0.34	4233	3957.2
	min) + scale(SPEI max) + scale(elevation) +			
M24	scale(LAIm)	0.22	20(4.4	2600 5
MZ4	$\log[NDVI LOSS] \sim scale(water balance) + scale(-SPEI min) + scale(SPEI more) + scale(slower) + $	0.33	3964.4	3698.5
	mmj + scale(SPEI max) + scale(elevation) +			

	<pre>scale(NDVIm) + Forest type + Protection status+ Previous landcover</pre>			
M25	log(NDVI Loss) ~ scale(Water balance) + scale(-SPEI min) + scale(SPEI max) + scale(elevation) + scale(NDVIm) + Forest type + Protection status + Previous landcover	0.34	3968.7	3701.3
M26	log(LAI Loss) ~ scale(Water balance) + scale(-SPEI min) + scale(SPEI max) + scale(elevation) + scale(LAIm) + Forest type + Protection status	0.36	4127.8	3921.9
M27	log(LAI Loss) ~ scale(Water balance) + scale(-SPEI min) + scale(SPEI max) + scale(elevation) + scale(LAIm) + Forest type + Protection status+ Previous landcover	0.36	4124.1	3920
M28	log(NDVI Gain) ~ scale(Water balance) + scale(-SPEI min) + scale(SPEI max) + scale(elevation) + scale(NDVIm)	0.27	6664.3	6550.5
M29	log(LAI Gain) ~ scale(Water balance) + scale(-SPEI min) + scale(SPEI max) + scale(elevation) + scale(LAIm)	0.26	6803.9	6725.3
M30	log(NDVI Gain) ~ scale(Water balance) + scale(-SPEI min) + scale(SPEI max) + scale(elevation) + scale(NDVIm) + Forest type + Protection status	0.28	6622.9	6545.6
M31	log(NDVI Gain) ~ scale(Water balance) + scale(-SPEI min) + scale(SPEI max) + scale(elevation) + scale(NDVIm) + Forest type + Protection status+ Previous landcover	0.28	6624.8	6547.6
M32	log(LAI Gain) ~ scale(Water balance) + scale(-SPEI min) + scale(SPEI max) + scale(elevation) + scale(LAIm) + Forest type + Protection status	0.27	6773.9	6721.6
M33	log(LAI Gain) ~ scale(Water balance) + scale(-SPEI min) + scale(SPEI max) + scale(elevation) + scale(LAIm) + Forest type + Protection status+ Previous landcover	0.27	6775.6	6723.4
M34	log(NDVI Gain/Loss) ~ scale(Water balance) + scale(- SPEI min) + scale(SPEI max) + scale(elevation) + scale(NDVIm)	0.16	5846.9	5815.5
M35	log(LAI Gain/Loss) ~ scale(Water balance) + scale(- SPEI min) + scale(SPEI max) + scale(elevation) + scale(LAIm)	0.16	6734.9	6697.8
M36	log(NDVI Gain/Loss) ~ scale(Water balance) + scale(- SPEI min) + scale(SPEI max) + scale(elevation) + scale(NDVIm) + Forest type + Protection status	0.17	5824.5	5809.6
M37	log(NDVI Gain/Loss) ~ scale(Water balance) + scale(- SPEI min) + scale(SPEI max) + scale(elevation) + scale(NDVIm) + Forest type + Protection status+ Previous landcover	0.17	5821.2	5807.9
M38	log(LAI Gain/Loss) ~ scale(Water balance) + scale(- SPEI min) + scale(SPEI max) + scale(elevation) + scale(LAIm) + Forest type + Protection status	0.17	6703.2	6685.8
M39	log(LAI Gain/Loss) ~ scale(Water balance) + scale(- SPEI min) + scale(SPEI max) + scale(elevation) + scale(LAIm) + Forest type + Protection status+ Previous landcover	0.17	6700.5	6684.5

SPEI=monthly SPEI values

 $\Delta$ SPEI=monthly SPEI change determined from M1

NDVI=monthly NDVI values

 $\Delta \text{NDVI}\text{=}\text{monthly}\ \text{NDVI}\ \text{change}\ \text{determined}\ \text{from}\ \text{M2}$ 

NDVIm=average NDVI (2000-2017)

LAIm= average LAI (2000-2017)

 $CGW = \gamma_G = Short$ -term covariance between NDVI and SPEI determined from M3

CCI= $(\alpha_G - \alpha_P)^*$ 215=Long-term effect of SPEI on NDVI determined from M3 as monthly change between observed NDVI and potential NDVI

-SPEImin=Minimum SPEI during the period of NDVI loss representing water deficit SPEImax=Maximum SPEI during the period of NDVI gain representing water surplus



## **S1.6 Summary of negative NDVI trends**

#### Figure S1.6 Spanish forest greenness trends.

Other broadleaves

(a) Summary of the autocorrelative regression model studying greenness trends; (b) density distribution of greenness trend in terms of % greening in the past 18 years for different forest types; (b) density distribution of greenness trend in terms of % greening in the past 18 years for protection statuses.

-0.11

Forest type	% plots with significant negative trends in LAI	Average change in forest LAI for declining plots							
Q. robur & Q. petraea	9	-0.18							
Fagus spp.	5	-0.20							
P. sylvestris	13	-0.23							
Other Quercus spp.	9	-0.22							
Castanea spp.	11	-0.20							
<i>Eucalyptus</i> spp.	26	-0.43							

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#### Table S1.2 Forests canopy greenness across forest types and protection statuses.

P. pinaster	20	-0.24
Other Pinus spp.	11	-0.28
Other conifers	10	-0.23
Protection status		
Unprotected areas	13	-0.30
Sites of community Importance ZEC	12	-0.22



#### Figure S1.7 Fitted relationship between losses and gains.

(a) For different forest types; (b) and different protection status. Fitted regression lines were back-transformed from log–log scale to match original axes. Differences in regression coefficient in the log-log relationship. (c) For different forest types, and (d) different protection statuses. Error bars represent the standard error of the coefficient estimates.



Figure S1.8 Summary coefficients for the forest types of the spatial autoregressive model performed to evaluate resilience components determined from NDVI time-series.

(a) Relationship between the loss, gain and the short-term response to drought of forest types; (b) gain-to-loss ratio (log scale); (c) long-term climate change influence on greenness. Value for forest type indicates mean response for forests outside of protected areas. Overall mean for forest outside protected areas indicated by the black dot in (a) and the dashed lines in (b) and (c), and the error bars represent 99% confidence intervals. Note losses and gains were log-transformed to improve normality of residuals since both measurements are right-skewed, and because gains tend to be smaller when losses are large.





S1.7 Maps of Spanish forest resilience to drought at different timescales

Figure S1.9 Drought accumulation time best coupled with NDVI.



Figure S1.10 Forest greening trend in Spain from 2000 to 2017.

(a)



**Figure S1.11** Covariance between greenness (NDV) and changes in water availability. (a) CGW using SPEI; (b) CGW using SPEI plotted against CGW using Water Balance.



CCI on NDVI when using Water Balance

Figure S1.12 Long-term Climate Change Influence (CCI) on greenness (NDVI).

(a) CCI on NDVI over Spain; (b) CCI on NDVI when using SPEI plotted against CCI on NDVI when using Water Balance.





0.05

0.10

0.00

Figure S1.13 NDVI Loss during drought events.

0.1

0.0

-0.05

(a) Distribution of NDVI loss measures over Spain; (b) NDVI loss plotted against short-term covariance between SPEI and NDVI.

## (a)

(a)



Short-term forest response to drought



(a) Distribution of NDVI gains following drought over Spain; (b) NDVI gains plotted against short-term covariance between SPEI and NDVI.



Figure S1.15 Gain/loss ratios over Spain relating to short-term Gain-to-Loss ratio.

# Supplementary information 2

# S2.1 Allometric relationship to determine canopy cover in FunDivEurope plots.

Table S2.1: Comparison of allometric models of the relationship between basal areas, height and crown area.

Model formulae evaluated against lm(log(CrownArea)~log(BasalArea)	ΔΑΙϹ
lm(log(CrownArea)~log(BasalArea)+log(Height)	-114
lm(log(CrownArea)~log(BasalArea)+log(Height)+Species)	-208
lmer(log(CrownArea)~log(BasalArea)+log(Height)+(1 PlotID))	-688
lmer(log(CrownArea)~log(BasalArea)+log(Height)+Species+(1 PlotID))	-685
lmer(log(CrownArea)~log(BasalArea)+log(Height)+(1 Sp.compo/PlotID))	-998
lmer(log(CrownArea)~log(BasalArea)+log(Height)+(log(BasalArea) Sp.compo/PlotID))	-774
lmer(log(CrownArea)~log(BasalArea)+log(Height)+(log(Height) Sp.compo/PlotID))	-827

## S2.2 Classification

### Table S2.2: Extra vegetation indices used in classification taken from the Index DataBase

(Henrich et al., 2009).

Numbers between parentheses refer to band wavelengths, while those preceded by 'range'

correspond to a range of wavelengths in which bands were averaged.

Indices to cover >1000nm				
Name	Formula			
Aerosol.free.veg.index.1600	((800)-0.66*( (1600)/( (800)+0.66* (1600))))			
Aerosol.free.veg.index.2100	((800)-0.5*( (2100)/( (800)+0.56*(2100))))			
Cellulose.absorption.index	(0.5*( (2030)+(2210))-(2100))			
Lai.difference.1725.970	(1725)-(970)			
Normalized.difference.1094.1205.leaf.water	((1094)-(1205))/( (1094)+ (1205))			
Normalized.difference.1094.983.leaf.water	((1094)-(983))/( (1094)+ (983))			
Normalized.difference.leaf.canopy.biomass	((2160)-(1540))/( (2160)+ (1540))			
Normalized.difference.leaf.mass.per.area	((2260)-(1490))/( (2260)+ (1490))			
Simple.ratio.water.content	(1193)/(1126)			
Simple.ratio.lai.determining.index	(1250)/(1050)			
	(-0.2848* range(450,520)-0.2435*			
	range(520,600)-0.5436*			
Tasselled.cap.vegetation	range(630,690)+0.7243*			
	range(760,900)+0.0840* range(1150,1750)-			
	0.1800* range(2080,2350))			

### Table S2.3: Vegetation indices used in the classification of Sentinel 2 products taken from

the Index DataBase (Henrich et al., 2009).

Indices which can be computed from Sentinel 2 bands as extracted from Index database.					
Name	Formula				
ATSAVI	1.22*((b9-1.22*b4-0.03)/(1.22*b9+b4+1.22*0.03+0.08*(1+1.222)))				
AFRI1600	(b9-0.66*(b11/(b9+0.66*(11))))				
AFRI2100	(b9-0.5*(b12/(b9+0.56*(12))))				
ARI	(1/b2)-(1/b4)				

*'bX' refers to the sentinel 2 band number (X) starting the count at 0.* 

ARVI	(b9-(b4-1*(b4-b0)))/(b9+(b4-1*(b4-b0)))
ARVI2	-0.18+1.17*((b9-b4)/(b9+b4))
BWDRVI	(0.1*b9-b0)/(0.1*b9+1)
BRI	((1/b2)-(1/b4))/b9
CCCI	((b9-b4)/(b9+b4))/((b9-(3))/(b9+b3))
CARI	(h4/h3)*((sort(((h4-h3)/150)*670+h3+(h2-(((h4-
onnu	(01/00) ( $(01/00)$ ) $((((01/00))$ ) $((((01/00))$ ) $((01/00))$
CARI2	(2)/(150)/(150)/(150)/(1502)/(1502)/(1502)/(150)/(15
CANZ	(abs(((b+b2)/150) b5+b5+b2-(((b+b2)/150) b2))/((((b+b2)/150) b2)))
Chlaroon	$(b_1/b_2) \times (1)$
Clancon	$(107/102)^{-1}$
Clyreen	(09/02)-1
Cireaeage	(09/04) - 1
Chied-edge	$(b6/b4)^{**}(-1)$
CVI	b9*(b4/(b22))
CI	(b4-b0)/b4
CTVI	((((b4-b2)/(b4+b2))+0.5)/abs(((b4-b2)/(b4+b2))+0.5))*sqrt(abs(((b4-
	b2)/(b4+b2))+0.5))
Datt1	(b7-b4)/(b7-b3)
Datt4	b3/(b2*b4)
Datt6	b(8)/(b2*b5)
D800/550	b7-b2
D800/680	b7-b3
GDVI	h9-h2
EVI	$25^{\circ}$ 52 2 5*((h9-h4)/((h9+h4*6-7 5*h0)+1))
CFMI	(((2*(h92-h42)+1)5+b4+0)5+b4+0)((h9+h4+0)5))*(1-0)25*((2*(h92-h42)+1)5+b4+0)((h92-h42)+1)5+b4+0)((h92-h4)+0)(h92-h4)
	$(((2 (0)2^{-}0+2)^{+}1.5 0)^{+}0.5 0+)/((0)^{+}0+(0.5)) (1^{-}0.25 ((2 (0)2^{-}0+(0.5))) (1^{-}0.25 ((2 (0)2^{-}0+(0.5))))$
CUI	$(b^{2})^{+1.5} b^{-1.5} b^{-$
	$(D2^{-}2^{-}D4^{-}D0)/(D2^{-}2^{+}D4^{+}D0)$
GNDVI	$(D_{2}-D_{2})/(D_{2}+D_{2})$
GUSAVI	(09-02)/(09+02+0.10)
GSAVI	$((D9-D2)/(D9+D2+0.5))^{*}(1+0.5)$
GRNDVI	(b9-(b2+b4))/(b9+(b2+b4))
Н	atan(((b4*2-b2-b0)/(30.5))*(b2-b0))
IPVI	(((b9)/(b9+b4))/2)*(((b4-b2)/(b4+b2))+1)
Intensity	$(1/30.5)^{*}(b4+b2+b0)$
LCI	(b7-b4)/(b7+b3)
Maccioni	(b6-b4)/(b6-b3)
MVI	b9/b(11)
MCARI	((b4-b3)-0.2*(b4-b3))*(b4/b3)
MCARI1	1.2*(2.5*(b7-b3)-1.3*(b7-b2))
MCARI2	(1.5*((2.5*(b7-b3)-1.3*(b7-b2))/(sqrt((2*b7+1)2-(6*b7-5*sqrt(b3))-
	0.5))))
mNDVI	(h7-h3)/(h7+h3-2*h0)
mSR	(b7-b0)/(b3-b0)
MSAVI	(2*h9+1-sart((2*h9+1))-2*(h9-h4)))/2
MSAVIhunor	$(2^{-}0^{-}1^{-}3q1((2^{-}0^{-}1^{-}2^{-}0^{-}0^{-}0^{-}1))/2$ 0 5*((2*b7+1)-cart((2*b7+1)2-8*(b7-b2)))
мтил	1.2*(1.2*(h7 h2) - 2.5*(h2 h2))
	1.2 $(1.2 (0)^{-}02)^{-}2.3 (00^{-}02))$ 1 $f^{*}((1.2 (0)^{-}02)^{-}2.3 (00^{-}02)) (22^{-}1)^{-}2.3 (2^{+}02)^{-}2.3 (00^{-}02)^{-}2.3 $
MIVIZ	$1.5^{(1.2^{(0)}-0.2)-2.5^{(05-02)}/Sql((2^{0})+1)2-(0^{0})-5^{(01-5)}Sql((05))-0.5)}$
	U2/(U7+U4+U2)
NORM NIK	D9/(D9+D4+D2)
Norm R	b4/(b9+b4+b2)
GNDVIhyper	(b6-b2)/(b6+b2)
ND790/670	(b6-b3)/(b6+b3)
PSNDc1	(b7-b(1))/(b7+b(1))

GNDVIhyper2	(b7-b2)/(b7+b2)
ND800/680	(b7-b3)/(b7+b3)
NDMI	(b7-b(11))/(b7+b(11))
NGRDI	(b2-b4)/(b2+b4)
NDVmirnir	(b12-b7)/(b12+b7)
BNDVI	(b9-b0)/(b9+b0)
GNDVI	(b9-b2)/(b9+b2)
MNDVI	(b9-b12)/(b9+b(12))
GNDVI	(b9-b2)/(b9+b2)
NDVI	(h7-h3)/(h7+h3)
NBR	(h9-h(12))/(h9+h(12))
RI	$(b^{2},b^{$
NDVI690-710	$(b^{-}b^{-}b^{-}b^{-}b^{-}b^{-}b^{-}b^{-}$
OSAVI	(1+0.16)*((h7-h3)/(h7+h3+0.16))
	$(hQ_{1}(hQ_{2}+hA_{2}+hQ))/(hQ_{2}(hQ_{2}+hA_{2}+hQ))$
	$(b^{-}(b^{2}+b^{4}+b^{0}))/(b^{-}(b^{2}+b^{4}+b^{0}))$ $(b^{-}(b^{2}+b^{2})/(b^{-}(b^{2}+b^{4}+b^{0}))$
	$(D^{-}D^{-})/(D^{+}D^{-})$ (D.5) (D.5)
	(D/+DS)/(Sq1)(D/+DS)
	$(D^{2}-(D^{4}+D^{2}))/(D^{2}+(D^{4}+D^{2}))$
	$700+40^{\circ}(((103+100/2)-104)/(105-104))$
REIPZ	$(02+40^{\circ}((03+06/2)-04)/(05-04))$
REIP3	$(15+35^{((0)}+06/2)-04)/(05-04))$
RDVI	(D'-D3)/sqrt(D'+D3)
IF	(2*b4-b2-b0)/(b2-b0)
MSI	b(11)/b7
BGI	b0/b2
SR550/800	b2/b7
GI	b2/b3
SR672/550	b3/b2
SR675/700	b3/b4
SR700	b0/b4
SR700/670	b4/b3
SR735/710	b5/b4
PSSRc1	b7/b(1)
SR800/550	b7/b2
RVI	b7/b3
SR833/1649	b7/b(11)
RDI	b(12)/b9
SRNir/700-715	b9/b4
GRVI	b9/b2
DVI	b9/b4
SLAVI	b9/(b4+b(12))
SIPI1	(b7-b0)/(b7-b3)
SIPI3	(b7-b(1))/(b7-b3)
GVI	(-0.2848*b(1)-0.2435*b2-0.5436*b3+0.7243*b7+0.0840*b(11)-
5 T A	0.1800*h(12))
TVI	sart((h4-h2))/(h4+h2))+0.5)
тсі	1 2*(h4-h2)-1 5*(h3-h2)*cart(h4/h2)
VARIrododao	$(h_{-}h_{3})/(h_{+}h_{3})$
v AINI CUEUge	נט ב טט ו / נט די טט ו

Table S2.4: Classification accuracies obtained from running three different algorithms on sampled hyperspectral data.

Delineate	Method	Pixel leve	1		Crown level		
d crowns & ground 70:30 partition		Overall accurac y	Average user's accuracy	Average produce r's accuracy	Overall accurac y	Averag e user's accurac y	Average producer' s accuracy
With dark-	LDA	0.71	0.71	0.72	0.86	0.86	0.86
pixel	PLS-DA	0.87	0.86	0.87	0.90	0.89	0.92
filtering	RF	0.82	0.82	0.82	0.86	0.84	0.87
Without	LDA	0.77	0.76	0.77	0.81	0.82	0.82
dark-pixel	PLS-DA	0.92	0.90	0.90	0.95	0.96	0.96
filtering	RF	0.83	0.83	0.85	0.90	0.89	0.93
Averaged	LDA	0.70	0.68	0.66	0.70	0.70	0.70
repeated	PLS-DA	0.89	0.86	0.91	0.80	0.78	0.88
flight data over pixel	RF	0.70	0.69	0.68	0.65	0.60	0.65

## S2.3 Eye-trained Sentinel 2 imagery using known pixel compositions.

In an effort to evaluate the effectiveness of quick by-eye classification that can be implemented by volunteers in the context of "Citizen Science", we used high-resolution Google Maps and our knowledge of the area during the field trip to label sentinel pixels as belonging to one of the five classes. We then trained our candidate Sentinel 2 product as described in the chapter to determine the accuracy of such a method at mapping the species over the landscape. We also trained the classifier on the second product which was mosaiced using a least cloudy pixel score from the Sentinel 2 image collection over 06/2017 - 06/2018 (a total of 94 scenes). The month of the year of the selected pixel was added as a band. The idea behind this second product was to test if information taken from different seasons would improve the classification accuracy. While that was true for the by-eye trained dataset, it wasn't true for the hyperspectral-derived training set (Table S2.3). By-eye training of random forest classifiers led to high accuracy in GEE (average accuracy of 0.89), however, when compared to classification done on georeferenced tree crowns the agreement between the maps were low (average accuracy 0.44). Considering both Sentinel 2 candidate products, training the random forest classifier on a stratified sample from the hyperspectral-derived classification map led to only to a 4% increase in overall accuracy at the pixel level (Table S2.3).

#### Table S2.5: Accuracy of classifications of Sentinel-2 data using random forest modelling.

Summer median vs yearly composite with random sampling and stratified sampling of the four species of interest. Numbers in bold are the maximum accuracy reached in each category. Background category not shown.

Sentinel 2	Training and validation	Overall accurac	User's accuracy			Producer's accuracy				
innage	vanuation	У	Pn	Ps	Qf	Qi	Pn	Ps	Qf	Qi
	Eye-trained			0	.92			0.	93	
	& validated on by-eye dataset	0.93	0.9 2	0.93	0.89	1	0.96	0.93	0.84	0.92
Vearly	Trained &			0	.46			0.4	46	
composite (June 2017-June	validated on airborne- classified map	0.47	0.5 4	0.56	0.54	0.42	0.44	0.61	0.56	0.44
2018)	Eye-trained		0.45					0.4	48	
	& validated on airborne- classified map	0.45	0.5 0	0.65	0.32	0.43	0.45	0.68	0.54	0.28
	Eye-trained		0.86			0.83				
	& validated on by-eye	0.86	0.9 4	0.92	0.73	0.67	1	0.71	0.85	0.94
	Trained &			0	.51		0.50			
Summer	validated on airborne- classified man	0.49	0.4 7	0.59	0.59	0.28	0.46	0.67	0.53	0.44
median	Eye-trained			0	.43			0.4	46	
(June- August 2017)	& validated on airborne- classified man	0.43	0.5 3	0.58	0.50	0.32	0.39	0.63	0.57	0.23
	Trained & validated on			0	.49			0.4	47	
	classified map – SRTM variables excluded	0.49	0.4 6	0.70	0.62	0.21	0.48	0.48	0.59	0.33

# S2.4 Composition agreement by looking at contingency matrix of MODIS size pixel composition

Pixel composition from 100 m<sup>2</sup> spaceborne-derived map and 100 m<sup>2</sup> downscaled airborne-derived map were compared by constructing contingency tables per MODIS sized pixel, and the level of agreement resulting from matrix diagonals reported in percent (methodology and results demonstrated in Figure S2.1a). The similarity between

the maps ranged from 0 to 100% with an average of 64% and a mode of 100 % (Figure S2.1b).



Figure S2.1 Accuracy of Sentinel 2 prediction over MODIS 250 m pixels in relation to plane-truth data.



Figure S2.2: Alto-Tajo species map derived from classified hyperspectral data to the left and multispectral setinel2 data to the right.

## S2.5 Modelling MODIS pixel composition by looking at canopy cover

Table S2.6: Logistic regression of species cover predicted from Sentinel-2 imagery vs 250m pixels as a function of species covered airborne-derived pixel composition and summary metrics.

 $\Delta AIC$  column reports the difference in AIC between the simple model and one with multiple explanatory variables backward-selected model. X = sqrt(airborne-derived tree cover); Y = total tree cover; Z = Number of Species; W=oaks or pines (0) or both (1)

Species	Formula	ΔΑΙϹ	R2
P. nigra	- 3.96 + 5.65 X	0	0.53
	- 1.75 + 3.51 X - 1.94 Y- 0.63 Z + 0.71 W+ 6.67 X:Y	-53.8	0.60
P. sylvestris	- 3.51 + 7.23 X	0	0.52
	- 3.80 + 4.95 X - 0.83 Y- 0.620 W+ 11.09 X:Y	-34.65	0.56
Q. faginea	- 3.20 + 6.76 X	0	0.47
	- 2.34 + 3.28 X - 3.40 Y+ 12.66 X:Y	-4.72	0.50
Q. ilex	- 2.62 + 5.31 X	0	0.45
	- 1.15 + 4.72 X - 3.35 Y- 0.37 Z + 0.80 W	-51.8	0.53

## S2.6 Variable importance in random forest classification



**Figure S2.3: The ten most important variables in airborne data trained random forest classifier.** PRI531/570: photochemical reflectance index 531 570, REP: red edge position linear interpolation, REIP3: normalized difference 1094 1205 leaf water, LWVI-2: modified soil adjusted vegetation index hyper, REIP2: red edge inflexion point 2, MSAVIhyper: modified soil adjusted vegetation index hyper, reNDVI: red edge NDVI, PSNDb1: pigment specific simple ratio b1, SAVI: soil adjusted vegetation index, OSAVI: optimized soil adjusted vegetation index.



**Figure S2.4: The ten most important variables in spaceborne data trained random forest classifiers in google earth engine.** a) Variable importance in classifier which includes SRTM data vs b) classifier which trained on Sentinel 2 summer median product only.

## **Supplementary information 3**
# S3.1 MODIS vegetation indices



**Figure S3.1:** Spatial linear model result comparing predicted R<sup>2</sup> of the time-series regressions between AWP and three MODIS-derived vegetation indices on a yearly basis.

# S3.2 Computing above-ground wood production

# Table S3.1: Predicting missing crown illumination index (CI) for recruited trees in the second FunDivEuope census.

Reported are  $\Delta$ AIC: difference in Akaike Information Criterion between the basic model and the model in question,  $\Delta$ BIC: difference in Bayesian Information Criterion between the basic model and the model in question; and R<sup>2</sup>: the conditional pseudo-R<sup>2</sup> computed for generalized mixed-effect models using the "r.squaredGLMM" function from the "MuMIn" package in R. Model in bold was used to predict CI.

Formulae evaluated against the linear model:	∆AIC	∆BIC	R <sup>2</sup>
CI~DBH+Height+SR+Composition+Species			
CI~DBH×Height×Composition+Species×Composition	-288	-12	0.54
CI~DBH+Height+SR+Composition+Species+(1 PlotID)	-210	-205	0.75
CI~DBH+Height+Species+(1 PlotID)	-185	-243	0.77

#### Table S3.2: Choosing equation for species biomass estimation.

Reported are  $\Delta$ AIC: difference in Akaike Information Criterion averaged across the four focal species between the basic model and the model in question, R<sup>2</sup>: the conditional pseudo-R<sup>2</sup> computed for generalized mixed-effect models using the "r.squaredGLMM" function from the "MuMIn" package in R. Model in hold was used to compute tree biomass.

Formulae evaluated against the linear model:	ΔAIC	R <sup>2</sup>
log(Biomass) ~ log(DBH)+(1 Plot)		
log(Biomass) ~ log(DBH)+CI + Species richness+(1 Plot)	-11.0	0.78
log(Biomass) ~ log(DBH)+CI + Functional composition +(1 Plot)	-	0.77
	12.30	
log(Biomass) ~ log(DBH)+CI + Functional richness+(1 Plot)	-9.9	0.78

# S3.3 Determining significance of variables in maximum likelihood

## models.

Table S3.2: Maximum likelihood models tested to determine the significance of canopy area, species proportions and diversity on AWP and LAI metrics.

Formulae	Variance
y – b	$\sigma$ or $\sigma_1 + \sigma_2 \times CA$
y – b×CA	$\sigma$ or $\sigma_1 + \sigma_2 \times CA$
y – b×CA <sup>a</sup>	$\sigma$ or $\sigma_1 + \sigma_2 \times CA$
$y - b \times CA^a \times (1 + d \times SRe)$	$\sigma$ or $\sigma_1 + \sigma_2 \times CA$
$y - b \times CA^a \times (1 + c \times Pp)$	$\sigma$ or $\sigma_1 + \sigma_2 \times CA$
$y - b \times CA^a \times (1 + c \times Pp) \times (1 + d \times SRe)$	$\sigma$ or $\sigma_1 + \sigma_2 \times CA$
$y - b \times CA^a \times (1 + c \times Ppn + c1 \times Pps + c2 \times Pqf)$	$\sigma$ or $\sigma_1 + \sigma_2 \times CA$
$y - b \times CA^a \times (1 + c \times Ppn + c1 \times Pps + c2 \times Pqf) \times (1 + d \times SRe)$	$\sigma$ or $\sigma_1 + \sigma_2 \times CA$

Best model was selected based on AICc difference > -2. Best model was tested with variance fixed variance sigma and temporal variance  $\sigma_1 + \sigma_2 \times CA$ .

# S3.4 Diversity effects on productivity and crown area.



Figure S3.2 Plot basal area and Shannon index relationship to wood productivity and canopy area.

a) Back-transformed fit between AWP, basal area, and Shannon index. Light blue and dark blue curves represent respectively the predicted fit at the minimum and maximum Shannon index for this dataset, and shaded areas are 95% confidence intervals. b) Back-transformed fit between canopy area and basal area.



### S3.5 Relating sensitivity to stability

Figure S3.3: Relating stability to sensitivity in AWP (a) and LAI on average (b).

Maximum likelihood prediction for the relationship between stability and sensitivity. Dark shaded areas indicate 95% confidence intervals and light-shaded areas indicate prediction intervals (1 sd).

# S3.6 Relating AWP and LAI on average

The net increase in leaf area was positively related to mean AWP in the matched sites (Figure S3.4a) (28 sites in total), however, we did not find differences related to species richness or proportions, which is probably due to the low number of samples. AWP sensitivity was also negatively related to LAI sensitivity, suggesting that forests whose wood productivity slowed the most during droughts had relatively tolerant canopies that maintain their leaf area (Figure S3.4b). The negative pattern is mostly driven by the extreme differences between *Q. ilex* and *P. nigra* as the difference between the predictions of M4 and M3 indicate (Figure 4.6b). These results suggest that drought-tolerant species such as *Q. ilex*, that do not lose much wood productivity, do not necessarily have a tolerant leaf area, and the opposite is true for species that keep their foliage but lose their productivity.



#### Figure S3.4: Relating AWP and LAI on average.

Maximum likelihood prediction for the relationship between AWP and LAI metrics. Dark shaded areas indicate 95% confidence intervals and light-shaded areas indicate prediction intervals (1 sd).



#### **S3.7** Relative drought strength in the region.

**Figure S3.5**: Average relative water availability (SPEI 12 month time-scale) over the MODIS pixels in central Spain used in Chapter 4. Mapped change in SPEI<sub>1</sub> from 2000 to 2018 from the linear trend over the SPEI<sub>1</sub> time-series and extent of the area being studied as a small black rectangle.



S3.8 Manual computation vs. automatic detection of resilience indices.

**Figure S3.6**: Underestimation of resilience metrics when computed manually with a fixed oneyear pre- and post- drought measurement vs. automatic detection of sensitivity and recovery in ecosystem state variables. Solid lines are predicted fit from linear models and shaded bands are 95% confidence intervals.

#### S3.9 Spatial auto-correlation

Moran's I on distance classes was computed for both the ground and satellite-derived variables as well as for model residuals using the *"pgirmess"* package in R (Giraudoux *et al.*, 2018). Plotting Moran's I allowed us to visualise the patterns of spatial auto-correlation in our datasets (e.g. Figure S3.7a and S3.7b) and in model residuals (e.g. Figure S3.7c and S3.7d). Spatial auto-correlation for our two main variables, greenness and productivity became negative around 5 km. Buffer distances in which to construct the weighting matrix to be used in the spatial regression model (Figure S3.7) were tested between 300m and 7000m with 100 m increments; models with

the lowest AIC are reported below for two logarithmic models. Pixels/plots within the buffer area were assigned a weight equivalent to the inverse of their distance when computing their errors in the regression model, i.e. errors associated with pixels/plot which are further away would have a smaller weight in determining the relationship in question, while the error of pixels/plots lying outside the buffer distance would have a weight of zero. Functions "dnearneigh", "nbdists", "nb2listw", "errorsarlm" from the packages *"spdep"* and *"spatialreg"* were used in sequence to run spatial regression models (Bivand *et al.*, 2015; Bivand & Piras, 2019). Given the low number of plots at very small distances classes in the field inventory dataset, the spatial regression model did not significantly improve on the linear models in that dataset and was instead only used on the NDVI dataset.



**Figure S3.7:** Correlograms showing Moran's I vs. distance classes in meters for the average AWP (MgC ha<sup>-1</sup> yr<sup>-1</sup>) in the FunDivEurope plots (a) and average NDVI in the MODIS pixels datasets (b). Red dots indicated significant positive auto-correlation (p < 0.01). Correlograms showing Moran's I vs. distance classes in meters for model residuals in c) and d).

Table S3	3.3: 5	Spatial	autoregressive	model	result.
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Model tested	Pseudo-R <sup>2</sup>
18 yr NDVI trend ~ Canopy Area%	0.53
log(NDVI stability) ~ log(Canopy Area%)	0.53



Figure S3.8: Spatial autoregressive model prediction for the NDVI dataset

# Supplementary information 4

#### S4.1 Climate conditions

We sampled trees in late June and early July of 2017, during the summer period. Depending on the cumulative timescale we look at, the standard precipitation evapotranspiration index indicates that this period was following a few months of moderately dry conditions (Figure S4.1a) or during a period of moderately dry conditions (Figure S4.1b) (Vicente-Serrano *et al.*, 2010, 2017).



Figure S4.1: SPEI over Alto-Tajo during fieldwork.

#### S4.2 Tree level traits

As stated in the paper, plots for this study were selected from a wider plot collection pertaining to the FunDivEurope project. To support our results, we evaluated tree-level traits collected by the project in 2011 (Figure S4.2).



**Figure S4.2: Tree level traits:** a) Diameter at breast height (DBH); b) height; and c) age of tree growing in mixed plot and monocultures, as taken from the FunDivEurope permeant plots data.

### References

**Vicente-Serrano SM, Beguería S, López-Moreno JI**. **2010**. A multiscalar drought index sensitive to global warming: The standardized precipitation evapotranspiration index. *Journal of Climate* **23**: 1696–1718.

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