Universitat Autònoma de Barcelona

Recent Forest Expansion in Europe (1985-2015).
Patterns, Drivers, and Implications on Forest Growth

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Doctoral thesis

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To apply for the degree of Doctor

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Abstract

Human societies have increased their awareness of the magnitude and extent of deforestation mostly in the tropics and the fatal consequences it has for these ecosystems. However, the overall decline in forest cover has fallen in recent decades due to forest transition in many developed countries and especially in the Northern Hemisphere, which has witnessed a change from net deforestation to net reforestation. Particularly in Europe, forest area has been increasing in many regions since the early 20th century, mainly due to the abandonment of farmland that has induced widespread forest expansion across the continent. Despite the relevance of this phenomenon, many questions remain poorly understood mostly due to the lack of studies addressing the issue at a global scale.

In this thesis, we aimed at exploring the spatial patterns of the forest expansion in Europe for the last decades (1985-2015) and its main socioenvironmental drivers in order to investigate its consequences on secondary forests establishment and growth and on landscape composition and configuration. To achieve this goal, we used different land-cover maps and other remote sensing datasets, which allowed us to analyse spatial patterns and functioning of vegetation at different temporal and spatial scales. In Chapter 2, we addressed the association between forests cover increase and its spatial pattern change in Europe through a set of classical landscape metrics regarding land cover diversity and habitat fragmentation and connectivity. Here, we used data from the European Spatial Agency (ESA) and the Global Land Cover Facility, and we performed GLMs on a 752 randomly selected landscapes where we detected recent forest increase to characterize land cover changes between 1990 and 2012. This analysis showed that landscapes experiencing forest area increase exhibit a significant decrease in their land cover diversity, and an increase in both forest defragmentation and connectivity. However, these changes in land cover diversity were not directly attributable to forest increase but to the land cover initial composition. In addition, we determined that forest expansion patterns also depended on elevation and geographical position, with forest defragmentation being more frequent in forest-dominated landscapes concentrated in northern and eastern Europe and new patch proliferation in the less forested landscapes in southern and western regions. In

Chapters 3 and 4, we aimed at addressing at a continental but also at a regional (Spain) scale, the spatial pattern and the socioenvironmental drivers promoting forest expansion and the implications on forest establishment and growth, accounting also for differences in functional traits such as leaf-habit. In Chapter 3, we examined the magnitude and distribution of recently established forests (1992-2015) across and extensive socioecological gradients in Europe. We combined ESA land cover maps of 1992 and 2015, and we classified the established forests between these dates into regenerating after disturbances or secondary forests expanded into agricultural areas after abandonment, and we used a set of GIS datasets to determine main socioenvironmental factors associated with both forest regrowth processes. In addition, we evaluated the effect of these patterns and the land use legacy (i.e. regeneration vs. expansion) on forest productivity by using the Enhanced Vegetation Index. Results determined that forest area increased Europe (0.06% year^{-1}) caused mainly by forest expansion in Mediterranean and in Eastern temperate regions, while regeneration was particularly relevant in the boreal region. Both forest expansion and regeneration processes had a greater magnitude in highly forested and/or highly diverse landscapes, suggesting that landscape composition largely determined the local forest increase across Europe. Conversely, the rest of socioenvironmental factors (i.e. distance to metropolitan areas, elevation, temperature and water deficit) showed contrasting association with forest expansion and regeneration depending on the climatic domain (i.e. Mediterranean, temperate and boreal). Moreover, the analysis of EVI temporal trends revealed that expanding forests had higher EVI values than regenerating forests except in the warmer and drought-prone areas where, probably, they cannot benefit from the biological and physicochemical legacies of former agricultural soils for tree growth. In Chapter 4, we put the focus on the Iberian Peninsula, a hotspot of land use changes during the second half of the 20th and early 21th century and an excellent laboratory to study forest expansion due to the contrasting climatic and topographic gradients. Here, we used fine resolution Landsat land cover maps, combined with ESA aboveground biomass (AGB) maps and topographic and climatic data, to explore changes in the pattern of secondary forest establishment from 1985 to 2014 and its implications for forest growth (AGB), for the main forest leaf-habit types. Results showed expansion rates in the Iberian Peninsula (0.31% year^{-1}) above average Europe and that secondary forests were increasingly established in places with better environmental conditions (i.e. higher water availability, at lower elevations and on less steep slopes). In addition, results highlighted a key role of summer precipitation, temperature, slope and forest cover, and the lesser role of drought events, on secondary forest growth. Particularly, we observed that warm temperatures compromise the growth of needleleaf forests while broadleaf secondary forest benefits more from summer precipitation. Ultimately, these chapters points that spatial patterns of forest expansion may also be responsible of the observed proliferation of secondary broadleaf forests in detriment of needleleaf ones due to its different life strategies.

We think that the results of this thesis may improve the knowledge of forest expansion in Europe and may provide valuable information for the development of management strategies to adapt to Climate Change. The European Union has committed to achieving climate neutrality by 2050. As part of the European Green Deal, three billion new trees will be planted across the 27 member states. Our results can be useful in addressing this ambitious strategy because they provide valuable information about which sites may be prioritized, where afforestation can contribute more to carbon sequestration or to forest defragmentation and landscape diversification. Moreover, results raises the debate on whether afforestation should be thorough active tree plantation or thorough the management of the passive expansion of forests which can be a cost-effective strategy for ecosystem restauration.

Chapter 1

General Introduction

Changes in land use (human utilization of the land) and land cover (biophysical attributes of the earth's surface) have a direct impact on ecosystems functions and services (Pimm and Raven 2000; Foley et al. 2005) and alter Earth's biogeochemical cycles and energy balance (Le Quéré et al. 2018; Song et al. 2018) being one of the most important drivers of global changes (Lambin et al. 2001; Foley et al. 2005; Song et al. 2018).

In recent decades, human societies have increased their awareness on the intensity, magnitude, and extent of human alterations of the Earth's land surface. Humans have transformed world landscapes from the moment we entered for the first on a new environment (Lewis and Maslin 2015), but probably the most important anthropogenic alteration of the natural environment has been the clearing of forests by agricultural societies to establish cropland and pasture, and the exploitation of forests for fuel, wood and construction materials (Kaplan et al. 2009). This has supposed a continuous dynamics of planetary deforestation that has been closely linked to the increase of the human population and the socioeconomic development, first observed on temperate and subtropical regions and actually on tropical ones (Williams 2010). Some estimates suggest that global forest area has decreased by around 1.8 billion hectares in the past 5000 years, a decline equivalent to nearly 50 percent of today's total forest area (FAO 2016; Sandker et al. 2017).

However, in the last two centuries a change in this trend has been observed in some regions of the planet where the forest area increases for the first time to the detriment of the agricultural surface. This was described by Mather (1992) as forest transition, and describes the turning point where forest surface change from shrinking to expanding. This phenomenon involves the recent forest expansion in many regions of the world and, in turn, important changes in forest landscapes dynamics, characteristics and in ecosystems functions and services.

In this thesis, we will explore the patterns of forest expansion in Europe in the last decades, and will study some implications on the landscape dynamics and on the productivity of these secondary forests. The following sections will address the main socioecological processes driving this forest expansion, their rationale and associated methodological approaches.

1.1 - Socioecological framework of forest expansion

1.1.1 - Forest expansion

The conversion from non-forest to forest is named forest expansion and occur through active afforestation, i.e., the planting of trees on land that was not previously classified as forest, or through passive expansion of forest, i.e., natural successions on land that was previously under another land use (e.g., forest succession on agricultural land) (FRA 2018). Secondary forests established on former farmlands are often small but numerous, and together with remnants of ancient and semi-natural managed forests, provide essential ecosystem services (e.g., CO_2 sequestration, water, air and climate and regulation, preservation of habitats and biodiversity) (Foley et al. 2005; FAO 2020). Secondary forests may constitute a large proportion of the total forested area in many regions (e.g., Foster et al. 1998; Falcucci et al. 2007; Vilà-Cabrera et al. 2017; FAO 2020). For example, in the Iberian Peninsula secondary forests established on former farmland may account 20-25% of current forest surface (Baśnou et al. 2013; Vilà-Cabrera et al. 2017) while in China or Costa Rica may account more than 50% of the forests surface (FAO 2016).

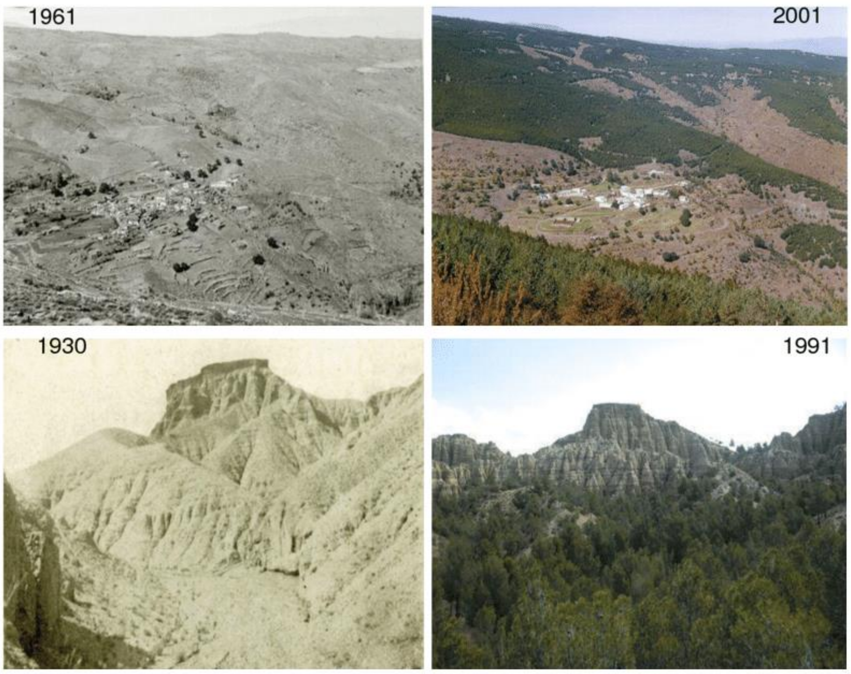

Figure 1.1. Differences in forest cover in two locations in South Eastern Spain before and after forest expansion. Upper pictures are Sierra Filabres (Almería) and lower pictures are Torreón (Granada). Source: Montero et al. (2007).

1.1.2 - Forest transition

The expansion of forests is part of a much larger phenomenon named the forest transition. The forest transition denotes a process through which a region moves from net loss to net gain of forest area (Mather 1992; Mather and Needle 1998). This term was introduced by Alexander Mather who suggested that a country's forest cover generally declines as it develops socially and economically, but eventually this trend could be reversed and forest cover begins to expand. The result is an inverted "U-shaped curve" for forest cover as a function of time (Figure 1.2), and the turning point at which forest decline halts and begins to rise is called the forest transition.

This phenomenon has occurred in many industrialized countries on temperate regions along the last centuries (Meyfroidt and Lambin 2011) and authors that have studied it emphasized the multiple and interrelated causes of forest transitions, involving economic, political, institutional, and cultural processes (Rudel et al. 2005; Kuemmerle et al. 2009; Lambin and Meyfroidt 2011; Pagnutti et al. 2013). Nevertheless, specialized literature agrees that forest transition is driven primarily by economic development and/or by forest scarcity (Rudel et al. 2005; Barbier et al. 2010; Meyfroidt and Lambin 2011):

a) The economic development carries the industrialization and the growth of the service economy in the country that pull the labour force from rural areas to cities (Samson et al. 1985; Antrop 2004; Terres et al. 2015). It also carries the agricultural intensification that increases national food production and profitability, which cause depopulation and agricultural decline in the least suitable regions of a country (Evenson and Gollin 2003; Rudel et al. 2009b; Lasanta et al. 2017). More recently, the pressure of global markets favours international land-use displacement and accelerates land abandonment in less competitive regions (Lambin et al. 2001; Lambin and Meyfroidt 2011). These processes changed the spatial patterns of agriculture on a national scale depending on the suitability of the land, allowing the regrowth of forests in marginal regions, especially those that are less connected to economic centres and are in less productive agricultural regions (Jongman 2002a; Rudel et al. 2009b; Keenan et al. 2015; Jadin et al. 2016).

b) Forest decline caused by agricultural expansion or wood extraction in the pre-forest transition phases creates a scarcity of forest products and decreases the ability of forests to deliver ecosystem goods and services to local communities (Rudel et al. 2005; Lambin and Meyfroidt 2010). This causes the reassessment of forests products (e.g., raising timber prices) accelerating the intensive forest management. Forest scarcity also drives cultural and political responses, inducing national policies to restrict forest exploitation, create protected areas, promote more sustainable management practices or invest in forest reforestation (Zhang and Song 2006; Kull et al. 2007; Meyfroidt et al. 2010). Reforestation is therefore expected to occur in regions with low forest cover, poor land suitability for agriculture but well-connected to wood markets (FAO 2016; Song et al. 2018).

However, with land use across the world becoming increasingly integrated via international trade and globalized economies, trends in forest loss and gain can no longer simply be explained by national dynamics, but are rather the result of complex drivers across scales, from local to global (Pendrill et al. 2019). Recent empirical studies suggest the globalization pathway as a modern version of the economic development pathway in which national economies are increasingly integrated into and influenced by global markets and global ideologies, and together with global and national forest policies, drives forest transition in developing countries (FAO 2016).

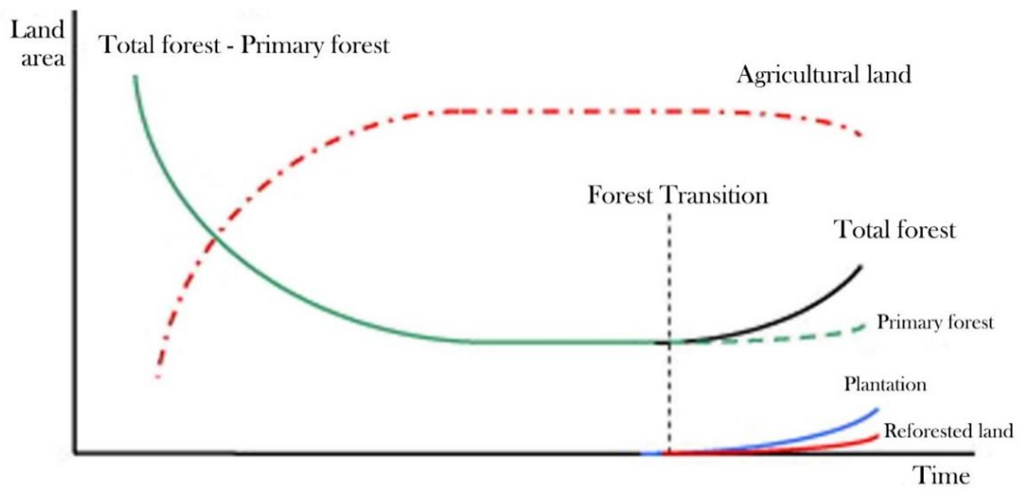

Figure 1.2. Land use changes in the forest transition model, modified from Barbier et al. 2010.

1.1.3 - Forest transitions across the world

The initial focus of forest transition studies was the historical experiences of industrial countries in Europe (Mather, 1992; Walker, 1993; Mather et al., 1999) and North America (Foster et al. 1998). In Europe many countries experienced the turning point from shrinking to expanding forest area in the late 1800s (Meyfroidt et al. 2010), as a result of industrialization and associated urbanization, the replacement of wood by coal as the main source of fuel and the Agricultural Revolution that increased considerably crops productivity (Pagnutti et al. 2013; FAO 2016). However, the beginning of a significant forest recovery in Europe was in the mid-20th century when it occurred a massive land abandonment in response to the collapse of mountain societies (Lasanta et al. 2017), influenced by the Green Revolution in 1960 (Evenson and Gollin 2003) and the economic modernization (Meyfroidt and Lambin 2011). The forest transition in the United States was similar to the European ones, occurring through a regional redistribution of land use since the beginning of 20th century (Foster et al. 1998; Pfaff and Walker 2010) where cropland and pastures spread to the South and West, while agricultural abandonment and reforestation occurred specially in Eastern United States (Ramankutty et al. 2010).

More recently, forest transition has been observed in China (Zhang and Song 2006), India (Ashraf et al. 2015), Vietnam (Meyfroidt and Lambin 2008), Chile (Heilmayr et al. 2016) or Costa Rica (Jadin et al. 2016) among other countries with developing economies (Meyfroidt and Lambin 2011; Pagnutti et al. 2013; FAO 2016; Pendrill et al. 2019). Generally, this later forest transitions differs from the initial ones on Western temperate nations as industrialization become less important in explaining reforestation, than globalization - the global integration of markets and internationalization of ideas and culture (Rudel 2009). Moreover, in densely populated and poorer countries of Asia, the forest scarcity pathway is usually more prominent, while in the richer and less densely populated countries of America, the economic development pathway is more frequent (Rudel et al. 2005).

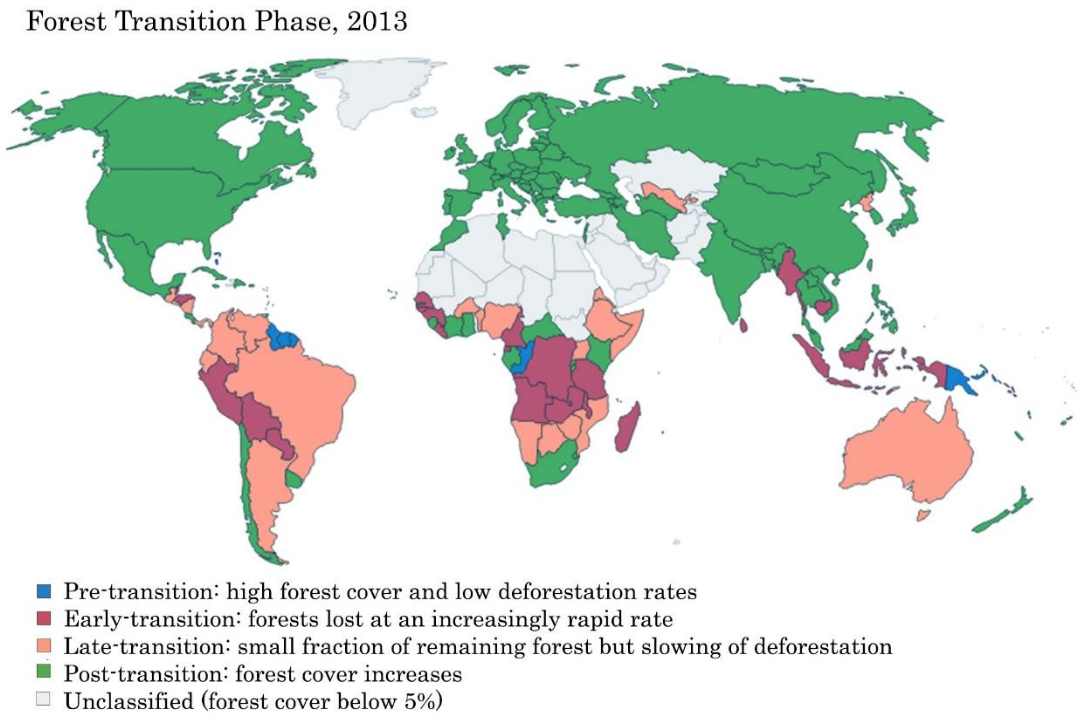

Figure 1.3. Map showing countries classified into different forest transition stages. Countries marked as 'unclassified' are primarily those with a forest cover below 5%. Modified from Pendrill et al., (2019)

1.1.4 - Forest transition in Europe

In Europe, forest cover has been recovering since the beginning of the 20th century (Fuchs et al. 2015a; Kauppi et al. 2018) and has increased 25–30% on average since the 1950s (Gold et al. 2006; Fuchs et al. 2015a). Forest transition in Europe is closely linked to farmland abandonment, the major land cover and land use changes in Europe since the19th century (Ramankutty and Foley 1999; MacDonald et al. 2000; Sitzia et al. 2010). Apart from alternative forms of human land use, such as urbanization, the main consequence of land abandonment in many areas is the beginning of plant succession and the establishment, either passively or actively, of secondary forests under favourable local climate and soil conditions (Bowen et al. 2007). The scientific literature agrees that farmland abandonment in Europe is due to a set of global and local causes that vary in time and space and is triggered by ecological, social and economic factors (Ramankutty et al. 2010; Prishchepov et al. 2012; Terres et al. 2015; Leal Filho et al. 2017; van der Zanden et al. 2017; Perpiña Castillo et al. 2021).

In Europe, three large-scale socio-economic processes determined the land abandonment in the last two centuries (Lasanta et al. 2017). First, the collapse of mountain societies in Europe that pushed the rural population to emigrate to cities and industrial sites causing a massive land abandonment in many European mountain areas: e.g., the Alps, the Pyrenees, the Carpathian Mountains, the Central System and the Apennines among many others (Kopylova 2000; Chauchard et al. 2007; Baumann et al. 2011; Lasanta et al. 2017; Vidal-Macua et al. 2018). The process started in early decades of the 19th century in France, Denmark, Switzerland, or United Kingdom (Mather and Needle 1998; Mather and Fairbairn 2000; Chauchard et al. 2007) and spread to other countries in Western and Southern Europe in the early decades of the 20th century (Terres et al. 2015; Lasanta et al. 2017). Second, a massive cropland abandonment occurred in Europe during the application of the Common Agricultural Policy (CAP) in 1988–2008 (Gold et al. 2006; Fuchs et al. 2013). This policy subsidized set-aside land abandonment or land retirement to force agriculture to be more competitive in global markets, causing the agriculture redistribution and intensification in the most productive regions (Jongman 2002a). The most important changes took place in Portugal, Ireland and the Czech Republic (Feranec, Jaffrain, Soukup, & Hazeu, 2010) but were also important in the Mediterranean countries, and the former socialist states (Fuchs et al. 2013, 2015a). Unlike the land abandonments attributed to the collapse of mountain societies, this occurs mainly in plains and it was closely linked to water scarcity problems, salinization or low soil fertility (Terres et al. 2015). Third, the drastic socio-economic and political changes that occurred after the breakdown of socialism triggered widespread land abandonment in the soviet countries in Central and Eastern Europe. After the fall of the Iron Curtain in 1989 the agricultural system in the post-soviet countries was not competitive in the international market (i.e. low productivity, high-pollution machinery and high energy consumption) and the value of wood production became more important, resulting in afforestation areas and fallow cropland (Baumann et al. 2011; Prishchepov et al. 2012, 2013).

While this global causes has been the most decisive in land use changes in Europe, regional and local factors are the ones that made abandonment more or less severe (Lambin et al. 2001; FAO 2016). In one hand, there is the local or regional socio-economic drivers which include market incentives, politics, technology, industrialization, farm characteristics, farmer age, accessibility (e.g. roads) or proximity to cities among others (Rey Benayas et al. 2007; Feranec et al. 2010; Prishchepov et al. 2013; Kosmas et al. 2015; Lasanta et al. 2017). On the other hand, there are a set of biophysical or ecological drivers including elevation, geological substrate, slope, aspect, fertility, soil depth, soil erosion, climate, or climate change when they constrain agricultural production (Rey Benayas et al. 2007; Terres et al. 2015; Lasanta et al. 2017). Biophysical factors always interfere in land abandonment because they determine the productivity and profitability of agricultural holdings. Regional studies in Europe have observed, for example, that patterns of abandonment are controlled by topography and accessibility (MacDonald et al. 2000; Sluiter and De Jong 2007; Van Doorn and Bakker 2007; Kuemmerle et al. 2009; Baumann et al. 2011; Nainggolan et al. 2012; Regos et al. 2015) and/or by poor and low fertility soils (Gellrich and Zimmermann 2007; Sluiter and De Jong 2007; Arnaez et al. 2011; Stellmes et al. 2013). Climate factors are also considered to be important for land abandonment, especially in the Mediterranean mountains as well as in arid and semi-arid areas in Southern Europe (Arnaez et al. 2011; Stellmes et al. 2013; Kosmas et al. 2015).

1.2 - Ecological implications of forest expansion

1.2.1 - Forest expansion and changes in landscape patterns

Forest expansion can have profound effect on landscape structure and ecological functions bringing about positive, as well as negative consequences. It is largely known that forest cover increase is affecting biodiversity conservation in Europe, with a generalized recovery of forest species including threatened species targeted in conservation initiatives (Plieninger et al. 2013; EEA 2016a) but also a local extinction of species living in open habitats, including butterflies, birds and plants (Plieninger et al. 2013; Melero et al. 2016; Regos et al. 2016). Forest expansion may also affect landscape heterogeneity and promote vegetation homogenization which may increase the functional connectivity among forests (e.g. seed dispersal potential) and may facilitate migration and gene flow among tree populations in response to climate change (Breed et al. 2011), while at the same time, may increase the danger of propagation of extreme wildfires in large areas, especially in southern Europe (Bowen et al. 2007).

Forest spatial pattern and landscape attributes resulting from forest increase may depend on the original landscape composition and configuration. For example, Fahrig (2017) suggests that the ecological responses to habitat fragmentation are largely dependent on habitat amount. Furthermore, the spatial arrangement of these secondary forests may influence forest functional diversity of tree species by modifying the connectivity, centrality and modularity of forest landscapes (Honnay et al. 2002; Gerard et al. 2010; Geri et al. 2010; Messier et al. 2019). This suggests the importance of forest spatial pattern in the conservation of biodiversity and ecosystem functions, especially in highly transformed landscapes (e.g. Guirado et al. 2007; Ramage et al. 2013).

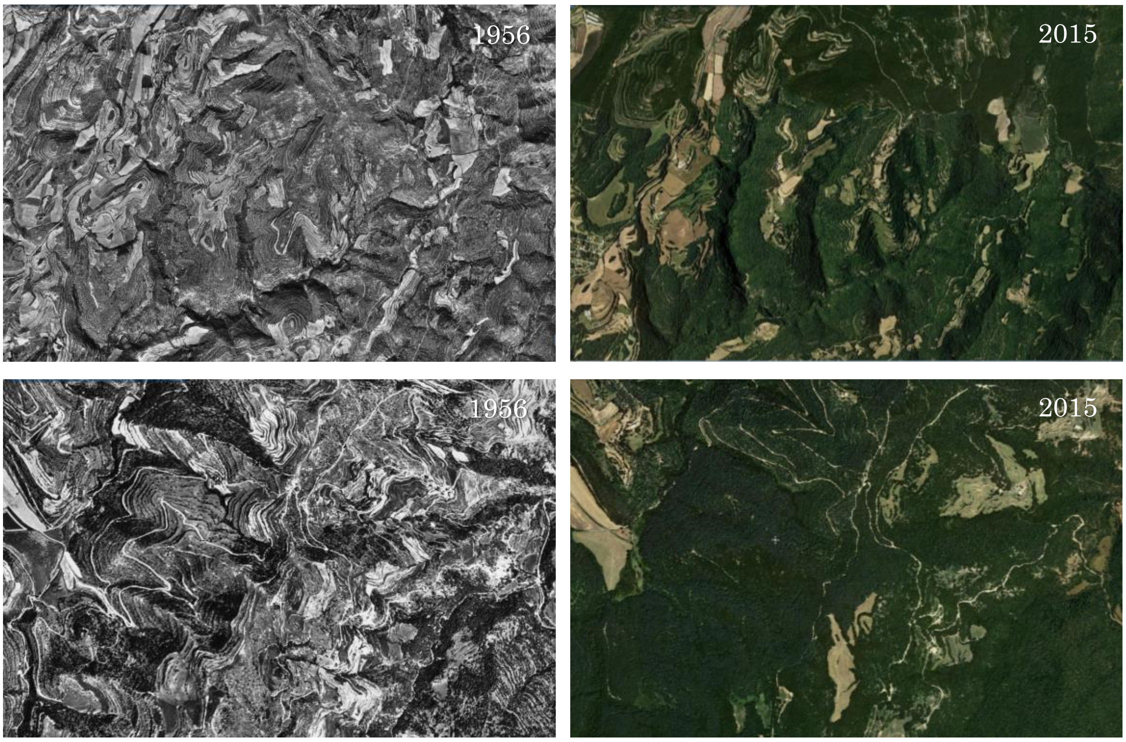

Figure 1.4. Differences in landscape in two locations in North Eastern Spain before (left) and after forest expansion (right). Source: AMS and PNOA.

1.2.2 - Secondary forest productivity and growth

The spatial patterns of forest expansion is mostly determined by farmland abandonment closely linked to low productivity. The biophysical conditions involving forest expansion may influence the recruitment, growth and mortality of tree species affecting the whole plant community (Tsujino et al. 2006; Thompson et al. 2009; Ruiz-Benito et al. 2017) which may ultimately determine secondary forest productivity and its capacity to carbon accumulation (Hooker and Compton 2003; Thompson et al. 2009; Pan et al. 2011; Jucker et al. 2014). Some studies suggest that the expansion of secondary forests may contribute in a relevant way on carbon sequestration (Hooker and Compton 2003; Pan et al. 2011; Fuchs et al. 2015b; Vilà-Cabrera et al. 2017) but again little is known about the influence of expansion patterns on secondary forests growth.

Moreover, forests established on former agricultural land may differ from long-established forests in species composition, and structural and functional attributes (Espelta et al. 2020). Several studies have suggested that these forests can benefit from land-use legacies because agricultural soils tend to be richer in N and P and exhibit faster mineralization rates (Compton and Boone 2000; Fraterrigo et al. 2005). These characteristics may enhance tree growth and productivity (Freschet et al. 2014; Leuschner et al. 2014; Vilà-Cabrera et al. 2017; Alfaro-Sánchez et al. 2019) although it may also cause greater sensitivity to climate due to changes in some functional attributes (e.g. lower wood density in Alfaro-Sánchez et al. 2019). This may be especially relevant for forests under a context of climate change (i.e. rising temperatures and extreme events), especially in the Mediterranean Basin (Scarascia-Mugnozza et al. 2000). Understanding the effect of the environmental factors (i.e. climatic and topographic) and past land use legacies on the establishment and growth of expanding forests can contribute to develop management practices enhancing the ecosystem functions and services.

1.3 - Remote sensing to study forest expansion

It is difficult to know the exact extent of forest expansion in Europe due to the lack of studies that can show a global and temporal perspective of this phenomenon. Most of the studies related to forest expansion cover regional or local scales, mostly due to the absence of a cartographic source before 1990 which makes it possible to analyse large areas and large periods (Zanchi et al. 2007). Moreover, despite their great usefulness for large-scale studies, the available datasets (e.g., national inventories) vary in forest definition among periods, which made it difficult to integrate afforestation and deforestation processes across Europe. Under this perspective, remote sensing offers unprecedented capabilities for global forest mapping and health assessments and may be the most effective way of monitoring Earth's forested areas as provide homogeneous and reliable information in different levels of detail in a cost effective way (Manakos and Braun 2014). Spectral reflectance signatures of Earth's surface reveal information about the state, biogeochemical composition, and structure of a leaf and canopy which allows detecting and classifying the land cover composition and also monitor the estate of vegetation (Huete 2012). In the field of remote sensing applications, scientists have developed vegetation indices (VIs) which are quite simple and effective algorithms for qualitatively and quantitatively evaluating vegetation cover conditions based on the electro-magnetic wave reflectance information from canopies. Spectral VIs are spectral measures of canopy greenness, which is expressed by several biophysical variables related to the amount (cover fraction and leaf area) and chlorophyll content of the canopy foliage allowing determine plant type, aboveground biomass, water content within tissues or aboveground net primary productivity among others (Glenn et al. 2008; Vicente-Serrano et al. 2016; Xue and Su 2017). One of the most used and implemented VIs is the Normalized Difference Vegetation Index (NDVI) and the later improved Enhanced Vegetation Index (EVI) widely used to characterize canopy growth and vigour, the Leaf Area Index (LAI) and indirectly the aboveground productivity of vegetation (Prince 1991; D'arrigo et al. 2000; Turner et al. 2005; Huete 2012; Ogaya et al. 2015).

1.4 - Objectives

Despite the relevance of the phenomenon of forest expansion most of the works addressing the issue have been performed till now at local and regional scales. Little is known about the influence of the context on the changes in the spatial pattern following forest recovery in Europe, which is the previous essential step for understanding the effects of these changes on biodiversity or C sequestration. It is also key to understand spatial patterns of forest expansion and how local factors affect secondary forest growth to be able to evaluate the potential of mitigation strategies aimed at maximizing carbon sequestration. Moreover, most studies underlying changes on forest growth due to land use legacies have been performed at local and regional scales and focused on particular tree species while large-scale studies including different biogeographical regions are absent. Yet, understanding the interactions between land use legacy and climate and the differences for the main forest leaf-habit types is also key to anticipate and assess changes in forest productivity and growth under an uncertain climate change scenario.

In this thesis we address recent (approx. 1985-2015) patterns of the forest expansion in Europe and its implications on landscape characteristics and on the secondary forests establishment and growth. We aim to understand the changes on forest patterns and the effect on landscape composition and configuration that involve recent forest increase in Europe (Chapter 2). We also aim to examine the main socioenvironmental factors, especially the ecological ones, related to this phenomenon and address the implications for the growth and productivity of secondary forests for the main leaf-habit types (Chapter 3 and 4). We approach this issue from a global perspective, analysing forest expansion on the European continent, but also on a regional scale, studying the case of the Iberian Peninsula (Chapter 4), whose contrasting climatic, topographic and socioeconomic conditions made its forests an excellent laboratory. The specific objectives for each chapter are listed below:

Chapter 2: In this chapter we aimed at addressing the association between forests cover increase and spatial pattern change in the European landscapes, while considering the landscape land cover composition and the altitudinal and geographical gradients. We characterized landscape spatial pattern through a set of classical landscape metrics regarding land cover diversity and habitat fragmentation and connectivity. Data was obtained from the European Spatial Agency and the Global Land Cover Facility land-cover maps and other GIS layers and a set of GLM were performed on randomly selected 752 landscapes with recent (1990-2012) forest increase. Particularly, we examine whether forest increase determines i) a decrease in the overall landscape diversity, ii) a forest defragmentation and iii) an increase in forest connectivity across Europe.

Chapter 3: In this chapter we aimed at addressing the spatial pattern and the socioenvironmental drivers that influence recent (1992-2015) forest regeneration and expansion across Europe, considering the main forest leaf-habit types across the continent. For that we used European Space Agency land cover maps and a set of GIS datasets and performed GLMM to determine main socioenvironmental drivers. We also aimed at evaluating the effects of these patterns and the past land use legacy (i.e. regeneration vs. expansion) on forest productivity by using Enhanced Vegetation Index obtained from NASA and performed randomized block design ANOVAs. Here, i) we compare differences among forest expansion and regeneration extent across Europe according to bioclimatic and socio-economic factors and ii) we examine whether forests established in former agricultural lands show higher EVI values than regenerating forest owing to the benefits of land use legacies, considering climatic conditions and the forest leaf habit.

Chapter 4: In this chapter we aimed at addressing recent (1985–2014) patterns of secondary forest establishment in the Iberian Peninsula (IP) and examine how environmental factors affects the growth of the main forest leaf-habit types. We used Landsat land cover maps, combined with European Space Agency aboveground biomass (AGB) maps and topographic and climatic data, to explore recent (1985–2014) patterns of secondary forest establishment in the Iberian Peninsula and performed GLM to determine its implications for forest growth (AGB). In particular, we examine i) environmental factors associated to secondary forests emergence and ii) its effect on its growth (AGB), for the main leaf-habits in the Iberian Peninsula.

Finally, we expose the main conclusions of this thesis in the **General Conclusions** section.

Chapter 2

Changes in forest landscape patterns resulting from recent forest increase in Europe (1990-2012): Defragmentation of pre-existing forest versus new patch proliferation

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2.1 - Abstract

Recent forest cover increase in Europe might involve deep changes on landscape composition and configuration. We show that increasing forest area promotes defragmentation of pre-existing forests and new patch proliferation, in forest-dominated and non-forest-dominated landscapes respectively, while it is not associated to decreasing landscape diversity. These processes are modulated by geographic factors and might affect functional connectivity and biodiversity conservation in newly forested landscapes. Recent forest increase in Europe might drive changes in landscape pattern, with increasing forest defragmentation and connectivity but decreasing land cover diversity that, in turn, might affect biodiversity conservation. However, little is known about these patterns of change, and their association with the environmental context. To explore the association of forest cover increase with changes in the spatial pattern of European landscapes, while considering their original landscape composition, geographical position and elevation. We obtained data from ESA and GFC land-cover maps and other GIS layers and performed a set of GLM on randomly selected 752 landscapes with recent (1990-2012) forest increase. Decrease in landscape diversity in the last decades was not associated to forest increase but to high cropland and low scrub-grassland cover. Forest increase promoted the defragmentation of already existing forests and new patch proliferation in forest-dominated and non-dominated landscapes, respectively. These processes also depend on elevation and geographical position, with forest defragmentation concentrated in Northern and Eastern Europe and new patch proliferation in southern and western regions, and in mid-elevation areas. Changes in landscapes due to forest expansion are more complex than expected and cannot be solely attributable to forest increase, but also to landscape composition and location across elevation and geographical gradients across Europe.

Keywords: *Forest transition, forest spatial pattern, land-cover change, landscape diversity, landscape metrics.*

2.2 - Introduction

Deforestation is a primary land-use changes on a world scale (Pagnutti et al. 2013) yet the overall decline in forest cover has fallen in recent decades due to forest transition (Meyfroidt and Lambin 2011), which has determined a change from net deforestation to net reforestation at both national and regional scales particularly in the Northern Hemisphere (Rudel et al. 2009a). Indeed, forest transition has been taking place in many European and North American regions since the beginning of the twentieth century (Rudel et al. 2005) and, more recently, in the northern Mediterranean Basin (Mazzoleni et al. 2004). Gerard et al. (2010) detected an overall increase in forest cover in Europe in the second half of the 20th century using land cover maps for a specific set of landscape samples. Recent works have highlighted that forest transition continues nowadays in Europe, with a net gain of 1.4% of forest surface between 1992 and 2015 detected from the European Space Agency global Land Cover maps (Palmero-Iniesta et al. 2021).

It is largely known that forest cover increase is affecting biodiversity conservation in Europe, with a generalized recovery of forest organisms including threatened species targeted in conservation initiatives (Plieninger et al. 2013; EEA 2016a). However, it also promotes a rarefaction and local extinction of species living in open habitats, including butterflies, birds and plants (Plieninger et al. 2013; Melero et al. 2016; Regos et al. 2016). In contrast, the effects of forest expansion on changes in the spatial pattern of the European landscapes are mostly unknown. In a seminal review on habitat loss and fragmentation (i.e. the reverse process to that analysed here), Fahrig (2003) observed a primary effect of habitat loss on biodiversity conservation, while the effects of habitat fragmentation per se (i.e. changes in habitat configuration but not in habitat cover) were much weaker and both positive as negative (see also Fahrig 2017). This would disagree with other works showing the importance of forest spatial pattern in the conservation of biodiversity and ecosystem functions, especially in highly transformed landscapes (e.g. Guirado et al. 2007; Ramage et al. 2013) where local disturbance regimes favour the extinction of forest specialists and the colonization by non-forest ones (Vellend et al. 2007; Basnou et al. 2015). As most of these works have been performed at local and regional scales, specific socio-environmental context might largely determine the effects of landscape configuration on biodiversity. Once again, little is known about the influence of this context on the changes in the spatial pattern following forest recovery in Europe, which is the previous essential step for understanding the effects of these changes on biodiversity.

The present work is aimed at addressing the association between forests cover increase and spatial pattern change in the European landscapes, while considering the landscape land cover composition and the altitudinal and geographical gradients. The study takes profit of a recent set of medium- to high-resolution land use and cover (LC) maps worldwide available: those of the Climate Change Initiative (CCI), which are derived from ENVISAT, POES and SPOT images by the European Spatial Agency (ESA 2017), and the forest cover change maps of the Global Land Cover Facility (GLCF) from the University of Maryland, which are derived from Landsat images (Hansen et al. 2013; Kim et al. 2014). Changes in landscape and in forest spatial pattern have been addressed through a set of classical landscape metrics regarding land cover diversity and habitat fragmentation and connectivity. We hypothesized that forest increase is determining i) a decrease in the overall landscape diversity, ii) a forest defragmentation and iii) an increase in forest connectivity across Europe. Yet, these effects might depend on the initial forest cover if the association between forest cover increase and landscape change is not linear as observed by Fahrig (2003) in the reverse case of habitat fragmentation. Still, geographical position determining climatic conditions responsible for differential forest recovery may modulate these landscape changes.

2.3 - Materials and Methods

2.2.1 - Study system

The study was performed in Europe as the region bordered by the Arctic Ocean to the north, the Atlantic Ocean to the west, the Mediterranean Sea to the south and the Ural Mountains and the Caspian Sea to the east, and including the natural region of the Caucasus and the Anatolian Peninsula. It comprises around 10^7 km^2 from 30 to 80º of latitude and -30 to 70º of longitude in the Northern Hemisphere. Latitudinal and longitudinal climatic gradients and orography determine strong climatic variety in Europe (EEA 2016b). The relief of Europe is dominantly flat

(66% of the territory is below 200 m a.s.l.) although the influence of the mountains gives the territory a high ecological heterogeneity (IGN 2019). The current European landscape is the outcome of a long history of human land-use changes (Perlin and Journey 1989) in which forests and other wooded land now constitute the largest land-cover type, extending over more than 43% of its area (EEA 2016b).

2.2.2 - Data sets on forest change and landscape composition

Forest cover and its spatial pattern in 1990 and 2012 were derived from the GLCF datasets (Hansen et al. 2013; Kim et al. 2014) covering all Europe, but only including forests. We used the oldest dataset available (1990-2000; www.landcover.com) to obtain a 1990 forest cover map with three categories: i) forest, which included those pixels with already existing forest and forest lost between 1990 and 2000, ii) non-forest, which included the non-forest and the forests gain between the same period, and iii) noise, which include shadow, clouds and no data pixels in the GLCF 1990-2000 that were excluded in later steps. A similar forest cover map was obtained for 2012 (http://earthenginepartners.appspot.com/science-2013-global-forest/download_v1.4.html), the most recent one in the GLCF datasets by categorizing the pixels of already existing forest and of forest gain between 2000 and 2012 as forest, and the rest as non-forest. We also assessed the overall landscape composition through the land cover maps annually produced within the Climate Change Initiative of the European Spatial Agency (ESA CCI-LC), which are the complete land-cover maps with the highest spatial resolution (300 m of pixel size) covering the overall Europe (Diogo and Koomen 2016). We selected 1992 and 2012 land cover maps for the present study. The original CCI-LC land cover categories were reclassified into those proposed by the Intergovernmental Panel on Climate Change (IPCC; Eggleston et al. 2006), using the correspondence tables of the CCI-LC Product (see Appendix 1 Table A1.1; ESA 2017).

2.2.3 - Sampling design and landscape metrics

To assess changes in forest spatial pattern and in landscape composition due to forest increase, we randomly selected 2000 circular landscapes of 5-km radius across the study area. As the original GFC 1990-2000 had some noise (e.g. clouds, shadows), we discarded those landscapes with any type of noise (a total of 667 points) to avoid misinterpreting changes. Then, we calculated forest cover area (ha) in 1990 and 2012 for the remaining landscapes and we selected those with a positive forest increase between these dates (n= 752).

Changes in forest spatial pattern between the study dates were assessed from the 30-m pixel sized binary (forest/non-forest) maps mentioned above, through a set of landscape metrics aimed at describing forest fragmentation and forest connectivity (McGarigal and Marks 1994; Kupfer 2012). Their selection was based on: (1) comparability with previous landscape ecological studies (ex. Turner 2005; Weng 2007); (2) and appropriateness for indicating ecological conditions (Debinski and Holt 2005; Kupfer 2012) and (3) for describing contrasting dimensions of the selected landscape attributes (McGarigal and Marks 1994; Fahrig 2003). Patch number and both mean and largest patch size were chosen as metrics of forest fragmentation. Moreover, patch size is known to be related with species richness and abundance (Boulinier et al. 2001; Debinski and Holt 2005). Total forest edge was also selected as a proxy of relevant fragmentation effects related to habitat alteration (Saunders et al. 1999). We finally selected effective mesh size (ha) for its high sensitivity to contrasting fragmentation processes (Jaeger 2000). Regarding forest connectivity, we selected the percentage of like adjacencies, which measures the degree of aggregation of patch types, and the Euclidean nearest neighbour distance, which measures distance among patches of the same type and deals explicitly with the degree to which patches are spatially isolated from each other (McGarigal and Marks 1994).

On the other hand, to assess changes in land cover diversity, we calculated the Shannon diversity index for 1992 and 2012 for each study landscape using the CCI-LC map (300-m of pixel size). Landscape diversity is considered a key attribute of landscapes, indicative of its ability of housing a variety of organisms and habitats (Turner 1989).

All these metrics were calculated for the selected study dates and study landscapes, using the datasets mentioned above and the R 'landscapemetrics' package (Hesselbarth et al. 2019).

2.2.4 - Environmental covariates

In order to assess the modulating role of environmental context on the association between forest increase and landscape change, we included a set of variables regarding geographical position, topography, and initial composition of the study landscapes in the study following the related literature (Heilman et al. 2002; Geri et al. 2010; Fernandes et al. 2011; Nagendra et al. 2013). The geographical position of landscapes is a proxy of their position along the observed climatic and socio-environmental gradients across Europe (Jongman 2002a; Metzger et al. 2005), and it was described from the geographic coordinates of the landscape central point (latitude and longitude in UTM coordinates). Topography included mean elevation, obtained from the Global 30 Arc-Second Elevation dataset (GTOPO30) provided by the USGS (http://edcwww.cr.usgs.gov/landdaac/gtopo30/gtopo30.html). Initial composition of landscapes (i.e percentage of each land-cover category), was inferred from the CCI-LC map of 1992. We calculated the cover percentage of the dominant land cover categories, namely forest and cropland (mean cover and standard error 39.02 ± 1.27% and 37.34 ± 1.31%, respectively; see Table 1 Appendix 1). We then summed cover of grasslands, wetlands, shrublands and sparse vegetation into a shrub/grassland category, noticeably represented in the study landscapes (10.94 ± 0.65%). We did not include the agroforestry mosaics, as this category is an undefined mixture of forest, scrubland, grassland and croplands, although its relevance in the study landscapes (9.32 ± 0.54%).

2.2.5 - Statistical analyses

In order to test if these landscape metrics differed between 1990 and 2012 (1992 and 2012 for the Shannon diversity index), we performed eight non-parametric Wilcoxon signed rank tests for paired samples for each landscape metric, after confirming the non-normal distribution of these metrics through the Kolmogorov-Smirnov test with Lilliefors modification. The significance of these tests was also adjusted with Bonferroni correction.

We performed eight general lineal models – one for each landscape metric - to test the association of changes in landscape metrics with forest increase, the environmental variables mentioned above and the interaction between both. To avoid multicollinearity, we firstly generated a correlation matrix with a Spearman rank and choose those less correlated variables (r<|0.7|) (Appendix 1 Table A1.2). So that, explanatory variables finally used on the linear models were forest increase (ha), forest cover (%), cropland cover (%), shrub/grassland cover (%), elevation (m), latitude and longitude (degree) and the second order interactions among the forest increase and the remaining variables. These interactions were included as we were particularly interested in exploring if the association between forest increase and landscape metrics varied according to environmental factors.

Simplest general lineal models were selected following a dredge procedure using MuMIn R package (Barton and Barton 2019), which removed non-significant variables from the general model, and assessed significant changes in model predictions using the Akaike information criterion (AIC). From the models with a difference in AIC relative to AICmin < 2 we chose the most parsimonious model by selecting the model with fewest predictor variables following the procedure described in Crawley (2007) (see Appendix 1 Table A1.3). In addition, we carefully considered all plausible models in order to not leave out an important explanatory variable by exploring model averaging based on an information criterion (see Appendix 1 Table A1.4). Moreover, null models were also performed for each landscape metric to investigate whether an observed pattern could have arisen by chance producing a type I error (Gotelli and Graves 1996). All the analyses were carried out with software R 2.15.0 (R Development Core Team 2012).

2.4 - Results

On average, a significant increase in the size of both the largest and the mean forest patch and in the forest effective mesh size was observed in the studied landscapes (

Table 2.1**¡Error! No se encuentra el origen de la referencia.**). Forest total edge and the number of forest patches also significantly increased as the Euclidean nearest neighbour distance did (

Table 2.1**¡Error! No se encuentra el origen de la referencia.**). In contrast, the Shannon diversity index significantly decreased in the same landscapes. Our analyses failed to detect any significant change on the percentage of forest like adjacencies during the study period.

Table 2.1. Changes in the studied metrics in our study landscapes between 1990 and 2012. Wilcoxon test (paired samples) used to test significant differences. Significate codes: '.' >0.05, '*' = 0.05, '**' = 0.01, '***' = 0.001

	Mean 1990 (SE)	Mean 2012 (SE)	V-value	p-value	Sign.
Forest largest patch size (ha)	1,490 (76.75)	1,860 (88.87)	29,816	<0.0001	***
Forest mean patch size (ha)	36.6 (2.84)	46.4 (6.92)	205,050	<0.0001	***
Forest total edge (m)	190,000 (6764.11)	257,000 (8611.18)	32,186	<0.0001	***
Forest effective mesh size (ha)	819 (56.34)	1140 (71.19)	26,197	<0.0001	***
Number of forest patches	56.4 (2.04)	129 (4.56)	18,583	<0.0001	***
Euclidean nearest neighbour distance (m)	152 (9.47)	131 (4.41)	94,471	0.046	*
Percentage of forest like adjacencies (%)	67.8 (1.31)	72.3 (0.97)	125,796	0.276	
Shannon diversity index	0.738 (0.02)	0.620 (0.02)	110,262	<0.0001	***

The best adequate model for each one of the eight landscape metric variables included the effects of the environmental factors specified in Table 2.2. There were between 5 to 10 other plausible models for each metric (difference in AIC in relation to AICmin <2) that varied in the presence of lower relative importance variables but always included the effects of all the selected variables in the selected model (see model averaging results in Appendix 1 Table A1.3 and Table A1.4). As shown in Table 2.2, explanatory variables accounted for a substantial proportion of total variability for some landscape metrics, as the increase in forest largest patch size and forest effective mesh size, but not for others (increase in forest mean patch size or Euclidean nearest neighbour distance). Selected models suggest that forest increase during the study period was not significantly associated with the increase in all the studied metrics (Table 2.2). It was positively associated with the increase in forest largest patch size, effective mesh size, total edge and the number of forest patches while test failed to detect any significant association with the increase in the Shannon diversity index and in the percentage of like adjacencies.

Several environmental context variables were also significantly associated with the increase in the studied landscape metrics, sometimes through significant interactions with forest increase (Table 2.2Table 2.2). Initial forest cover showed a significant interaction with forest increase in both forest largest patch and effective mesh size, as these metrics increase more rapidly with forest increase in forest-dominated landscapes than in the rest (Appendix 2 Figure A1.1 A and B). There was also a significant interaction between initial forest cover and forest increase in both forest total edge and the number of forest patches, but in this case the increase in these metrics with forest increase was lower in forest-dominated landscapes than in the rest (Appendix 2 Figure A1.1 C and D). Figure 1 illustrates the different new forest distribution pattern in forest-dominated landscapes, where new forest grew coalescent to the pre-existing forest, and in non-forest-dominated landscapes, where forest grew in isolated patches.

Table 2.2. Summary of GLM results showing the association of forest increase and the landscape and geographic variables with changes in the studied landscape metrics. Each column shows the factor effect estimate (standard error) and the significate codes: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.'

	Forest largest patch size	**Forest effective mesh size**	**Forest total edge**	**Number of forest patches**	**Shannon diversity index**	**Percentage of forest like adjacencies**	**Forest mean patch size**	**Euclidean nearest neighbour distance**
Intercept	272.43 (14.42) ***	162.11 (14.06) ***	92344 (4706) ***	95.35 (40.2) ***	-0.12 (0.01) ***	3.13 (0.65) ***		
Forest increase (FI)	473.09 (22.73) ***	168.09 (23.57) ***	94337 (8252) ***	57.55 (7.10) ***		-1.67 (1.11)	-15.57 (8.85)	18.39 (12.13)
Forest cover	146.06 (14.67) ***	299.90 (14.83) ***	-21084 (5182) ***	-40.13 (7.12) ***			26.39 (5.73) ***	
Crops cover				-38.37 (7.10) ***	0.05 (0.01) ***	3.04 (0.76) ***		
Shrub/grassland cover				-21.90 (4.59) ***	-0.02 (0.01) *	1.82 (0.57) **		
Elevation			13730 (7132) .	1.16 (6.18)	-0.04 (0.01) **			
Longitude		38.76 (13.85) **	-23907 (4447) ***	-26.15 (3.68) ***		1.26 (0.59) *	13.22 (5.01) **	20.42 (9.16) *
Latitude		-35.29 (16.03) *	29849 (6111) ***	0.74 (5.41)	0.10 (0.01) ***	-3.48 (0.64) ***		
FI: Forest cover	221.9 (16.22) ***	469.65 (19.67) ***	-88460 (6561) ***	-53.97 (5.59) ***			26.99 (6.32) ***	
FI: Crops cover						-4.10 (1.12) ***		
FI: Elevation			43153 (12026) ***	29.26 (10.19) **				
FI: Longitude		44.45 (19.25) *	-18909 (6167) **					-25.01 (11.52) *
FI: Latitude		-154.47 (23.45) ***	67268 (8434) ***	14.61 (6.72) *				
Model fit ▼								
Residual standard error	341.4	324.5	10350	0.75	0.31	14.35	132.8	207.7
R-squared	0.85	0.84	0.31	0.27	0.17	0.16	0.08	0.02
AIC model	10913.19	10826.24	19512.46	8882.77	395.77	6141.62	9494.42	7936.39
AIC null model	12280.84	12212.15	19771.98	9101.12	524.99	6256.30	9552.35	7943.53

Initial cropland cover showed a negative association with the number of forest patches and positive with the Shannon diversity index and the percentage of like adjacencies. It also showed a significant interaction with the increase in forest cover on that in some metrics. Thus, the increase in the percentage of like adjacencies following that in forest cover was higher in cropland-dominated landscapes than in the rest (Appendix 2 Figure A1.1 E). Shrub/grassland cover showed a negative association with the increase in both the number of forest patches and the Shannon diversity index and positive with that in the percentage of like adjacencies.

Besides, longitude and latitude showed a significant association with the increase in most of the metrics and some significant interactions with forest increase, and different patterns of forest growth were observed throughout Europe (Table 2.2, Figure 2.). Longitude showed a positive association with the increase in both the effective mesh size and the percentage of like adjacencies, and negative with the increase in forest total edge and in the number of forest patches. Latitude showed a positive association with the increase in both forest total edge and the Shannon diversity index, and negative with that in forest effective mesh size and in the percentage of like adjacencies. Further, the increase in effective mesh size following forest cover increase was higher when higher longitude and latitude (Appendix 1 Figure A1.2 A and B, respectively). Contrarily, the increase in the forest total edge in relation to forest cover increase was higher when lower the longitude and latitude (Appendix 1 Figure A1.2 C and D, respectively). The increase in the number of forest patches following that in forest cover was higher when the lower the latitude (Appendix 1 Figure A1.2 E).

Finally, elevation showed a positive association with the increase in the forest total edge, but negative with that in the Shannon diversity index. The increase in both forest total edge and in the number of forest patches following that in forest cover was highest between 500 and 1000 m above sea level (Appendix 1 Figure A1.3 A and B).

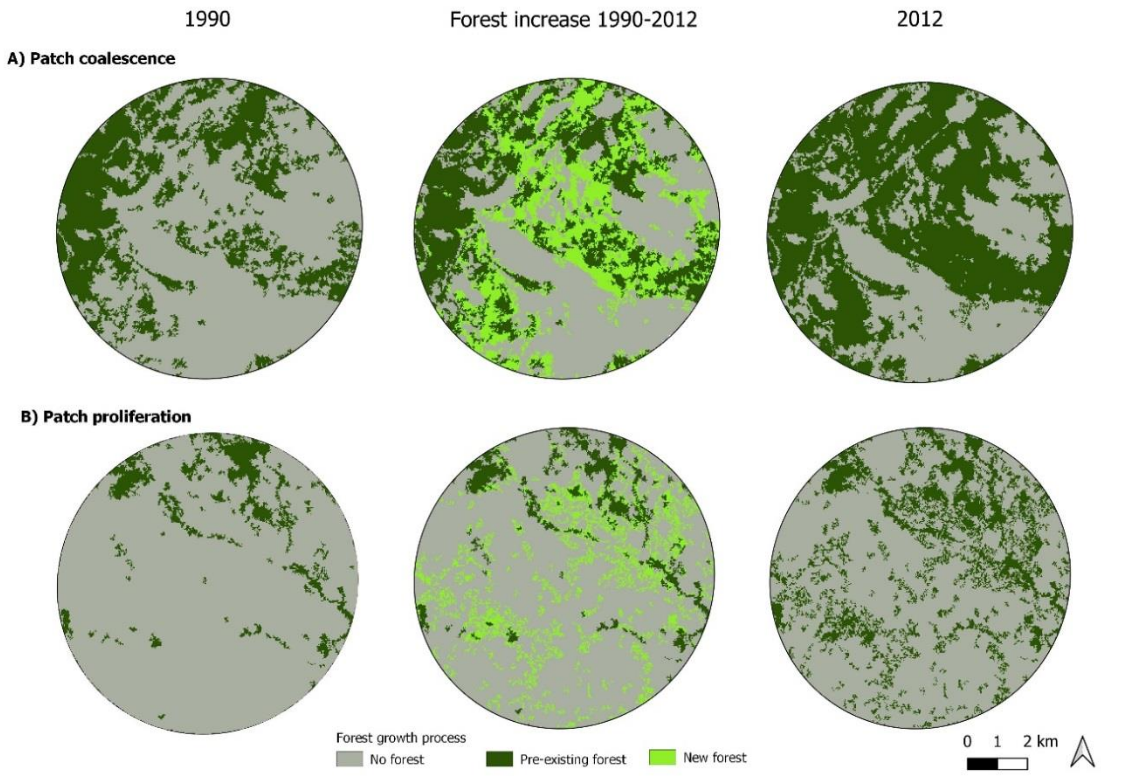

Figure 2.1. Examples forest-dominated and non-dominated landscapes, where pre-existing patch coalescence and new patch proliferation were respectively observed.

2.5 - Discussion

Our results confirm our first hypothesis that European landscapes experiencing forest recovery in the last decades also exhibit a significant decrease in their land cover diversity, and an increase in both forest defragmentation and connectivity. However, not all these changes are directly attributable to forest increase, as our models show that some of them were only concurrent with it. This is the case of land cover diversity, which decreases in landscapes where the forest increased, yet this decrease is not associated with forest increase or even to forest cover as suggested in previous regional-scale studies (e.g. Marull et al. 2015; Otero et al. 2015). Instead, we observe a significant effect of other land cover categories, namely cropland and scrub-grassland, on the land cover diversity of these landscapes. This striking result brings some additional dimensions to the complex debate about the conservation of agroforestry mosaics, considered as biodiversity hotspots in Europe and especially threatened by afforestation (Marull et al. 2015; Otero et al. 2015). Positive association with cropland cover suggests that forest recovery leads to higher landscape diversity in cropland-dominated landscapes that often result from agricultural intensification (Perfecto and Vandermeer 2010; Otero et al. 2015). In contrast, its negative association with scrub and grassland cover, frequently originated from crop and pasture abandonment, might indicate that forest increase is especially detrimental for landscape diversity where traditional agroforestry mosaics have been abandoned (Otero et al. 2015). Concerning environmental drivers, changes in land cover diversity were also associated with elevation and latitude. Negative association with elevation might be related to the already known deep transformation of lowland landscapes, in which urban sprawl and road construction might substantially increase land cover diversity (Falcucci et al. 2007; Baśnou et al. 2013). Positive association with latitude might be due to the inverse latitudinal gradient in land cover diversity (r-spearman= -0.21, $p<0.001$): i.e. forest gain might increase land cover diversity more in the less diverse northern landscapes than in the southern ones.

Results regarding the effects of forest increase on changes in forest attributes suggest the coexistence of contrasting landscape processes on forest spatial pattern. On the one hand, forest gain determines a significant increase in both forest largest patch and effective mesh size, which are mostly related to the growth and coalescence of pre-existing forest patches indicative to forest defragmentation. On the other hand, forest recovery also determines an increase in the number of forest patches and in total forest edge. These results might be viewed, paradoxically, indicative of forest fragmentation due to small patch proliferation, as edge per area unit increases more rapidly with new small isolated patches than with the growth of old big patches. Fahrig (2003) described a similar paradoxical situation regarding the opposite case of habitat loss, which might determine both habitat fragmentation and defragmentation depending on the spatial loss pattern (i.e., the loss and fragmentation of big versus small, or nearby versus far habitat patches). The coexistence of these landscape patterns is probably the reason that there are non-significant changes in mean patch size associated with forest increase across Europe.

Our study also demonstrates that these landscape changes associated with forest increase depend on the original landscape composition (especially forest, but also cropland cover) and on a set of geographic and topographic variables. The first point illustrates the above-mentioned dichotomy of pre-existing patch growth and coalescence *versus* new patch proliferation associated with forest increase (Figure 2.). Thus, this last mostly determines patch growth and coalescence in forest-dominated (>50% of forest cover) landscapes, but new patch proliferation in non-forest dominated ones. Regarding the second point, our study shows the existence of significant geographic gradients in landscape change due to afforestation. While defragmentation (i.e. forest patch growth and coalescence) is especially concentrated northwards, new patch proliferation (indicated by increasing the patch number and, secondarily, by total edge) particularly affects the lowest latitudes (see Figure 2.2). This pattern is probably due to a combination of climate and human land-use legacy, since new forests mostly are originated from old pastures and wet grasslands in northern landscapes with colder climates while they come mostly from croplands in the rest of landscapes (Palmero-Iniesta et al. 2021). Moreover, pre-existing patch growth and coalescence concentrates eastwards where the landscape matrix is a forest-cropland mosaic, while the new patch proliferation is especially important in the western boundary where landscapes are especially affected by intense urbanization and fragmentation by infrastructures (Jongman 2002a; Jaeger et al. 2016). Still, the study indicates that forest increase especially determines the new patch proliferation (as indicated by the increase in the total edge and in the number of patches; Appendix 1 Figure A1.3) in medium elevations, probably because a concentration of crop abandonment in uplands as suggested in previous works (Baśnou et al. 2013; Cervera et al. 2019).

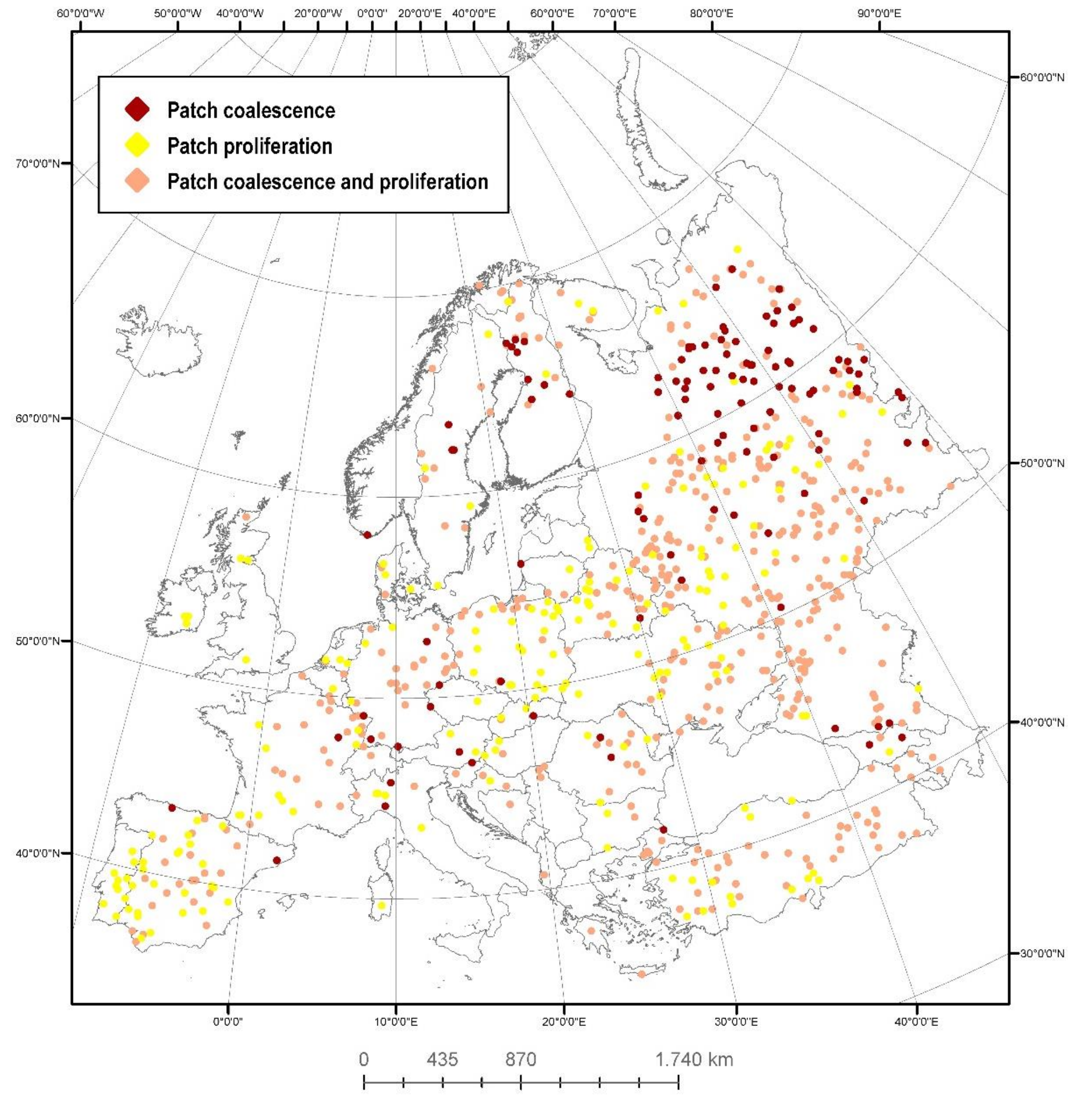

Figure 2.2. Distribution of the study landscapes classified as: Patch coalescence (effective mesh size increase over the median of the sample while number of forest patches under the median of the sample), patch proliferation (effective mesh size increase under the median of the sample while number of forest patches over the median of the sample) and both patch coalescence and proliferation (the remaining landscapes).

These results are, in turn, relevant for improving the strategies of forest biodiversity conservation, as they put in value the importance of considering the original composition of landscape and the socio-environmental context. Yet, the spatial arrangement of these new forests may influence forest resilience by increasing the functional diversity of tree species and by modifying the connectivity, centrality and modularity of forest landscapes (Messier et al. 2019). Forest defragmentation in already highly forested landscapes will clearly promote the recovery of forest specialist species commonly occupying large and connected forest areas and often of large conservation concern (e.g. Saura and Pascual-Hortal 2007; Gil-Tena et al. 2013; Deinet et al. 2017) and this will help to reconnect both the existing populations and potential habitats, particularly in Northern and Eastern Europe and in main mountain ranges, thus reinforcing the ecological network of protected areas in Europe (EEA 2012). In contrast, the proliferation of new forest patches in lowland, highly anthropized landscapes in Southern and Western Europe might favour forest generalist species that commonly have less conservation concern, and even non-forest and alien species (Guirado et al. 2006; Basnou et al. 2015; Regos et al. 2016; Liebhold et al. 2017). Conversely, the new patch proliferation observed southwards and westwards suggest an increase in functional connectivity among forests (e.g. seed dispersal potential) and may facilitate migration and gene flow among tree populations in response to climate change (Breed et al. 2011) while, at the same time, preventing, especially in the south, the danger of the coalescence of large forest areas in light of the propagation of extreme wildfires (Bowen et al. 2007). Moreover, the new habitat availability may be especially relevant in Southern Europe, as habitat loss and fragmentation effects on species density and/or diversity is greatest in areas with high maximum temperatures and in areas where average rainfall has decreased more over time (see Mantyka-Pringle et al. 2012).

2.6 - Conclusions

To sum up, our study shows that forest recovery in Europe is guessed by landscape changes in recently afforested landscapes. However, these changes are more complex than expected and they cannot be solely attributable to forest increase, but also to the original landscape composition and position across elevational and geographical gradients across the mainland.

Results may be especially relevant for the preservation of forest biodiversity and ecosystem services since they highlight the importance of the landscape context on the new forest spatial distribution pattern including forest fragmentation and connectivity and landscape diversity. Specific management policies might help to redirect these trends by designing both large forest recovery and priority connection areas in order to ensure large patch coalescence yet combined with prevention plans to avoid the deleterious effects of forest continuity in some of these regions (e.g. wildfires in Southern Europe; Duane et al. 2016).

Chapter 3

Recent forest area increase in Europe: expanding and regenerating forests differ in their regional patterns, drivers and productivity trends

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3.1 - Abstract

In Europe, forest area is increasing. These recently established forests can be classified into regenerating after disturbances or expanding into agricultural areas after abandonment. We used European Space Agency land cover maps and MODIS data to investigate which socioenvironmental drivers influenced recent forest expansion and regeneration in Europe from 1992 to 2015 and to compare their productivity by means of the Enhanced Vegetation Index (EVI). Our results showed that forest area increased in Europe by 1.4% from 1992 to 2015. The 66% of this forest area increase corresponded to forest expansion mostly in Mediterranean and temperate regions, while regeneration (34%) dominated in boreal areas. Forest area and land cover diversity in 1992 were the main drivers of local forest area increase from 1992 to 2015. Forest expansion occurred on the warmer zones far from urban areas in the boreal region while it was the opposite in temperate and Mediterranean areas. On the other hand, forest regeneration showed mostly a positive relation with the distance to urban areas and water availability but no relation with temperature. The EVI values in 2015 were higher in expanding than in regenerating forests except in the warmer and drier bioclimates of Europe. These EVI trends suggests a higher productivity of expanding forests, except in areas where they cannot benefit from biological and physicochemical legacies of abandoned agricultural soils for tree growth, owing to water shortage. In sum, our results highlight that recent forest area increase in Europe is mostly caused by forest expansion into former agricultural areas but this is mostly occurring in less productive (warmer and drought-prone) bioclimates where advantages of agricultural legacies may not occur. Ultimately, this casts doubts whether there may be a limit for the role of forest expansion into agricultural areas for carbon sequestration in the long term.

Keywords: *Enhanced Vegetation Index, forest regeneration, forest expansion, forest transition, land cover change, land use legacies*

3.2 - Introduction

Although deforestation is still a major global environmental threat (Song et al. 2018), net forest area decline is slowing down and even reversing in the Northern Hemisphere for some decades ago (FAO 2020). This process is the outcome of the so-called "forest transition" that refers to a set of interrelated demographic, socioeconomic, political, and cultural processes determining forest return (Lambin and Meyfroidt 2011). In Europe, forests have been recovering since the beginning of the 20th century (Fuchs et al. 2015a; Kauppi et al. 2018) and their area has increased 25-30% on average since the 1950s (Gold et al. 2006; Fuchs et al. 2015a). Changes in forest area are strongly modulated by multiple factors, including climate (Walther et al. 2002; Kelly and Goulden 2008), topography (Moeslund et al. 2013; Vidal-Macua et al. 2017) and specific socioeconomic characteristics of each country and region (Benayas et al. 2007; Vidal-Macua et al. 2017; Kauppi et al. 2018). Ultimately, this process may also be responsible of the shift among forests with species having different life strategies, such as the recently observed proliferation of broadleaved forests in detriment of coniferous in the Iberian Peninsula (Vidal-Macua et al. 2017).

For a given period, forest area increase may be the result of two different processes: *regeneration*, in areas where a previously existing forest had been disturbed (i.e. cut, burned, fell by storms) and forest *expansion* into areas, such as abandoned croplands, where forest had been absent for decades or even centuries (UNECE-FAO 2001). Interestingly, forests established on former agricultural land may differ from long-established forests in species composition, and structural and functional attributes (Espelta et al. 2020). Moreover, they can benefit from land-use legacies because agricultural soils tend to be richer in N and P and exhibit faster mineralization rates (Compton and Boone 2000; Fraterrigo et al. 2005). These characteristics may enhance tree growth and productivity (Freschet et al., 2014; Leuschner, Wulf, Bäuchler, & Hertel, 2014, Vilà-Cabrera, Espelta, Vayreda, & Pino, 2017, Alfaro-Sánchez, Jump, Pino, Díez-Nogales, & Espelta, 2019). Yet, the effect of land use legacies on forest development may exhibit complex interactions with climate. For example, Vilà-Cabrera et al. (2017) observed that growth differences between secondary forest established in former crops and pastures vs. long-established ones were greater in warmer and dryer climates, while Alfaro-

Sánchez et al. (2019) found a greater sensitivity to climate in recently established forests.

Understanding the interactions between land use legacy and climate may be of key interest to anticipate and assess productivity and growth changes in forests under an uncertain climate change scenario (Zang, Hartl-Meier, Dittmar, Rothe, & Menzel, 2014). Yet, most studies have been performed at local and regional scales (Freschet et al., 2014; Vilà-Cabrera et al., 2017) or focused on particular tree species (i.e. *Quercus petraea* in Von Oheimb et al., 2014; *Fagus sylvatica* in Mausolf et al., 2018, Alfaro-Sánchez et al., 2019), while large-scale studies including different biogeographical regions are absent. Increasing availability of remote sensing data makes this possible (Gregorio and Jansen 2005), as they inform of the vegetation conditions based on its differential absorption (Tucker 1979; Vicente-Serrano et al. 2016). In recent decades, the Normalized Difference Vegetation Index (NDVI) and the Enhanced Vegetation Index (EVI) have gained attention to assess the canopy biophysical parameters (i.e. LAI, canopy cover) and vegetation dynamics across time, as they exhibit a strong relationship with green biomass (Gutman 1991; Wylie et al. 2002; Ogaya et al. 2015) and indirectly with aboveground net primary productivity (Prince 1991; Hunt Jr 1994; D'arrigo et al. 2000; Turner et al. 2005). Yet, to the best of our knowledge we do not know any study that has used these indices to evaluate potential differences in productivity between expanding and regenerating forests.

The present study aims at assessing the spatial pattern and the socioenvironmental drivers that influence forest regeneration and expansion across Europe in recent decades, considering the main different forest types across the continent. It also aims at evaluating the effects of these patterns and the past land use legacy (i.e. regeneration vs. expansion) on forest productivity by using EVI. We used a recent set of medium-resolution land cover (LC) maps worldwide available from the Climate Change Initiative (CCI), derived from AVHRR, ENVISAT MERIS, PROBA-V and SPOT-VGT images (ESA 2017), and EVI products obtained from MODIS (NASA; Didan 2015). We hypothesize that i) forest expansion and regeneration extent across Europe will differ according to bioclimatic and socio-economic factors; ii) forests established in former agricultural lands will show higher EVI values than regenerating forest owing to the benefits of land use legacies for the former; and iii) differences in EVI increase between forest originated from expansion and regeneration will be also mediated by climatic conditions and forest leaf habit. Ultimately, our results will help understanding the recent changes in forest land cover in Europe and envision the contribution of forest expansion on the potential services and disservices provided by forested landscapes.

3.3 - Materials and Methods

3.3.1 - Study area

The present study was focused in Europe, defined as the mainland bordered by the Arctic Ocean to the north, the Atlantic Ocean to the west, the Mediterranean Sea to the south and the Ural Mountains and the Caspian Sea to the east. The study area includes the Caucasus and the Anatolian Peninsula, and all the islands either constituting separate countries (i.e. Great Britain, Ireland, Iceland, Cyprus, and Malta) or belonging to the mainland ones. This study area comprises around 10^7 km^2 from 30º to 80º of latitude and -30º to 70º of longitude on the North hemisphere. Climate varies from north to south, but also from west to east due to the ocean-continental gradient. These gradients entail a wide temperature and precipitation ranges that include 12 bioclimates according to the Global Environmental Zones (GEnZs) defined in Metzger et al. (2012) from extremely cold and wet, through temperate both mesic and xeric to hot and dry zones. Relief is predominantly flat - 66% of the area is below 200 m asl - although mountain ranges increase environmental variability across the region (Körner et al. 2017). Despite forest would probably be the dominant vegetation across Europe, the current landscape is the outcome of a long history of human land-use (Bengtsson et al. 2000), with forests currently only covering ca. 43% of the total area (EEA, 2016). Finally, Europe has not only high climatic and landscape heterogeneity but also spatial heterogeneity in economic, sociocultural and population traits, with particularly pronounced divergences between western and eastern countries, but also between northern and southern ones (Vandermotten 2000).

3.3.2 - Changes in forest land cover patterns

In order to study changes on forest land cover, we used the oldest (1992) and the most recent available (2015) Climate Change Initiative (CCI) 300-m annual land cover (LC) time series (hereafter CCI-LC) developed by the European Space Agency, hereafter ESA (ESA 2017). The ESA CCI-LC time series is one of the best datasets available for studying global land cover changes because of its high temporal extent (23 years) and its LC classification accuracy and coherence between regions and dates (Diogo and Koomen 2016; ESA 2017). Moreover, the spatial resolution of this dataset is appropriate enough for analyses run at a continental scale although some inconsistencies may locally appear (Diogo and Koomen 2016). These maps describe the Earth's terrestrial surface in 22 global (legend level 1) and 37 regional (legend level 2) original LC categories based on the United Nations Land Cover Classification System (UN-LCCS; Di Gregorio, 2005). For the purposes of this study, we grouped the original LC categories describing vegetation into the main types (see Appendix 2 Table A2.1) proposed by the Intergovernmental Panel on Climate Change (IPCC; Eggleston, Buendia, Miwa, Ngara, & Tanabe, 2006) following the correspondence table included in the CCI-LC Product User Guide (ESA 2017). This allowed us determining which were the original land covers where forests developed during the study period (hereafter, forest origin) and the resulting main forest leaf habit (i.e. broadleaf vs. needleleaf; evergreen vs deciduous).

We combined the CCI-LC 1992 and the CCI-LC 2015 maps to determine total forest area increase (forest land cover area present in 2015 but not in 1992; km^2), forest expansion (forest land cover area in 2015 that in 1992 corresponded to agricultural area; km^2), forest regeneration (forest land cover area in 2015 that in 1992 corresponded to non-agricultural area: km^2) and forest area net change (difference between forest land cover area in 2015 and 1992, once forest loss during the same period had been discounted; km^2). Notice that for the forest expansion and the forest regeneration processes, we adopted the definitions used by the Forest Europe expert group of the Ministerial Conference on the Protection of Forests in Europe (Forest Europe 2015). Thus, forest expansion is considered to be the establishment of a forest on a land that, until then, was under a different use. It implies a transformation of land use from non-forest to forest (FRA 2018), while forest regeneration corresponds to the reestablishment of a forest stand by natural or artificial means following the removal of the previous stand by felling or as a result of other causes, i.e. fire or windstorm (TBFRA 2000). Disentangling recently felled or disturbed forests from other non-forested land cover categories (i.e. croplands) in land cover maps is not an easy task. Therefore, for practical reasons and based on the available land-cover maps, we considered as regenerated forests in 2015 those corresponding, in 1992 to the non-agricultural CCI-LC vegetation classes 110, 120, 130, 140, 150, 180 and 210 and as expanded forest those included in 1992 in the CCI-LC vegetation classes 10, 20, 30 and 40 (see Appendix 2 Table A2.1). We acknowledge that this may somewhat overestimate the extent of regeneration, as some areas corresponding to shrublands, wetlands, sparse vegetation and bare areas in 1992 may have been finally included as recently felled or disturbed forests with the potential of regenerating. Yet, previous studies indicates that in Europe transitions from non-agricultural lands to forests mostly correspond to the regeneration of previously felled or disturbed forests (Falcucci et al. 2007; Gerard et al. 2010; Baśnou et al. 2013).

To assess the spatial distribution and amount of the forest land cover changes previously described, we generated a grid of 10-km cell size covering Europe and calculated, for each $10km^2$ cell, the percentage of CCI-LC 300m pixels where forest area increase, expansion and regeneration occurred. The distribution of these three processes across the continent was assessed from the percentage of $10km^2$ cells in which the process was detected while the extent of the process was characterized as the average percentage of forest change considering all cells.

3.3.3 - Environmental and socioeconomic drivers of forest regeneration and expansion

To study the influence of environmental and socioeconomic factors on the two processes leading forest area increase (regeneration, expansion), we extracted for each of the 10-km grid cells abovementioned the following bioclimatic, topographic and socioeconomic factors. We selected 4 bioclimatic indicators based on Metzger et al., (2012): mean annual temperature, aridity index (AI) as a proxy of plant available moisture (Trabucco et al. 2008), and temperature and potential evapotranspiration (PET) seasonality as proxies of seasonality and continentally, respectively. We also selected 2 topographic variables, slope and elevation, calculated from the Global Elevation dataset (GTOPO30) from the U.S. Geological Survey. Finally, we selected five socioeconomic factors as potential drivers of land cover change: population density, proximity to urban areas, proximity to metropolitan areas (> 500.000 inhabitants), road density and gross domestic product (GDP). Distance to urban areas and to metropolitan areas was calculated from the Urban areas 1-km resolution dataset v.4 (https://www.naturalearthdata.com/downloads/10m-cultural-vectors/10m-urban-area/). We obtained population density in 1990 from the Global Population Count Grid Time Series Estimates (https://doi.org/10.7927/H47M05W2), road density from the Global Roads Open Access Data Set v.1 (https://doi.org/10.7927/H4VD6WCT) and gross domestic product per unit area (GDP) for year 1990 from the Global 15x15' Grids (https://doi.org/10.7927/H4NC5Z4X). All these data are provided by the Columbia University Center for International Earth Science Information Network (CIESIN) and the NASA Socioeconomic Data and Applications Center (SEDAC).

Finally, by means of the CCI-LC map from 1992, we calculated the forest land cover percentage and the Shannon land-cover diversity index at the beginning of the study period (1992), as these two factors have been suggested to mediate in the process of forest cover change (Palmero-Iniesta et al. 2020).

3.3.4 - Enhanced Vegetation Index (EVI) in expanding and regenerating forests

We explored the differences in productivity between forests originated from expansion and regeneration by using the Enhanced Vegetation Index (EVI) from the MOD13A1 (Didan 2015) version 6, obtained from the MODIS Terra platform. The Enhanced Vegetation Index stems from the modification of the Normalized Difference Vegetation Index (NDVI) to reduce sensitivity to high biomass values and artefacts of canopy background and atmospheric conditions (Liu and Huete 1995). The EVI has been proposed as a proxy for forest productivity as it is known to be related with density of photosynthetically active vegetation, such as leaf biomass density (Vicente-Serrano et al. 2016). With its 500-m resolution and 16-day compositing periods, MOD13A1 provides consistent spatial and temporal comparisons of terrestrial vegetation variations (Justice et al. 1998). To explore potential differences between forest expansion and regeneration we used EVI values in 2015 and the variation from 2000 to 2015 while values in 2015 were also used to compare differences among forest leaf habit types. We selected 2000 as the initial point because images are available from this year. So that, we used the CCI-

LC maps for the year 2000 and, after class reclassification (see point 2.2), we combined it with the 1992 and the 2015 LC maps. Then we selected those pixels that were purely cropland areas (CCI-LC classes 11 and 20) both in 1992 and 2000 and forest in 2015 to detect locations where forest expansion had occurred. We also selected pixels of pure natural vegetation classes in 2000 (CCI-LC class 120, 130, 150, 180 and 200) that were forest both in 1992 and 2015 to define points where forest regeneration was occurring. We selected non-tree covered classes at the year 2000 (see Table 7-2: conversion of CCI-LC classes to Plant Functional Types of the CCI-LC Product User Guide, ESA, 2017) to ensure that, when they became forest in 2015, those pixels had experienced an increase of at least 30% in tree cover. To account for potential differences related to leaf habit types, we classified forests into the most representative categories in the European continent: broadleaf deciduous, needleleaf evergreen, mixed and mosaic forests (CCI-LC classes 60, 70, 90 and 100) as other categories were much less present in most territories (see Appendix 2 Figure A2.3). Notice that in Mediterranean areas the category of mixed and mosaic forests corresponds to the usual mixture of broadleaf evergreen and coniferous species typical of recently established forests in the area (Ruiz-Carbayo et al. 2020). Ultimately, our classification resulted into 13917 and 20975 points where, expansion or regeneration occurred respectively (see Appendix 2 Figure A2.1). For each point we calculated the EVI annual maximum value for 2000 and 2015, with images corresponding to maximum yearly development of vegetation (DeFries, Hansen, & Townshend, 1995; Holben, 1986) and calculated increase (EVI increase) from their difference.

3.3.5 - Statistical analyses

In order to investigate the association of the occurrence of total forest area increase, expansion and regeneration with the environmental and socioeconomic factors we performed generalized linear mixed models (GLMM) with a binomial family transformation (presence, absence) using “lme4” R package (Bates et al. 2007). For these bionomial variables, presence/absence of forest expansion or regeneration was assessed by using the information of the process and the original land cover categories in the 10 km grid cells defined in the previous sections 2.2 and 2.3. We considered the occurrence of forest expansion (regeneration) in those points with an expansion (regeneration) percentage > 0 while we considered the process did not occur in those points where expansion (regeneration) equals 0% although agricultural (non-agriculural vegetation categories) existed and the process could eventually take place. Finally, the occurrence of overall forest area increase was considered when either expansion or regeneration occurred. Note that in the models we only compared points where a process occurred with the points where it did not but could eventually take place, and we excluded from the analysis those points where it could not occur (i.e. forest area = 100% in 1992). Moreover, in order to analyze areas with similar characteristics (see Appendix 2 Figure A2.1), we run these analyses after we subdivided Europe into boreal (extremely cold and mesic and cold and mesic bioclimates), temperate (cool temperate mesic and cool temperate xeric bioclimates) and Mediterranean regions (warm temperate mesic and warm temperate xeric bioclimates) by using Metzger et al. (2012) map. To avoid multicollinearity, we chose the less correlated variables ($r < |0.7|$) after performing a correlation matrix with a Spearman rank test (Online Appendix 2 Table A2.2). Final explanatory variables selected were a combination of land cover and socioenvironmental variables: i.e. forest percentage in 1992, land cover Shannon's diversity, aridity index, temperature seasonality, mean annual temperature, elevation and distance to metropolitan areas. Country was included in the models as a random factor to account for variability caused by local scale socioeconomic and management characteristics. The simplest general lineal models were selected following a dredge procedure using MuMIn R package (Barton and Barton 2019). Models differing by >2 points in AIC values were considered to be different, following (Crawley 2007a).

In order to evaluate the potential effects of land use legacy on the forest EVI, we performed 2 randomized block design ANOVAs. The response variables were either EVI increase or EVI value in 2015 (EVI 2015) while forest area increase process (expansion or regeneration) was included as a categorical explanatory variable. We also included in the models: i) forest leaf habit in 2015 to consider potential differences on EVI values due to the different forest classes, ii) the bioclimate (Metzger et al., 2012), and iii) the EVI maximum value in the year 2000 to consider the potential effects of initial EVI values. For this particular analysis we used bioclimates, rather than the main regions (boreal, temperate and Mediterranean), because it is a more detailed classification of climatic conditions, as it considers temperature but also mesic and xeric conditions.

After the randomized block design ANOVAs, post-hoc tests were performed with the “emmeans” function from the "lsmeans" R package (Lenth 2019). The choice of the "emmeans" package was determined by the need to account for an unbalanced number of regenerating and expanding forests. All SIG and dataset tasks were performed using ArcGIS 10 (ESRI Inc., Redlands, CA, USA), whereas statistical analyses were performed using R (R Development Core Team 2017).

3.4 - Results

3.4.1 - Forest cover changes

From 1992 to 2015, there was an increase of 237,131 km2 of forest area in Europe and a net forest area change of 55,341 km2 once forest area loss during the period is accounted (i.e. a 1.4% increase in 23 years). Forest area increase was widely distributed across Europe since it occurred in 46% of the 10km grid cells analyzed, although it was low to moderate in most cells, with an average of 4.60 ± 0.02 % (mean ± SE). Forest area increase mostly occurred from agricultural mosaics (57% of total area) and secondarily (22%) from areas classified in the land cover maps as wetlands (Appendix 2 Table A2.3 and Figure A2.2). The main forest leaf habit types resulting from forest area increase were needleleaf evergreen and broadleaf deciduous (34.6% and 33.3%, respectively; Appendix 2 Table A2.5).

The 66.1% of forest area increase from 1992 to 2015 corresponded to forest expansion and it occurred in 34.2% of the grid cells, while regeneration represented the 33.9%, and occurred in the 24.2% of grid cells. Both forest area increase processes occurred at different latitudes (Figure 3.1): the 92.2% of forest expansion mostly occurred under 60º of latitude while 84.0% of forest regeneration happened above it. The 44.5% of forests arisen from expansion were broadleaf deciduous, the 22.1% were mosaic forests, the 20.6% were needleleaf evergreen while the 10.2% were mixed leaf habit forests. Conversely, 62.7% of forests developing from regeneration were needleleaf evergreen, the 19.4% were mosaic forests, the 11.0% were broadleaf deciduous and the 9% were mixed leaf habit forests.

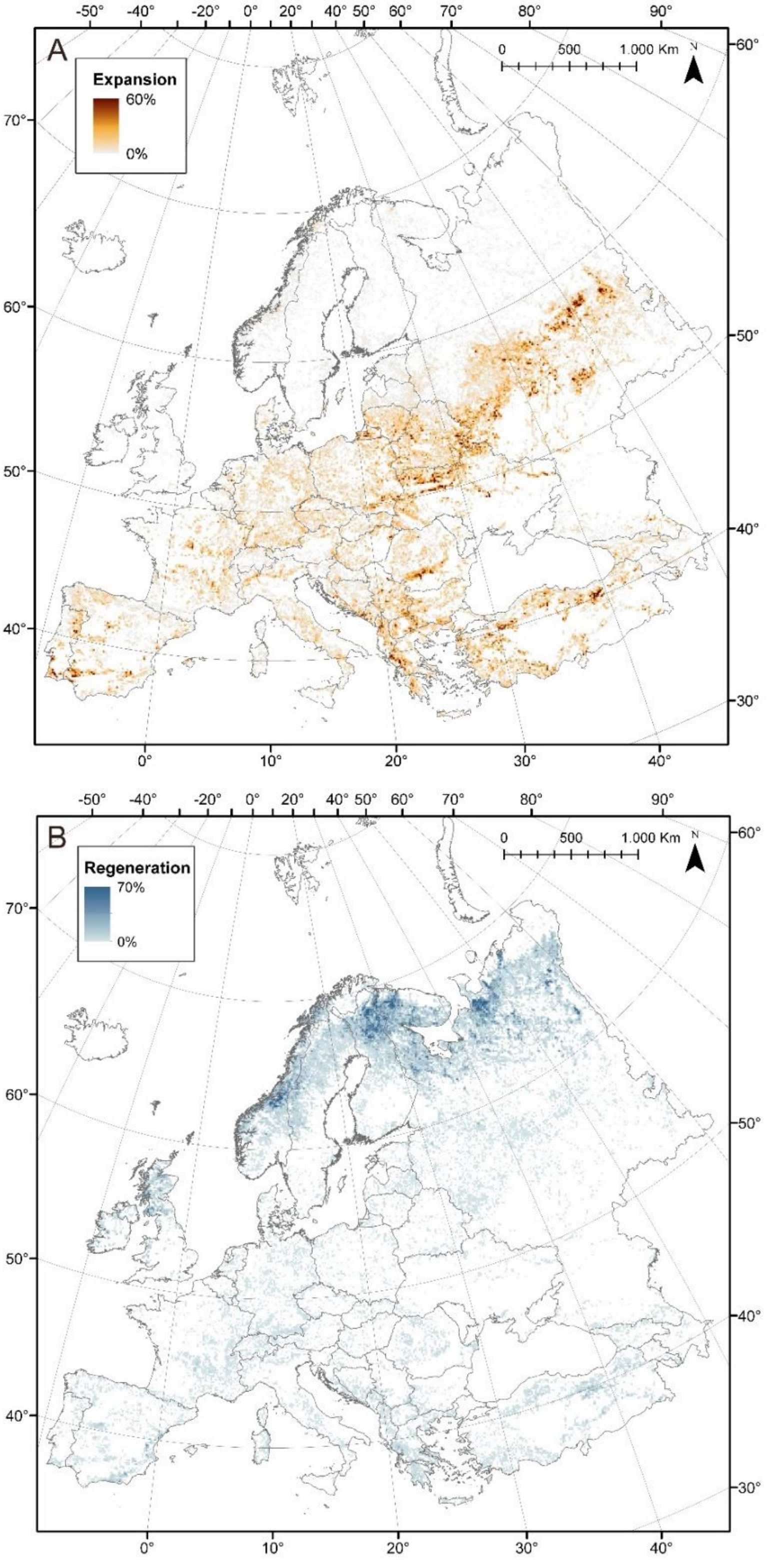

Figure 3.1. Forest expansion (A) and regeneration (B) in Europe between 1992 and 2015. Each pixel shows the percentage of forest expansion and regeneration relative to a 10-km grid cell. Note that these are absolute values and do not account for forest loss processes in the same pixels.

3.4.2 - Main drivers of forest change

Forest land cover area (%) and land cover diversity in 1992 were strongly and positively associated with forest area increase, expansion and regeneration in boreal, temperate and Mediterranean regions (see Table 3.1). The distance to metropolitan areas was positively associated with forest regeneration in all regions and with forest expansion in the boreal zone while it was negatively associated with forest expansion in temperate and Mediterranean regions. The elevation was positively associated with forest expansion in the boreal region and with forest regeneration in temperate and Mediterranean zones but negatively associated with forest expansion in temperate regions. Both the temperature seasonality and the mean annual temperature were positively associated with forest expansion and regeneration in the boreal region, while they showed a negative association with forest expansion in temperate and Mediterranean regions and no effects on regeneration except for the negative relation with temperature seasonality in temperate regions. Finally, the aridity index was positively associated with forest expansion in temperate region and negatively associated in boreal and Mediterranean ones while regeneration was positively associated in boreal and temperate and negatively in Mediterranean region. The inclusion of country as a random factor improved the model fit in all cases (see Appendix 2 Table A2.6).

Table 3.1. Results of the general linear mixed models (binomial family) exploring the association of total forest area increase, expansion and regeneration in Europe between 1992 and 2015 with the selected environmental and socioeconomic variables. Model standardized estimates and significance for fixed effects are shown. Green shadows indicate positive association while red marks negative association. Significance: '*' = 0.05, '**' = 0.01, '***' = 0.001.

	Forest cover in 1992	Land cover diversity 1992	Distance to metropolitan areas	Elevation	Temperature seasonality	Mean annual temperature	Aridity index
Forest area increase							
Boreal	0.73 ***	1.62 ***	0.61 ***	0.11 ***	1.19 ***	0.91 ***	0.16 ***
Temperate	1.06 ***	1.40 ***	-0.19 ***	-0.17 ***	-0.46 ***	-0.28 ***	0.64 ***
Mediterranean	0.88 ***	1.25 ***	-0.09 **	0.04	-0.39 ***	-0.19 ***	-0.10 **
Forest expansion							
Boreal	0.22 ***	1.53 ***	0.07 **	0.34 ***	1.12 ***	0.94 **	-0.06 *
Temperate	1.06 ***	1.35 ***	-0.20 ***	-0.19 ***	-0.61 ***	-0.39 ***	0.44 ***
Mediterranean	0.88 ***	1.20 ***	-0.15 ***	0.02	-0.36 ***	-0.24 ***	-0.09 **
Forest regeneration							
Boreal	1.18 ***	1.42 ***	0.82 ***	0.00	0.67 ***	0.18 ***	0.24 ***
Temperate	0.77 ***	1.23 ***	0.06 **	0.14 ***	-0.15 **	-0.01	0.37 ***
Mediterranean	0.67 ***	1.28 ***	0.06 **	0.33 ***	-0.07	0.05	-0.18 ***

3.4.3 - Forest EVI in expanding and regenerating forests

The EVI increase from 2000 to 2015 and the final value in 2015 were significantly different according to the process of forest area increase (expansion vs. regeneration), the bioclimate, the forest leaf habit and the initial EVI values (for EVI increase), with the interaction among several factors (Appendix 2 Table A2.7 and Table A2.8).

As indicated by the interaction between the forest area increase processes and bioclimate, expanding forests showed an EVI increase significantly higher than regenerating forests in all "cold sites" (i.e. extremely cold mesic, cold mesic, cold temperate mesic and cold temperate and xeric zones) but not in the warmest and driest ones (Figure 3.2 A). Concerning forest leaf habit, EVI increase was significantly higher in expanding than regenerating needleleaf evergreen, mixed leaf habit forest and mosaic forests but not in broadleaf deciduous ones (Figure 3.3 A, Appendix 2 Table A2.9). The final EVI values recorded in 2015 showed similar trends for the different factors analyzed that those described for EVI increase (Figure 3.2 B and Figure 3.3 B, Appendix 2 Table A2.10).

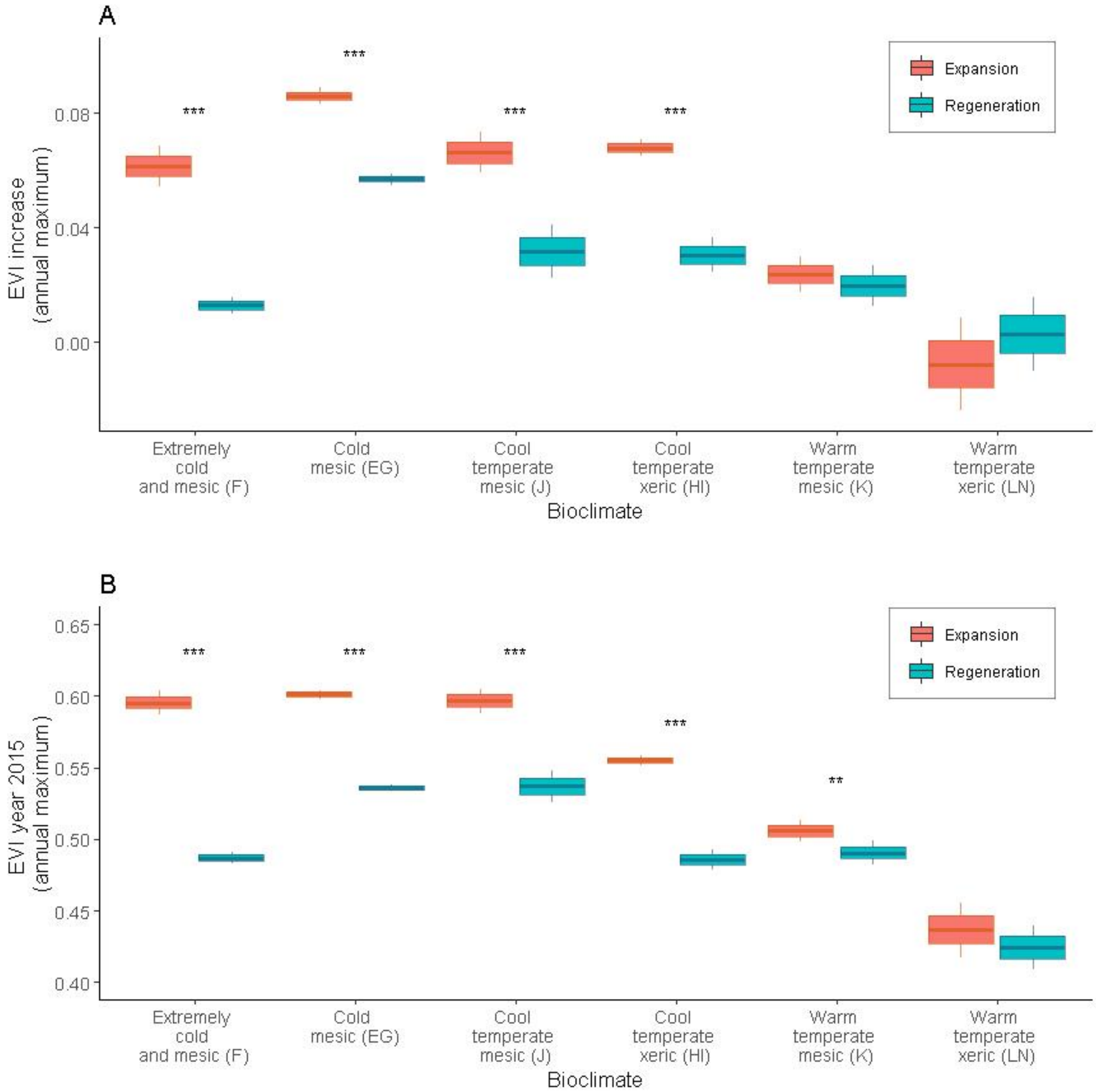

Figure 3.2. Interaction plot of the estimated marginal means of the Enhanced vegetation index (EVI) increase between 1992 and 2015 (A) and EVI annual maximum for the year 2015 (B) for forests arising from expansion or regeneration processes in different bioclimatic regions. Asterisk denotes significate differences from pairwise contrasts between expansion and regeneration for each bioclimate: '*' = 0.05, '**' = 0.01, '***' = 0.001.

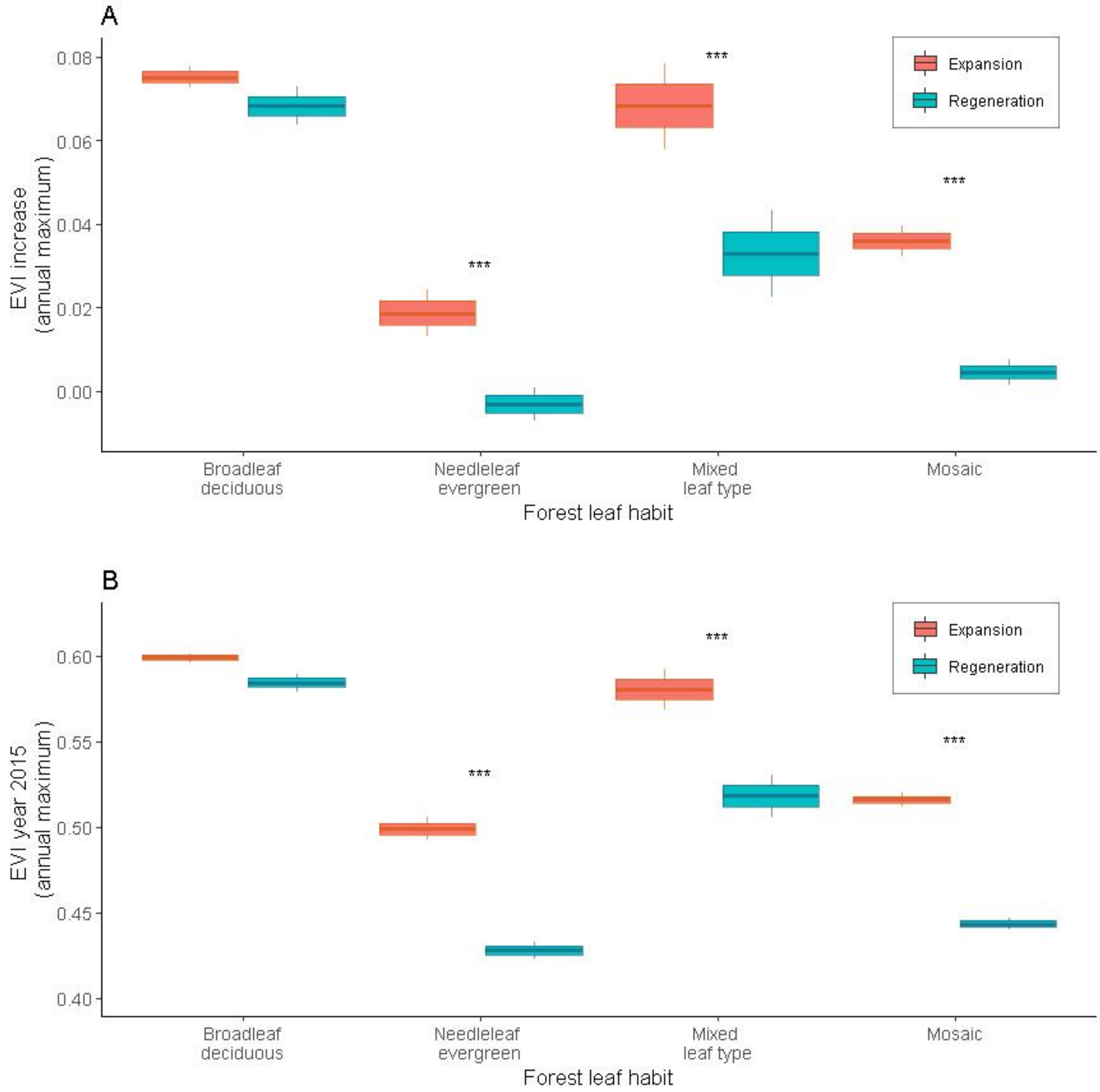

Figure 3.3. Interaction plot of the estimated marginal means the Enhanced vegetation index (EVI) increase between 1992 and 2015 (A) and EVI annual maximum for the year 2015 (B) for expansion and regeneration and for the main forest leaf habit (broadleaf deciduous, needleleaf evergreen, mixed leaf type and mosaic forests). Asterisk indicates significate differences from pairwise contrast between expansion and regeneration for each forest leaf habit: '*' = 0.05, '**' = 0.01, '***' = 0.001.

3.5 - Discussion

This study combined land cover and multi-temporal MODIS data to provide, apparently for the first time, a complete view of the two forest area increase processes (expansion and regeneration) leading recent changes in forest area in Europe, their main associated drivers and the potential implications for forest productivity through EVI. Results emphasize that forest expansion (i.e. forest establishment in former agricultural land) is still occurring across Europe but especially in Mediterranean and Eastern temperate regions, while regeneration (i.e. forest regenerated after disturbance) is particularly relevant in the boreal region. Moreover, the analysis of EVI temporal trends reveals that expanding and regenerating forests show different EVI values which suggest differences on productivity among the two forest area increase processes, depending also on climate and forest leaf habit type.

Forest area increase in Europe since the beginning of the 20th century has been widely acknowledged (Kauppi et al. 2018), while recent forest dynamics have been less documented. According to our results, forest area in Europe is still increasing, with an average net increase of 0.06% per year. This value is consistent with that of Keenan et al. (2015), who reported an annual increase of area of 0.08% for the same period but using the Global Forest Resources Assessment (FRA) data from the United Nations. However, compared to previous periods we observe a noticeable slowdown in increase rates: i.e. a 0.50% annual increase between 1950 and 2000 in Gold et al., (2006) and 0.42% between 1950 and 2010 in Fuchs et al., (2015). Despite the difficulties of comparing studies based on different methods, it should be noted that Gold et al. (2006) already detected a slowdown in forest area increase since the beginning of 1970s in most European regions. This suggests that forest area in Europe is reaching some stabilization in recent decades as indicated in the recent FAO (2020) report.

The study also shows that recent forest area increase is widely distributed across Europe and that most of this increase corresponds to forest expansion. Indeed, almost two thirds of recent forests occur in former agricultural land, especially under 60º of latitude in eastern and southern Europe (Figure 3.1 A). Thus, forest expansion is closely related to bioclimatic (temperature and rainfall) and socio-economic factors, as stated in our hypothesis. Several studies have attributed forest expansion in Europe to the application of the Common Agricultural Policy (CAP) since 1990, which forced agriculture to be more competitive in global markets causing massive cropland abandonment in the Eastern and in Mediterranean countries (Leal Filho et al. 2017). Probably, because of these geographic patterns, almost a half of forest expansion corresponds to broadleaf deciduous forests and one third to mosaic forests, which are dominant in Eastern Europe and in the Mediterranean Basin, respectively. However, it may also be related to the ecological traits that favor preeminent colonization by broadleaves over needleleaf species in expanding forests, such as dispersal mediated by vertebrates that facilitates the colonization of distant areas (Montoya et al. 2008). Moreover, regional studies have shown an increase in broadleaf forests due to the greater capacity of these species to respond to a wide array of disturbances through resprouting and their higher competitive ability (Vayreda et al. 2016; Petersson et al. 2019). Concerning the abundance of mosaic-like forests as the ones mostly expanding in the Mediterranean Basin, this may be due to the fact that recently established forests in former croplands in this region are often sparse and low-density forests made up by a mixture of conifers (Pinus spp.) and broadleaf evergreen (Quercus spp.) species (Basnou et al. 2016; Ruiz-Carbayo et al. 2020).

Although forests originated from regeneration occur in all regions, their area is mostly concentrated in northern Europe above 60º of latitude (Figure 3.1 B) thus suggesting that they are mostly related to the intense forest exploitation in Scandinavian countries (Ylitalo 2013). However, we cannot totally discard the role of extensive wildfires increasingly affecting the boreal regions in recent years (Krylov et al. 2014). Ultimately, the biogeographical pattern of forest expansion and regeneration is consistent with the distribution of economic activities in Europe (Kankaanpää and Carter 2004) and agrees with the land cover changes described in other studies (i.e. Prishchepov et al. 2012; Fuchs et al. 2015; EEA 2017).

The fact that the increase in forest area from 1992 to 2015, either by expansion or by regeneration, is positively related to initial forest cover percentage indicates that these processes mostly occur in partially forested landscapes. Additionally, our results show that this increase – especially forest expansion- mostly takes place in the most diverse landscapes, such as those dominated by agroforestry mosaics (Keenan et al., 2015). Both results support the idea that forest area increase may contribute to landscape simplification across Europe, where main land cover categories (i.e. intensive agriculture, intensive forestry or natural vegetation) are becoming more dominant and concentrated in different regions (Jongman, 2002). In previous studies (Palmero-Iniesta et al. 2020) we observed that forest area increase in Europe was leading to contrasting landscape patterns depending on previous forest cover: i.e. it promotes the coalescence among already existing forests in Northern and Eastern Europe, while it results in the proliferation of new forest patches in Western and Southern Europe.

Both forest expansion and regeneration in the boreal region show similar associations with climatic factors and the two processes are positively related to temperature, indicating that low temperatures are the main environmental constrain for forests and that the very low forest expansion is only taking place in the more suitable sites (Kumm and Hessle 2020). In the temperate region, forest expansion is negatively associated with temperature and positively associated with aridity index, probably reflecting the decline in cropland areas in Eastern Europe after the collapse of socialism (Kuemmerle et al. 2016). In the Mediterranean region, forest expansion is negatively related to the mean annual temperature, continentally and the aridity index reflecting a higher agricultural abandonment in northern and colder places (northern Spain, Italy, Greece in Kuemmerle et al. (2016). In this biome, conversely to norther latitudes in Europe (i.e. boreal zone), high temperatures seem to be limiting forest development in Mediterranean-type climates.

Concerning elevation, there is not a common pattern among climatic regions which may suggest that forest expansion into abandoned croplands is not only occurring in mountainous regions as it used to be in the past (Cervera et al. 2019). Forest regeneration in temperate and Mediterranean areas has a positive relation with elevation probably reflecting the exploitation of mountain forests in west Europe (Kuemmerle et al. 2016) and the regeneration after wildfires in mountain areas in the Mediterranean region (Díaz-Delgado et al. 2004).

A change in the type of cropland areas being abandoned is also reflected by the negative association of forest expansion from 1992 to 2015 with the distance to metropolitan areas in the temperate and Mediterranean region. This indicates that forests are expanding nearby highly populated areas where the traditional agricultural mosaic is being lost and the interface urban-forest increases (Basnou et al. 2016). This may have important consequences for the type of services provided by these new forests as they may turn into disservices such as favoring the spread of wildfires into urban areas (Mell et al. 2010; Basnou et al. 2013) or the presence of some problematic fauna (i.e. wild boar in Cahill et al. 2012)

As stated in the second hypothesis, from a functional perspective our analyses of EVI trends suggests that productivity is higher in forests resulting from expansion than in those resulting from regeneration, although this effect only occurred in some climatic zones and forest leaf habit types. The fact that the positive effects of agricultural land use legacies in forest growth are only significant in the coldest and wet climates but not in the hottest and driest ones (Figure 3.2), suggests that forest may not take profit of soil biological and physicochemical legacies when water is a limiting factor (Matías et al. 2011). Previous studies showed that temperate forests in former agricultural land may exhibit higher growth than long-established ones, particularly on wet years (Alfaro-Sánchez et al. 2019). Conversely, they perform worst under adverse climatic conditions (drought), probably owing to less appropriate water-related functional traits (lower wood density in Alfaro-Sánchez et al. 2019, less developed root system in Mausolf et al., 2018). Such a higher sensitivity to negative climatic events may result on a null effect of the benefits of a former agricultural land use in warm and temperate climates that are facing an increase in the frequency, intensity and duration of droughts (Allen et al. 2010). Concerning, tree species leaf habit the fact that EVI was significantly higher in expanding needleleaf evergreen forests but not in broadleaf deciduous ones may be due to the predominance of the former forest leaf habit in the coldest climatic areas, where the positive effects of land use legacy are also observed. This highlights the role that colder and wet regions in Europe may have in the future for carbon sequestration in contrast with the warmer regions where increasing water availability shortage may dramatically constrain forest growth (Lindner et al. 2010). On the other hand, EVI was significantly higher in expanding mixed and mosaic forests, probably by the influence of needleleaf evergreen in the first and that of higher germination of herbs in the second ones (Baeten et al. 2010).

3.6 - Conclusions

Our study highlights that forest area is still increasing in Europe and a great extent of this pattern is caused by forest expansion into former agricultural areas, although this process is mostly restricted to Eastern and Southern Europe. Forest expansion may increase forest connectivity, thus improving biodiversity conservation and forest resilience by increasing the functional diversity of forested landscapes (Messier et al. 2019). Moreover, it might enhance carbon sequestration in light of the greater growth and productivity often suggested for recent forests compared to long-established ones (Vilà-Cabrera et al. 2017; Alfaro-Sánchez et al. 2019). Yet, the geographical location of expanding forests in Europe highlights the paradox that a great part of this process is occurring in less productive areas (Sluiter and De Jong 2007; EEA 2012) where the benefits from an agricultural land use legacy may be less important compared to other constrains (i.e. water availability). This may have important implications for forest diversity and conservation, but also in the decision-making process that should set up the ecosystem services to be preserved and promoted beyond the usual of timber production and carbon sequestration (Roces-Díaz et al. 2018). In addition, the increasing expansion of forests near highly populated areas urges the need to develop management practices to enhance the ecosystem services they may provide while minimizing potential disservices (Von Döhren and Haase 2015).

Chapter 4

The role of recent (1985–2014) patterns of land abandonment and environmental factors in the establishment of secondary forest and its growth in the Iberian Peninsula

4.1 - Abstract

This study used Landsat land cover maps, combined with European Space Agency aboveground biomass maps and topographic and climatic data, to explore recent (1985–2014) patterns of secondary forest establishment in the Iberian Peninsula and its implications for forest growth. Our results highlight the fact that the amount of secondary forest cover is increasing in the Iberian Peninsula at a rate (0.31% year-1) that is above the European average. Yet, our study also indicates a directional change in the emergence of secondary forests towards regions with higher water availability, lower elevations, less steep slopes, greater forest cover, and subject to greater drought events. Our results show that environmental factors affect forest growth in different ways that depend on the forest leaf-habit, with needleleaf secondary forests being least favoured by high temperature and precipitation, and broadleaf deciduous forests most negatively affected by drought. Finally, the combination of spatial patterns of secondary forest emergence and the response of different forest leaf-habits to environmental factors explain why more broadleaf evergreen than broadleaf deciduous and, especially, than needleleaf secondary forests, developed during the study period (1985–2014). These results will improve knowledge of forest dynamics in the Iberian Peninsula in recent decades and provide an essential tool for understanding the potential effects of climate warming on forest growth.

Keywords: *Droughts, forest expansion, land-cover changes, land-use change, rural abandonment, secondary forests*

4.2 - Introduction

Changes in land use and land cover are one of the main drivers of global environmental change given that they affect the properties of land surfaces, the provision of ecosystem services (Song et al. 2018) and, ultimately, the Earth's energy balance and biogeochemical cycles (Foley et al. 2005; Alkama and Cescatti 2016). Although deforestation is still one of the main manifestations of changes in land use and land cover, worldwide the net rate of forest loss decreased substantially in 1990–2020 due to a reduction in deforestation in certain countries and active and passive afforestation in others (FAO 2020).

As major reservoirs of terrestrial biodiversity, forests provide key ecological functions and services (Thompson et al. 2009). They store around 90% of terrestrial vegetation carbon (C) and regulate the most important terrestrial fluxes of C between the atmosphere and the biosphere (Bonan 2008; Le Quéré et al. 2018; Harris et al. 2021). In this context, the expansion of secondary forests – i.e. forests established in areas where a different type of land use had once predominated – has gained much attention owing to their role in carbon accumulation (Hooker and Compton 2003; Pan et al. 2011). For example, Fuchs et al. (Fuchs et al. 2015b) determined that afforestation and cropland abandonment had made the greatest contribution to carbon sequestration in 1950–2010 in Europe, while Pan et al. (Pan et al. 2011) report that the C sink of China's forests increased by 34% in 1990–2007 due primarily to newly planted forests. Finally, Vila-Cabrera et al. (Vilà-Cabrera et al. 2017) testify that the secondary forests established from 1956 onwards represent 22% of the total C pool in Iberian forests.

Furthermore, it has been suggested that forests established on former agricultural land may differ from long-established forests in terms of species composition and their structural and functional characteristics (Espelta et al. 2020). These forests may benefit from land-use legacies since their soils tend to be richer in nutrients (Compton and Boone 2000) and exhibit greater enzymatic activity (Fichtner et al. 2014), which could explain why some secondary forests have higher growth rates than long-established forests: 35% greater plant biomass in (Freschet et al. 2014); 25% higher growth in (Vilà-Cabrera et al. 2017); but they may also be more sensitive to climatic processes due to differences in functional attributes (lower wood density in (Alfaro-Sánchez et al. 2019); finer root morphology in (Freschet et al. 2014; Mausolf et al. 2018). This may be of special relevance in a context of climate change as drought and heat-induced stress in trees could lead to a reduction in tree growth (Zhao and Running 2010) and to an increase in mortality rates (Allen et al. 2010, 2015). Moreover, the effect of land-use legacies on aboveground production in secondary forests may be the result of complex interactions between tree functional attributes and climate (e.g. there will be no advantageous effects due to land-use legacies under arid climates in (Palmero-Iniesta et al. 2021)). Finally, directional changes in forest composition have been reported consisting of a greater abundance of drought-tolerant species in recent decades (Trugman et al. 2020; García-Valdés et al. 2021) and an increase in broadleaf compared to needleleaf forests due to the greater competitive ability of the former species (Vayreda et al. 2016; Petersson et al. 2019). This may lead to less aboveground forest productivity owing to lower growth rates in drought-tolerant forest species (Ouédraogo et al. 2013; Zhang et al. 2018), although a greater resilience to water stress may allow these species to maintain their productivity under dry and warm conditions (Fauset et al. 2012).

Spatial patterns of land abandonment are strongly related to site biophysical conditions, which may ultimately determine secondary forest productivity (Thompson et al. 2009; Jucker et al. 2014). Indeed, topography and climate both influence the recruitment, growth and mortality of tree species, and also affect whole plant communities (Tsujino et al. 2006; Thompson et al. 2009; Ruiz-Benito et al. 2017). Thus, it is important to study current forest expansion rates and their spatial patterns. It is also vital to understand how local factors affect secondary forest growth by taking into account different forest leaf-habits to be able to evaluate the potential of mitigation strategies aimed at maximizing carbon sequestration by forests (Zhang et al. 2018).

The purpose of this study was thus to determine patterns of secondary forest establishment in the Iberian Peninsula in 1985–2014, and examine how environmental factors affect the growth of this type of forest, which will provide evidence of their potential to act as carbon sinks. The Iberian Peninsula is an appropriate study area given, on the one hand, the rapid and massive expansion of secondary forests that occurred there during the second half of the 20th century (Baśnou et al. 2013; Lasanta et al. 2017; Vilà-Cabrera et al. 2017) and, on the other, its diverse topoclimatic conditions and the increasing number of drought episodes in recent decades (Vicente-Serrano et al. 2014).

We thus established three main hypotheses: i) the distribution and magnitude of cropland abandonment is closely determined by the environmental characteristics that limit their productivity and, as such, secondary forests will appear first in poorly productive areas (i.e. areas with unfavourable climatic and topographic conditions) since the most productive areas will be the last to be abandoned; ii) due to the recent increase in drought frequency and severity in recent decades, a greater amount of drought-tolerant broadleaf secondary forests than needleleaf forests will develop; and iii) drought events will have a greater impact on needleleaf secondary forest growth than on broadleaf secondary forest growth.

4.3 - Materials and Methods

4.3.1 - Study area

The study was performed in the Iberian Peninsula (202,067 km^2; SW Europe), a region with great climatic and topographic diversity (Figure 4.1) and three biogeographic regions, namely, Mediterranean, Atlantic and Alpine. Mean annual temperatures range from 18 ºC (on the southern coast) to 1ºC (in mountainous areas), while mean annual rainfall varies from 340 mm to over 2400 mm (Topoclimatic Drought Atlas of the Spanish Iberian Peninsula; Domingo-Marimon 2016). The extraordinary number of mountain ranges (from sea level to more than 2600 m a.s.l) and steep coastal-inland gradients also contribute to the great environmental heterogeneity of this region. Forests cover 35% of the Iberian Peninsula (EEA Report No 5/2016). Broadleaf and needleleaf evergreen species are dominant in the study area; broadleaf deciduous forests are less frequent and mostly found in the Atlantic region and in mountainous areas (see Figure 4.1). The main needleleaf evergreen species in Mediterranean areas are *Pinus halepensis* and *P. pinea*, while *P. nigra* occurs in inland upland areas. *Abies alba* and *P. uncinata* are common in Alpine areas in the Pyrenees, while *P. sylvestris* is found widely from upland Mediterranean to Alpine areas. Broadleaf evergreen forests are dominated by *Quercus ilex* and *Q. suber* in lowland sites up to the limit of montane habitats, while *Q. coccifera* becomes increasingly common as continentality rises. Broadleaf deciduous forests mainly consist of *Q. humilis, Q. faginea*, and *Q. pyrenaica* in Mediterranean lowlands and uplands, and *Fagus sylvatica* in the Atlantic region.

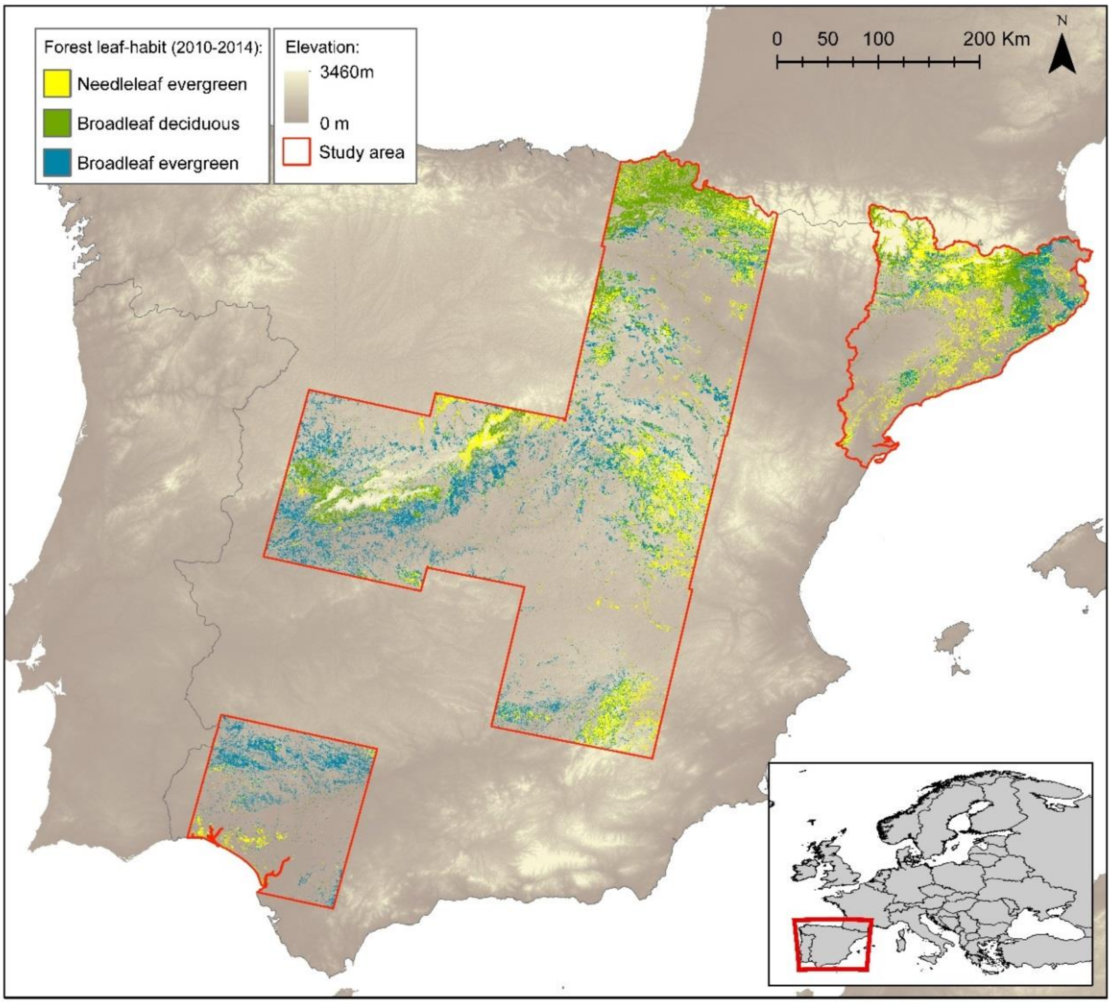

Figure 4.1. Secondary forest distribution in 2010–2014 by the main forest leaf-habit types in the Iberian Peninsula.

4.3.2 - Data sources

To detect secondary forest emergence we used Landsat images processed and classified by the Grumets Research Group at the Universitat Autònoma de Barcelona (www.ogc3.uab.cat/acapi/wms/USOS/index.htm; González-Guerrero and Pons 2020). We ensured that maps were only generated for those years with enough good-quality data and periodicity (i.e. from mid-80s). In order to have enough images for map classification, i.e. images that enabled us to identify correctly phenological variation in land cover categories, we worked with quinquennial periods and generated maps for every quinquennia from 1985 to 2014. From these maps, we selected a set of available scenes from the Landsat orbits (197, 198, 200, 201 and 202) distributed along a latitudinal gradient representative of the climatic variability present in the Iberian Peninsula (see Figure 4.1).

Secondary forest growth was estimated by relating the accumulated biomass to establishment date using the global maps of aboveground biomass from 2017 (100 m resolution) generated by the European Space Agency (ESA) Climate Change Initiative Biomass project (Santoro and Cartus 2019). Aboveground biomass (AGB) is defined as the amount of living biomass (organic matter) stored in vegetation above the soil including stem, stump, branches, bark, seeds and foliage, expressed as the weight of dry matter per unit ground area (i.e. Mg/ha-1) (ESA 2019).

4.3.3 - Detecting secondary forest establishment and growth throughout the study period

We detected new secondary forest that had appeared in the study period by combining maps relating to the different quinquennia. We defined secondary forest as those forests established on cropland or grassland that are a product of forest expansion, that is, of forests established in areas that for many years previously had been dominated by a different type of land use (FRA 2018). We did not consider as secondary forest the transition from shrubland to forest since this has been explored by previous studies (Palmero-Iniesta et al. 2021) and because this transition mostly corresponds to the regeneration of previously felled or disturbed forests(Gerard et al. 2010; Baśnou et al. 2013).

For each quinquennium, we identified pixels belonging to forest land cover that were cropland or grassland in the previous quinquennium (see classes in Appendix 3 Table A3.1). To avoid including pixels that had been falsely classified as new forests, we only selected forests in a quinquennium that appeared as forests in two consecutive subsequent quinquennium (i.e. cropland or grassland in 1995–1999 that was classified as forest in both 2000–2004 and 2005–2009). To account for potential differences related to leaf-habit types, we determined surface changes and annual rates of change for the main leaf habit types: i) broadleaf deciduous, ii) broadleaf evergreen and iii) needleleaf evergreen.

Finally, the growth of the selected secondary forests was assessed by estimating their biomass in relation to their age. Biomass was obtained by merging the detected secondary forests in 2010–2014 with the ESA aboveground biomass layer. We previously resampled the secondary forest dataset at a pixel size of 100 m (using the modal criterion of the most represented value) to fit with the resolution of the biomass dataset. Forest age was assessed in years as the difference between the final quinquennium (2010–2014) and the quinquennium of forest establishment.

4.3.4 - Environmental drivers of secondary forest establishment and growth

To assess the environmental context of the secondary forests in the study area, we selected a set of potential drivers of forest expansion and growth (Geri et al. 2010; Lindner et al. 2010; Vidal-Macua et al. 2017a; Palmero-Iniesta et al. 2020, 2021). Based on previous work (e.g. (Bonan 2008; Vanderwel et al. 2013; Palmero-Iniesta et al. 2020, 2021)), we chose a series of climatic, topographic and landscape factors known to affect forest composition, structure and growth.

Climatic variables

To characterize the main climatic conditions, we used the topoclimatic drought atlas of the Spanish Iberian Peninsula (Domingo-Marimon 2016), which includes monthly aggregates from 1950–2015 at a spatial resolution of 100 m of rainfall, mean temperature and Standardized Precipitation Evapotranspiration Index (SPEI) as an indicator of water deficit. We calculated the mean temperature (°C) and rainfall (mm) annually and seasonally for 1950–2015 (hereafter, the historic climate) and for the time that the secondary forests growth (hereafter, the recent climate). We used SPEI values calculated at a timescale of 12 months, which is an optimal and appropriate scale for studying the long-lasting dry periods that characterize hydrological droughts (Ivits et al. 2014; Li et al. 2015). We defined a drought event as a period of consecutive months in which SPEI values were equal or lower than −1, as suggested in the literature (Agnew 2000; Zargar et al. 2011; Li et al. 2015). For a statistical quantification of drought episodes, we calculated commonly used drought parameters (Mishra and Singh 2010; Zargar et al. 2011) for both the historic and recent climatic periods: i.e. drought frequency (number of episodes during a period divided by period; events/year), mean drought duration (average duration of drought events in the period; months), mean drought intensity (average of the mean SPEI values during the period of drought events), and mean drought severity (average of the accumulated SPEI values during the period of drought events).

Topography

We used the Digital Elevation Model of the Iberian Peninsula at a spatial resolution of 90 m generated by the Kraken group from the University of Extremadura (Reuter et al. 2007) to characterize the mean elevations (m) and slopes (degree) of emerging secondary forests.

Forest cover

Previous studies have observed that the amount of forest cover in the landscape has a positive influence on forest expansion and determines the distribution patterns of secondary forests (Palmero-Iniesta et al. 2020, 2021). Thus, we determined the percentage of forest land cover at the beginning of the study period by counting the number of forest pixels in a radius of 1 km of each secondary forest pixel. Finally, we resampled the spatial resolution of the abovementioned land-cover raster datasets from 30 m to 100 m to coincide with the resolution employed in most environmental datasets generated using the majority criterion (assigning the value of each pixel based on the most abundant value). We overlapped multiple environmental maps – after resampling and changing the coordinate systems wherever necessary – to determinate environmental values in all cells classified as secondary forests.

4.3.5 - Statistical analyses

We performed an ANOVA analysis of variance to test whether or not the environmental conditions of secondary forest establishment differed between forest leaf-habit types (broadleaf deciduous, broadleaf evergreen and needleleaf). Data were log-transformed when necessary to meet the assumptions of normality. Where significant differences occurred ($p < 0.05$), comparisons between means were performed using Tukey's HSD multiple comparison test.

We then performed a general linear model (GLM) to test the association between the secondary forest's time of establishment (quinquennium of establishment) and the environmental variables described above. For this analysis, we took the historic climatic variables from the period 1950–2015 as representative of the climatic conditions in the area. We decided to work with the absolute value of the severity and intensity of drought factors – all values were negative – so that the higher the value, the greater the severity or intensity of the drought, which facilitated the interpretation of the effect in the model. To prevent multicollinearity, we performed a correlation matrix with a Spearman rank test (Appendix 3 Figure A3.1) to avoid using highly correlated variables ($r < |0.7|$). Thus, when variables were correlated, we chose the best variable by selecting the one with the strongest effect on the response variable. The simplest general lineal models were selected following a dredge procedure using the MuMIn R package (Barton and Barton 2019), which removed non-significant variables from the general model, to assess significant changes in model predictions using the Bayesian information criterion (BIC). From the models with a difference in BIC relative to BICmin < 2, we chose the most parsimonious model by selecting the model with fewest predictor variables following the procedure described in Crawley (Crawley 2007a).

To study forest establishment, we performed ANOVA analyses of variance for each forest age to test whether or not secondary forest biomass differed between forest leaf-habit types, and performed pair-wise comparisons of means using Tukey's HSD tests wherever significant differences occurred ($p<0.05$).

Finally, we performed a GLM with lognormal distribution to test the association of environmental variables and secondary forest growth (AGB). We first selected those cells (100 m) in which secondary forest cover was 100% in the quinquennium 2010–2014. For this analysis, we used the recent climatic variables calculated from the year the secondary forest became established to the end of the study period (2015) to describe the climatic conditions in which secondary forests grew. Here too we used absolute values of drought severity and intensity factors. We employed the same criteria to prevent multicollinearity and avoid highly correlated variables as used in the abovementioned model (Appendix 3 Figure A3.2). Furthermore, we took into account forest leaf-habit as a factor and the environmental interactions with the forest leaf-habit. The simplest general lineal model was selected using the same criterion as described above. Finally, we check spatial autocorrelation of the model residuals to ensure that explanatory variables absorb any possible spatial autocorrelation of response variable (F. Dormann et al. 2007).

4.4 - Results

4.4.1 - Secondary forest establishment

The total forest surface area (i.e. the balance between gain and loses) in the study area increased by 7.7% in 1985–2014, which represents a mean annual increase of 0.31%. Broadleaf deciduous (BD) forests showed the highest increase from their initial surface area (30.3% during the study period, 1.21% annually). Broadleaf evergreen (BE) forests increased by 5.2% (annual increase 0.21%), while needleleaf forest (NE) showed no changes in their surface area.

Forest establishment occurred at an annual rate of 0.60 ± 0.15%. BD forests had the highest annual establishment rate (1.09 ± 0.21%), followed by BE (0.81 ± 0.32%) and NE (0.24 ± 0.11%). By the end of the study period, 14.8% of the forest surface area corresponded to secondary forests that had emerged in 1985–2014 (54.2% of BD, 31.1% of BE, and 14.7% of NE forests). Figure 4.2 shows spatial distribution of secondary forests by forest leaf-habit.

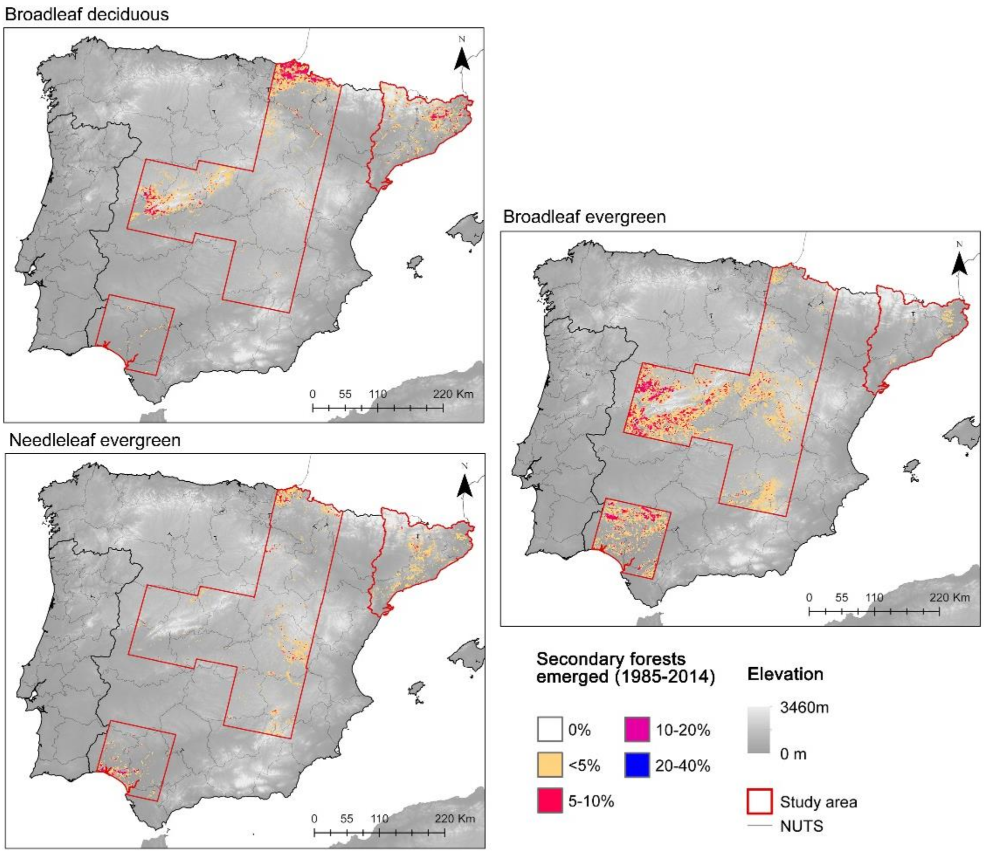

Figure 4.2. Secondary forest distribution and magnitude (percentage of 10 km pixels) in 1985–2014 by the main forest leaf-habit types in the Iberian Peninsula.

Secondary forest establishment occurred in areas with the following mean characteristics: elevation: 667 ± 0.8 m; slope: 6.2 ± 0.0%; and previous tree cover: 30.3 ± 0.05%. The mean climatic conditions of these areas were: annual temperature: 13.6 ± 0.01 ºC; annual precipitation: 710 ± 0.49 mm; 0.46 ± 0.00 droughts/year with 4.74 ± 0.00 months of duration; intensity of SPEI values: -1.30 ± 0.00; and severity of SPEI values: -6.91 ± 0.00. As shown in Table 4.1 for forest leaf-habit, BD secondary forests became established in areas with higher average annual precipitation rates, steeper slopes and more forest cover but with a lower mean annual temperature than BE and NE secondary forests. BE secondary forests became established at lower elevations, on less steep slopes and lower average annual precipitation, but with higher mean annual temperatures and greater drought intensity and severity than BD and NE secondary forests. NE secondary forests became established in areas of greater environmental variability with less drought duration, intensity and severity than either BD or BE.

Table 4.1. Mean values of environmental variables for sites with secondary forests and differences between secondary forest leaf-habit: broadleaf deciduous (BD), broadleaf evergreen (BE) and needleleaf evergreen (NE). Letters show significantly different means at p<0.05:

	Elevation (m)		**Slope (%)**		**Forest cover (%)**	
All	**667 ± 0.8**		**6.17 ± 0.01**		**30.3 ± 0.05**	
BD	681 ± 1.5	a	8.26 ± 0.02	a	36.7 ± 0.10	a
BE	666 ± 1.1	b	5.25 ± 0.02	b	27.6 ± 0.06	b
NE	684 ± 1.8	a	6.05 ± 0.03	c	29.2 ± 0.11	b
	Mean annual temperature (Cº)		**Annual precipitation (mm)**		**Drought frequency (event/year)**	
All	**13.6 ± 0.01**		**710 ± 0.49**		**0.46 ± 0.00**	
BD	12.5 ± 0.01	a	895 ± 0.87	a	0.46 ± 0.00	a
BE	14.0 ± 0.01	b	654 ± 0.59	b	0.46 ± 0.00	a
NE	13.7 ± 0.01	c	623 ± 1.00	c	0.48 ± 0.00	b
	Drought duration (months)		**Drought severity**		**Drought intensity**	
All	**4.74 ± 0.00**		**-6.91 ± 0.00**		**-1.30 ± 0.00**	
BD	4.72 ± 0.00	a	-6.88 ± 0.00	a	-1.29 ± 0.00	a
BE	4.79 ± 0.00	b	-6.98 ± 0.00	b	-1.31 ± 0.00	b
NE	4.60 ± 0.00	c	-6.74 ± 0.00	c	-1.30 ± 0.00	c
	SPEI		**Longitude**		**Latitude**	
All	**0.004 ± 0.000**		**435901 ± 440**		**4453824 ± 369**	
BD	0.005 ± 0.000	a	552225 ± 786	a	4604454 ± 642	a
BE	0.005 ± 0.000	b	349954 ± 535	b	4401588 ± 436	b
NE	0.004 ± 0.000	c	526596 ± 899	c	4404518 ± 733	c

The best model for describing the environmental factors associated with the time of establishment of secondary forests in 1985–2014 is shown in Figure 4.3. The time of establishment of the secondary forests was positively associated with mean summer precipitation, the mean SPEI, the mean drought intensity — but negatively associated with slope and forest cover. Models showed significant interactions between forest leaf-habit and certain environmental factors: both BE and NE had a more negative interaction with elevation, forest cover and drought intensity than BD, while BE had a more negative interaction with slope than both NE and BD.

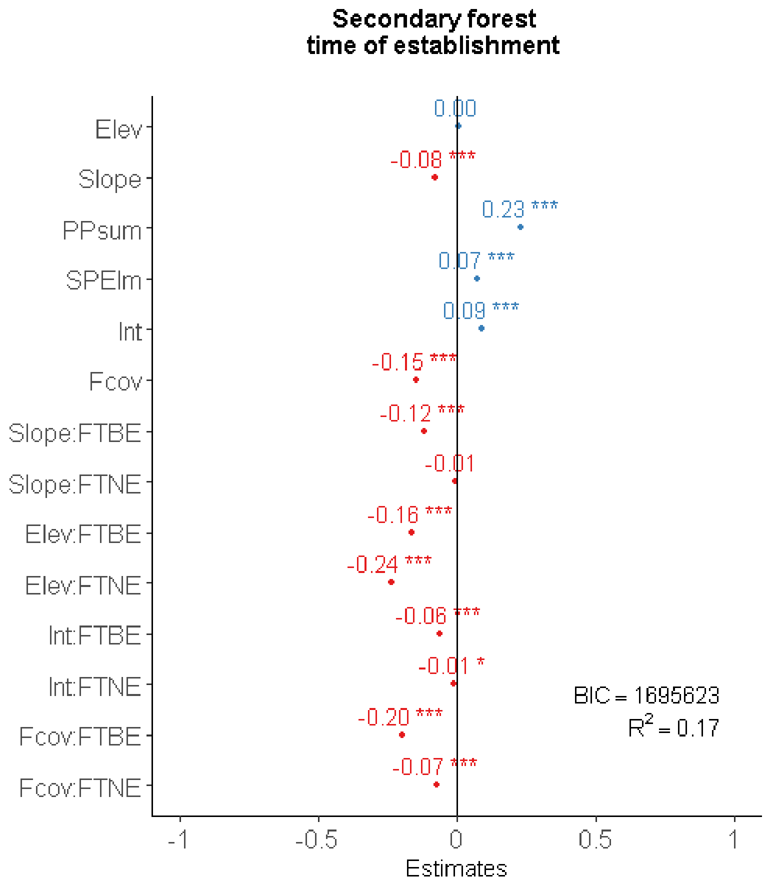

Figure 4.3. Estimates for the general linear model of the relationship between the time of secondary forest establishment (quinquennium) and elevation (Elev), slope, annual precipitation (PPm), mean annual SPEI values (SPEIm), drought intensity (Int), forest cover in a 1km radius (Fcov) and interaction (symbolized by ":") with forest leaf-habit (FT) broadleaf deciduous (BD), broadleaf evergreen (BE) and needleleaf evergreen (NE) secondary forests. Climatic values calculated from the mean of the period 1950–2015. Significance of p values is indicated by: '*' = 0.05, '**' = 0.01, '***' = 0.001.

4.4.2 - Secondary forest growth

Aboveground biomass (AGB) of secondary BD forests had mean values ranging from 61.3 ± 1.1 Mg ha^{-1} in the youngest forests (5 years) to 101.5 ± 0.9 Mg ha^{-1} in the oldest (25 years). These values were higher than those of BE and NE forests for most age groups (Figure 4.4). By contrast, secondary BE forests had the lowest AGB values for most age groups, ranging from 35.0 ± 0.7 Mg ha^{-1} to 58.3 ± 0.6 Mg ha^{-1}. Finally, NE secondary forests had mean AGB values ranging from 37.3 ± 1.4 Mg ha^{-1} to 77.9 ± 0.9 Mg ha^{-1}.

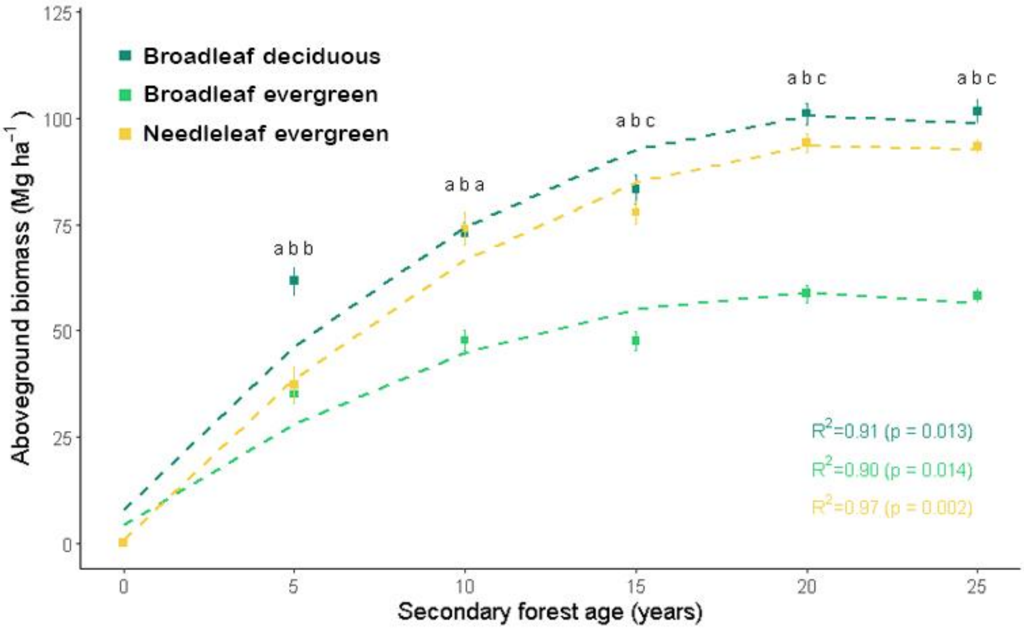

Figure 4.4. Average aboveground biomass (AGB) of secondary forests by age for the different forest leaf-habit types. Different letters indicate significant differences in AGB between forest leaf-habit types for the same age according to the Tukey's test ($p < 0.05$).

The GLM model for the effect of local environmental factors on the growth of secondary forests explained 42% of variance (Figure 4.5). The growth of secondary forests was positively associated with age, slope, forest cover, summer precipitation and mean annual temperature, but negatively associated with drought frequency and intensity. Additionally, BE had the lowest AGB, while NE had the highest AGB. In addition, the GLM revealed significant interactions between forest leaf-habit and climatic factors, that is, the positive effect of summer precipitation was higher for BE than for NE and BD, the positive effect of temperature was lower in NE than in BE and BD, while the negative effect of drought frequency and intensity was lower in BE and NE than in BD. Finally, both slope and summer precipitation had a negative interaction, which indicates that the greater the slope, the lower the positive effect of summer precipitation.

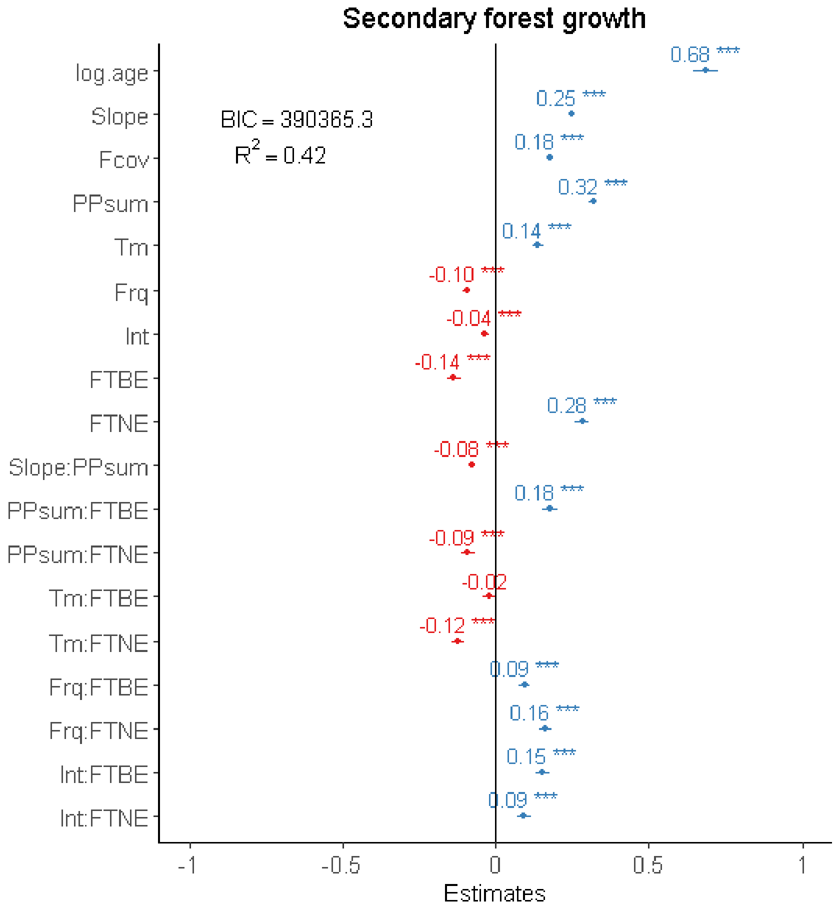

Figure 4.5. General linear model parameter estimates of the relationships between secondary forest growth (aboveground biomass; Mg ha^{-1}) and several explanatory variables, including the logarithm of age (log.age), slope, forest cover in a 1km radius (Fcov), mean precipitation in summer (PPsum), mean annual temperature (Tm), drought frequency (Frq), drought intensity (Int) and forest leaf-habit (FT) in broadleaf deciduous (BD), broadleaf evergreen (BE) and needleleaf evergreen (NE) forests. Interaction between factors is symbolized by " : " Climatic factors were calculated using the mean of the secondary forest establishment periods (from the quinquennium of establishment up to 2015). Significance of p values is indicated by: '*' = 0.05, '**' = 0.01, '***' = 0.001.

4.5 - Discussion

This study combined information from Landsat land-cover maps, ESA aboveground biomass maps from the CCI project, and topographic and climatic data to explore recent patterns of secondary forest establishment and growth in the Iberian Peninsula and their drivers. Results show that the establishment of secondary forests is still occurring in the Iberian Peninsula at a higher rate than the average rate reported for Europe (0.31 vs 0.08–0.06, respectively). They also indicate that secondary forests are increasingly becoming established in sites with better environmental conditions, as suggested by the directional change over time in their emergence in regions with higher water availability (i.e. higher average rainfall), and at lower elevations and on less steep slopes (Figure 4.3). This study also reveals the key role of summer precipitation, temperature, slope and forest cover, and the lesser role of drought events, on secondary forest growth. Finally, the results highlight the different response of forest leaf-habits to these environmental factors, which suggests that contrasting water economy strategies might favour the establishment and growth of broadleaf forests rather than needleleaf forests.

4.5.1 - Forest expansion in the Iberian Peninsula

According to our results, the forest surface area in the Iberian Peninsula is increasing at an average net rate of 0.31% year^{-1}, a rate that is much higher than the European average in recent decades (0.08% year^{-1} in 1990–2015 in (Keenan et al. 2015); 0.06% year^{-1} in 1992–2015 in (Palmero-Iniesta et al. 2021)) and closer to the European rate for the 20th century (0.50% year^{-1} in 1950–2000 in (Gold et al. 2006); 0.42% year^{-1} in 1900–2010 in (Fuchs et al. 2015a)). This reflects the current great dynamism of forests in the Iberian Peninsula (Regos et al. 2015), a tendency that may continue in the near future (Terres et al. 2015), compared to other regions of Europe where forest cover is stabilizing (Gold et al. 2006; Kuemmerle et al. 2016; FAO 2020). This phenomenon can be attributed to the massive cropland abandonment that occurred in southern (and eastern) Europe during the application of the Common Agricultural Policy (CAP) in 1988–2008, which forced agriculture to be more competitive in global markets (Gold et al. 2006; Fuchs et al. 2013; Lasanta et al. 2017; Leal Filho et al. 2017) and prompted the afforestation of former croplands. The program *Programa de Forestación de Tierras Agrarias* (FTA) had a great impact in Spain (Vadell et al. 2019).

The gross rate of secondary forest establishment determined in this study (0.60% year^{-1}) in 1985–2014 is generally consistent with the results reported by Vilà-Cabrera et al. (Vilà-Cabrera et al. 2017) for 1956–2007 (0.75–0.43% year^{-1}). Moreover, our results show that the secondary forest establishment rate differs according to the main forest leaf-habit types: NE had the lowest rate (0.24 % year^{-}

$^{-1}$) and represents only 14.7% of the total secondary forests, while BD and BE had higher rates (respectively, 1.21% and 0.81% year^{-1}) and represent 31.1% and the 54.2% of total secondary forests, respectively. This may be attributed to the prioritization of broadleaf species (i.e. *Quercus* spp.) in the FTA program: monospecific stands of broadleaf species represent 50% of the total afforested area in Spain since 1992, while stands of needleleaf species represent only 15% (Vadell et al. 2019). Nevertheless, it could also be due to the different responses of broadleaf and needleleaf species to the biophysical attributes of abandoned land, a question that we discuss in more detail below.

4.5.2 - Patterns of secondary forest establishment

According to our first hypothesis, the establishment of secondary forests is increasing over time in more favourable biophysical conditions, as shown by the GLM model. There is a directional change over time of secondary forest emergence towards regions with greater water availability (i.e. higher average summer precipitation and annual SPEI values) and lower elevations and less steep slopes (Figure 4.3). However, directional change in areas with greater drought intensity has been also detected. These changes over time suggest that, while global or external causes may trigger the abandonment of croplands and pastures, local or regional factors constrain the degree and location of the abandonment (Meyfroidt and Lambin 2011; Lasanta et al. 2017). Thus, in those regions where crop and pasture abandonment occurs, the first areas to be abandoned are the sites of least quality (e.g. in terms of climate limitations and slope steepness) that limit productivity and hamper the mechanization of tasks. Conversely, the directional change of forest expansion towards regions with a higher average drought intensity is difficult to interpret due to the heterogeneous spatiotemporal patterns of drought occurrence in the Iberian Peninsula (Vicente-Serrano 2006). Furthermore, although the average annual temperature and precipitation determine climatic conditions and thus the potential agricultural productivity and land abandonment (Meyfroidt and Lambin 2011; Lasanta et al. 2017), drought events may not have this effect because of their episodic occurrence over both space and time (Páscoa et al. 2017). In any case, the positive effect of drought intensity could be a collateral effect of the directional trends of forests towards lower elevations and thus higher annual temperatures, given that temperature rises play a key role in drought intensity in the Iberian Peninsula (García-Valdecasas Ojeda et al. 2021).

In addition, the effects of topographic factors interact with forest leaf-habit as indicated above (Figure 4.3). A decrease in forest establishment over time with elevation was detected in BE and NE but not in BD. We attribute this to the fact that BD forest distribution in the Iberian Peninsula is mostly constrained to mountain ranges with higher precipitation rates than surrounding lowland areas enjoying a typical Mediterranean climate (Gavilán et al. 2018). By contrast, NE secondary forest emergence has decreased most with elevation over time, probably because this forest leaf-habit has the widest altitudinal distribution, ranging from the *Abies alba* and *P. uncinata* stands at high elevations to the *P. halepensis* forests that dominate in lowlands. On the other hand, the directional change of secondary forest emergence towards lower slopes is far more evident in BE than in NE and BD. This may be due to the fact that secondary BE forests (i.e. dominated by *Quercus ilex*) are distributed from near the coast to the upper montane limit, and so the pattern of establishment may be better described by slope than by elevation.

We also detected that the time of establishment of secondary forests is negatively related to forest cover in the surrounding area, probably due to the change in forest emergence towards landscapes with lower elevations and less steep slopes. This may also explain why the negative effect of forest cover on secondary forest emergence is more negative in BE and NE than in BD secondary forests, given that the latter are mostly found in upland areas. In previous studies we detected a positive relationship between previous forest cover percentage and forest expansion (Palmero-Iniesta et al. 2021), which we attributed to the concentration of land abandonment in landscapes dominated by agroforestry mosaics (Keenan et al. 2015; Palmero-Iniesta et al. 2021). In addition, reforestation is more probable that occurs in regions with low forest cover, poor land suitability for agriculture, but good connections to wood markets (Meyfroidt and Lambin 2011).

4.5.3 - Secondary forest growth

The GLM assessing the effects of the diverse factors on forest growth explains 42% of the variability of secondary forest growth (Figure 4.5). As expected, age has the greatest effect on forest growth, although environmental and forest leaf-habit factors do also have important implications for forest growth.

Summer precipitation seems to be a key element in forest growth in the study area (Pasho et al. 2011), which is very dependent on the cumulative spring and summer water deficit (Vicente-Serrano 2007). This also depends on the forest leaf-habit, the effect being higher in broadleaf – especially evergreen – than in needleleaf forests. Our results corroborate the finding that under warm climatic conditions broadleaf species tend to be much more competitive than needleleaf species if soil moisture is available (Blanco et al. 1997), as their roots are able to penetrate into the deep-water table (Sardans et al. 2004). In addition, secondary forest growth is also positively related to mean annual temperature, this effect being greater in broadleaf than in needleleaf forests. This agrees with previous studies (Gómez-Aparicio et al. 2011; Coll et al. 2013) and can be attributed to the contrasting water economy strategies in broadleaf and needleleaf species (Carnicer et al. 2013): broadleaf – mainly oak species – have less strict stomatal control, which allows them to assimilate carbon for longer during warmer and drier periods; on the other hand, needleleaf – i.e. pine species – typically have more isohydric behaviour and reduce their stomatal conductance to a minimum during the warm and dry seasons (Klein 2014; Bartletta et al. 2016).

Our model also reveals a negative effect of the parameter of drought frequency and intensity on secondary forest growth. The magnitude of this effect depends on the forest leaf-habit, and the response to drought in BD secondary forests is more pronounced than in BE and NE. This may be caused by the fact that BD secondary forests in the study area are mainly found in the north of the Iberian Peninsula and consist in part of species at the southernmost limits of their ranges (e.g. *Fagus sylvatica* and *Quercus humilis*) that may have a lower buffering capacity than drought-tolerant species (Ivits et al. 2014). Moreover, recent studies suggest that beech forests established on former agricultural land have higher growth rates due to better soil attributes (i.e. higher N and P content and mineralization rates), which also implies lower wood density (Mausolf et al. 2018; Alfaro-Sánchez et al. 2019). This may also mean that BD secondary forests may be particularly vulnerable to drought-induced cavitation (Hacke et al. 2001). On the other hand, our model indicates that the growth of BE secondary forests is the least affected by drought frequency, while the growth of NE secondary forests is the least affected by drought intensity. Once again, variations in water-use strategies between the different leaf-habits may be key for understanding the response of ecosystems to average climate and drought episodes (Carnicer et al. 2013). Needleleaf species typically avoid drought by drastically reducing stomatal conductance at the first sign of water deficit (Ferrio et al. 2003; Klein et al. 2013), which implies that their growth is affected by drought frequency (Vicente-Serrano 2007; Allen et al. 2010) but not by intensity given that they will stop growing under a threshold of water deficit, thereby avoiding the adverse effects of intensity. Conversely, BE species usually maintain higher stomatal conductance even at low leaf water potentials (Ferrio et al. 2003; Klein et al. 2013), which may explain the higher effect of drought intensity on BE secondary forest growth. Despite this specific hypothesis, the contrasting effects of drought on the growth of secondary forests of different leaf-habits should be interpreted with caution as local adaptation processes, phenotypic plasticity and specific structure and composition of secondary forests may also greatly influence tree growth responses to temperature and drought (Gómez-Aparicio et al. 2011; Carnicer et al. 2013; Doblas-Miranda et al. 2017; Helman et al. 2017; García-Valdés et al. 2021).

In addition, our results suggest that slope has a strong effect on secondary forest growth. Different effects of slope on forest growth have been reported (Tateno et al. 2004; Ming et al. 2011; Coll et al. 2013; Laamrani et al. 2014; Helman et al. 2017) and attributed to associated biophysical properties (i.e. soil depth, solar radiation and mean elevation). Our results indicate a positive effect of slope on secondary forest growth, thereby suggesting that there has been more growth in upland areas than in lowland plains. This may be because land abandonment has mostly been prompted by low productivity (i.e. climatic limitation or soil degradation) in plains and topography (i.e. difficult access and a constraint on mechanization), and not necessarily by productivity in upland areas (Lasanta et al. 2017; Vidal-Macua et al. 2018). Our findings also reveal that the positive effect of summer precipitation on growth decreases as slope gradients increase, which suggests that forests in plains may grow under arid and semiarid conditions (Nainggolan et al. 2012) and thus that forest growth is most dependent on summer precipitation. Finally, the model shows that growth is higher in needleleaf than broadleaf secondary forests probably due to the lower wood density and faster growth rates in the former forest type (Gómez-Aparicio et al. 2011; Poorter et al. 2012).

4.6 - Conclusions

Our results show that forests continue to expand in mainland Spain at a rate that is above the European average. Although the analyzed period was not very long (25–30 years), a change in the conditions under which these secondary forests are being established is observable over time (greater water availability, on lower elevations and less steep slopes, and with less forest cover). This affects both the type of forests (leaf-habit) that are expanding in the Iberian Peninsula and their growth rates: compromise needlelef growth and establishment and favouring the establishment of broadleaf forests, as the latter cope better with warm temperatures, benefits more from summer precipitation and its dispersal mediated by vertebrates may facilitates the colonization of less forested landscapes (Montoya et al. 2008; Vayreda et al. 2016; Vidal-Macua et al. 2017a). This may have advantages for forest functioning under a context of climate change, as broadleaf evergreen species have stable production in wet and dry periods (García-Valdés et al. 2021) and are highly resilient to droughts (Carnicer et al. 2013) and wildfires due to their ability to reshoot (Paula et al. 2009; Fernandes et al. 2011). However, this may mean that there will also be a global reduction in the rate of carbon fixation by secondary forests in the Iberian Peninsula, as forests that are more tolerant to drought tend to be less productive (Zhang et al. 2018; García-Valdés et al. 2021). Finally, these results may help devise appropriate management policies, i.e. the promotion of forest diversity and richness based on a wide range of drought-tolerant species, or the application of early selective thinning as a way of enhancing both forest productivity and long-term resilience (Cameron 2002; Vilà et al. 2007; Vayreda et al. 2012; Duveneck et al. 2014; Phillips et al. 2016; García-Valdés et al. 2021).

General conclusions

- European landscapes experiencing forest area increase in the last decades exhibit a significant decrease in their land cover diversity, and an increase in both forest defragmentation and connectivity. However, not all these changes are directly attributable to forest increase, as in land cover diversity whose decrease is not associated to forest increase *per se* but to the effects on land cover composition. **(Chapter 2)**
- The increasing forest area in Europe promotes defragmentation of pre-existing forests in forest-dominated and new patch proliferation in non-forest-dominated landscapes, showing the importance of original forest area to predict changes in functional connectivity and biodiversity in forested landscapes. Moreover, these processes also depend on elevation and geographical position, with recent forest expansion concentrated in mid-elevation areas, forest defragmentation in Northern and Eastern Europe and new patch proliferation in southern and western regions. **(Chapter 2)**
- Thus, landscape changes due to forest expansion cannot be solely attributable to forest increase, but also to landscape composition (e.g., cropland cover) and location across elevation and geographical gradients across Europe. **(Chapter 2)**
- In the studied period, the forest area has continued increasing in Europe mainly due to forest expansion (i.e. forest establishment in former agricultural land), which occurred across Europe but especially in Mediterranean and Eastern temperate regions. In contrast, forest regeneration (i.e. forest regrowth after disturbance) is particularly relevant in the boreal region. **(Chapter 3)**
- The landscape composition (i.e. original forest area and land cover diversity) is one of the main factors determining the local forest increase in Europe, both forest expansion and regeneration were especially important in highly forested and/or highly diverse landscapes. Further, forest expansion shows contrasting association with socioenvironmental factors (i.e. distance to metropolitan areas, elevation, temperature and water deficit) depending on

the climatic region (i.e. Mediterranean, temperate and boreal) suggesting the importance of general context in determining the local drivers of forest expansion. **(Chapter 3)**

- The analysis of the Enhanced Vegetation Index (EVI) reveal that expanding and regenerating forests show different EVI values which suggest differences on productivity among the two forest increase processes. Expanding forests shows higher EVI values than regenerating forests except in the warmer and drought-prone areas where they cannot benefit from biological and physicochemical legacies of abandoned agricultural soils for tree growth. **(Chapter 3)**
- Forest is expanding in the Iberian Peninsula at a rate (0.31% year^{-1}) above the European average. The analysis temporal patterns of forest emergence shows that secondary forests are increasingly becoming established in sites with better environmental conditions, as suggested by their trend over time to concentrate their emergence in sites with higher water availability (i.e. higher average rainfall), lower elevations and flatter areas. **(Chapter 4)**
- Data on aboveground biomass of forests emerged in contrasting dates reveal the key role of summer precipitation, temperature, slope and forest cover, and the lesser role of drought events, on secondary forest growth in the Iberian Peninsula. **(Chapter 4)**
- Results highlight the different response of forest leaf-habits to these environmental factors: they constrain the establishment and growth of needlelef forests, most affected by warm temperatures, and favours broadleaf secondary forest, which benefits more from summer precipitation. **(Chapter 4)**
- Forests resulting from forest expansion are mostly dominated by broadleaf species. This trend is observed at a continental but also at a regional scale in the Iberian Peninsula and we attributed this to geographic patterns of forest expansion (i.e. mostly occurs in Mediterranean and temperate regions) but also to the contrasting water economy strategies that favour the establishment and growth of broadleaf rather than of needleleaf forests. **(Chapters 3 and 4)**

Appendix 1

Supplementary material - Chapter 2

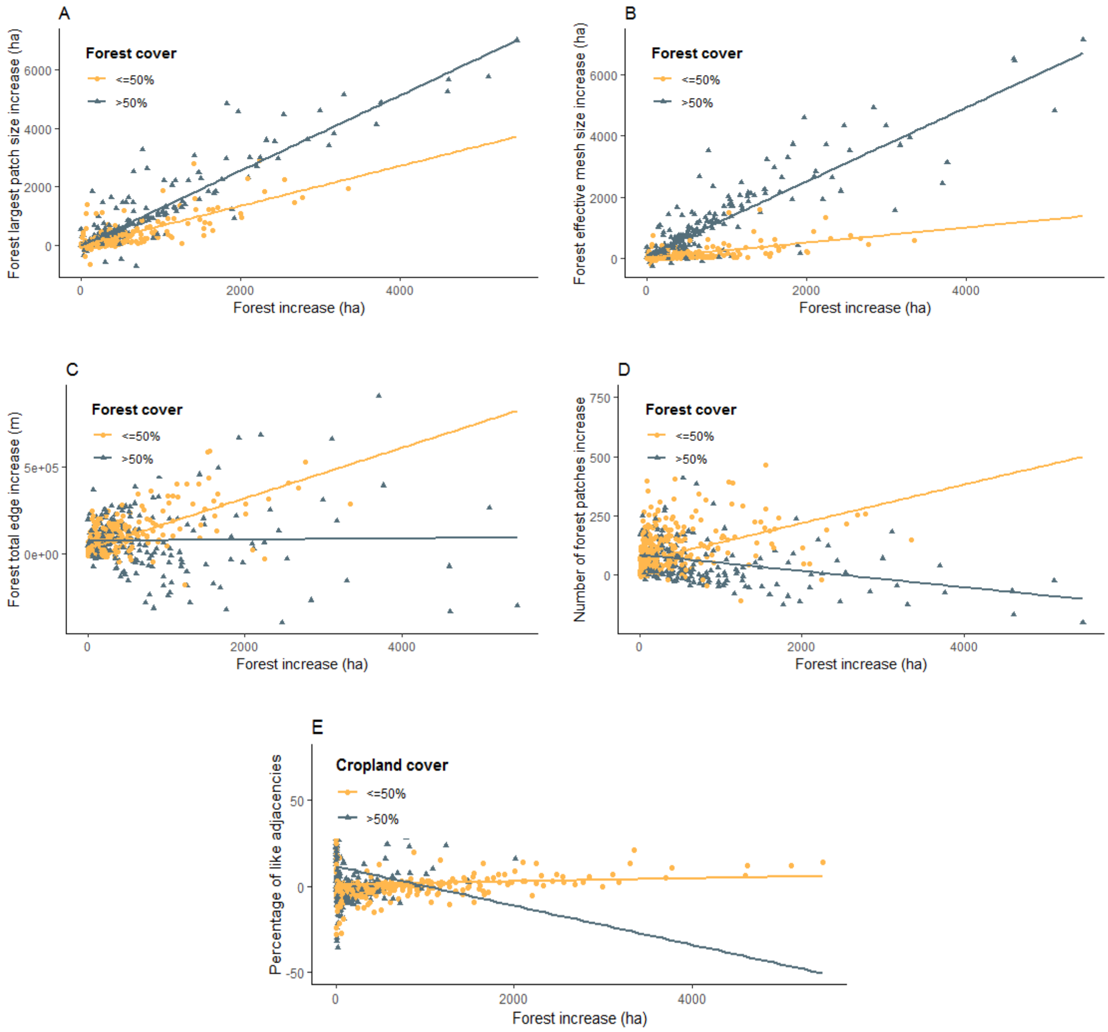

Figure A1.1. Association of forest increase between 1990 and 2012 with the increase in forest largest patch size (A), forest effective mesh size (B), forest total edge (C) and the number of forest patches (D) in the study landscapes, for two ranges of forest cover percentage (A,B,C,D) and cropland cover (E).

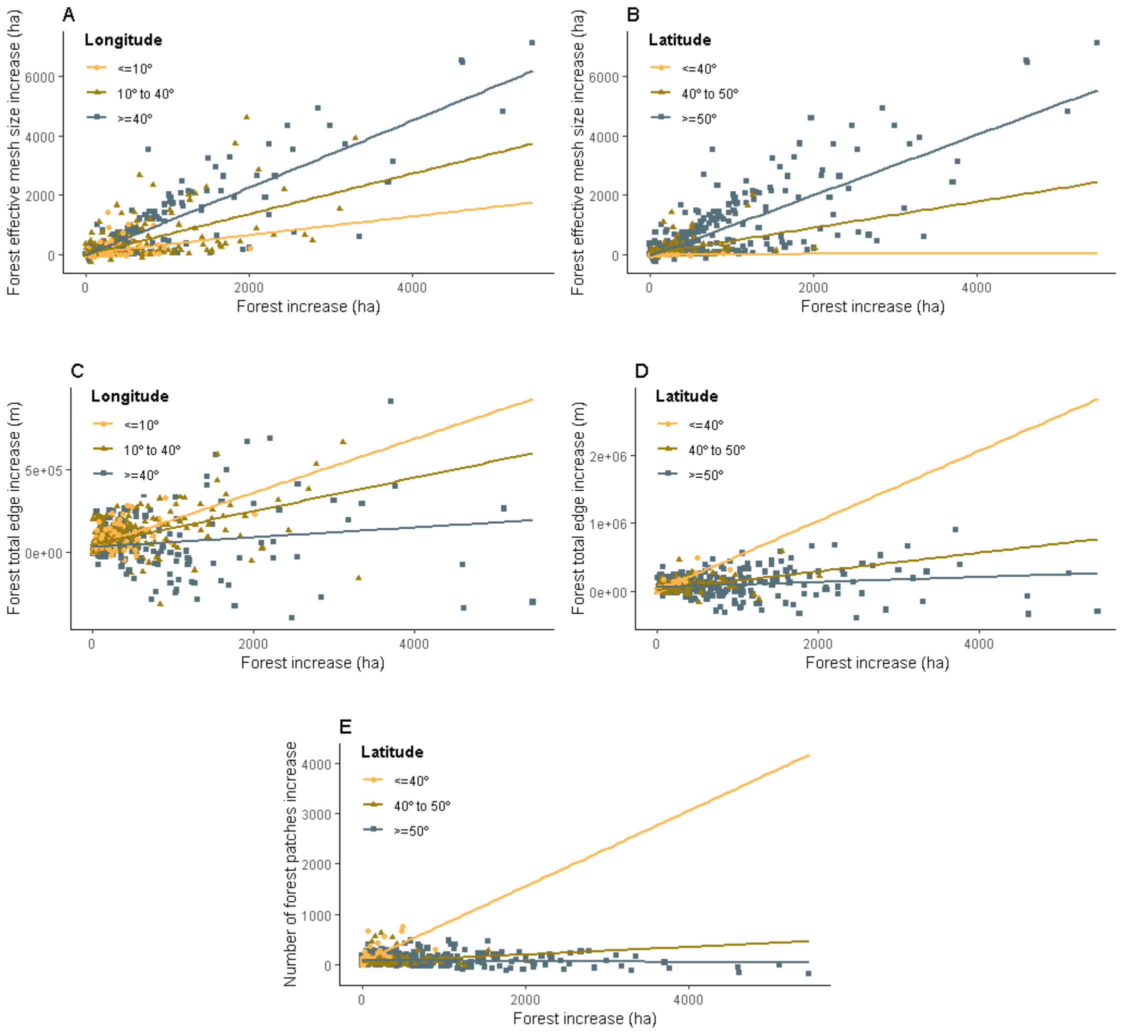

Figure A1.2. Association of forest increase between 1990 and 2012 in the study landscapes with their increase in forest effective mesh size (A, B), in forest total edge (C, D) and number of forest patches (E) for diverse latitude and longitude ranges.

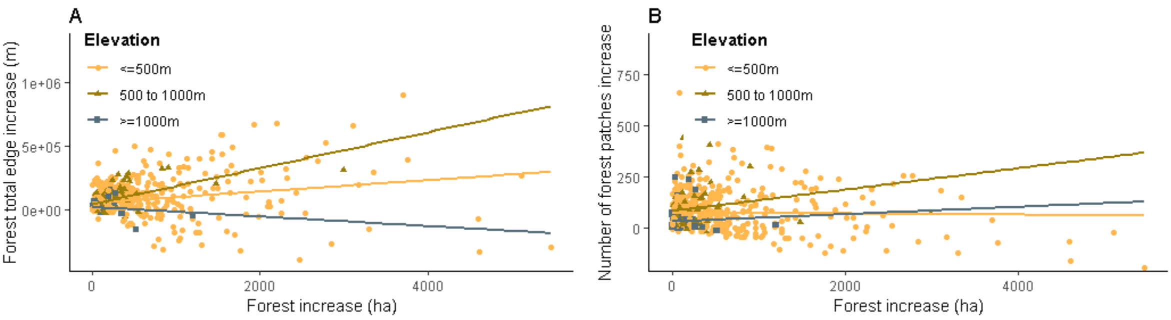

Figure A1.3. Association of forest increase between 1990 and 2012 in the study landscapes with their increase in forest total edge (A) and in the number of forest patches increase (B) for diverse elevation ranges.

Table A1.1. Summary of the composition of the 752 study landscapes randomly selected across Europe.

Forest (%)	Agriculture (%)	Agroforestry mosaics (%)	Grassland (%)	Settlement (%)
Min. : 0.00	Min. : 0.00	Min. : 0.00	Min. : 0.00	Min. : 0.00
1st Qu.: 2.99	1st Qu.: 1.64	1st Qu.: 0.72	1st Qu.: 0.00	1st Qu.: 0.00
Median : 26.49	Median : 25.99	Median : 5.49	Median : 0.41	Median : 0.00
Mean : 37.03	Mean : 37.35	Mean : 9.32	Mean : 6.18	Mean : 0.85
3rd Qu.: 68.75	3rd Qu.: 70.97	3rd Qu.: 14.99	3rd Qu.: 5.28	3rd Qu.: 0.21
Max. :100.00	Max. :100.00	Max. :86.30	Max. :93.63	Max. :60.78
Wetland (%)	**Sparse vegetation (%)**	**Shrubland (%)**	**Bare area (%)**	**Water (%)**
Min. : 0.00	Min. : 0.00	Min. : 0.00	Min. : 0.00	Min. : 0.00
1st Qu.: 0.00	1st Qu.: 0.00	1st Qu.: 0.00	1st Qu.: 0.00	1st Qu.: 0.00
Median : 0.00	Median : 0.00	Median : 0.00	Median : 0.00	Median : 0.00
Mean : 2.76	Mean : 1.17	Mean : 0.52	Mean : 0.31	Mean : 2.46
3rd Qu.: 0.21	3rd Qu.: 0.00	3rd Qu.: 0.00	3rd Qu.: 0.00	3rd Qu.: 0.62
Max. :76.65	Max. :54.27	Max. :71.88	Max. :30.38	Max. :98.76

Table A1.2. Correlation matrix with a Spearman rank (r) for the landscape covariates used in the general lineal models.

	Forest increase (ha)	Forest cover (%)	Crop cover (%)	Shrub/ Grassland cover (%)	Eleva tion (m)	Long. (º)	Lat. (º)
Forest increase (ha)	1,00						
Forest cover (%)	0,45	1,00					
Cropland cover (%)	-0,35	-0,64	1,00				
Shrub/Grass. cover (%)	-0,11	-0,15	-0,31	1,00			
Elevation (m)	-0,15	0,04	-0,14	0,13	1,00		
Longitude (º)	0,23	0,17	-0,09	-0,08	-0,14	1,00	
Latitude(º)	0,37	0,46	-0,38	0,03	-0,52	0,43	1,00

Table A1.3.Components of the plausible models (delta < 2) after model selection for the general lineal models performed for each landscape metric. Factors code: Crop cover (1), Forest cover (2), Forest increase = FI (3), Latitude (4), Longitude (5), Elevation (6), Grassland/shrubland cover (7), Crop cover:FI (8), Forest cover:FI (9), Latitude:FI (10), Longitude:FI (11), Elevation:FI (12) and Grassland/shrubland cover:FI (13).

Component models:	df	logLik	AICc	delta	weight
Largest patch size					
2/3/9	5	-5451.56	10913.19	0.00	0.07
2/3/5/9	6	-5451.10	10914.32	1.13	0.04
1/2/3/8/9	7	-5450.27	10914.69	1.50	0.03
2/3/4/9	6	-5451.39	10914.90	1.71	0.03
2/3/6/9	6	-5451.51	10915.13	1.93	0.03
Effective mesh size					
2/3/4/5/9/10/11	9	-5404.00	10826.24	0.00	0.17
1/2/3/4/5/9/10/11	10	-5403.53	10827.36	1.12	0.10
1/2/3/4/5/8/9/10/11	11	-5402.68	10827.72	1.48	0.08
2/3/4/5/7/9/10/11	10	-5403.81	10827.92	1.68	0.07
Mean patch area					
2/3/5/9	6	-4741.15	9494.42	0.00	0.07
2/3/5/9/11	7	-4740.55	9495.25	0.83	0.05
1/2/3/5/9	7	-4740.87	9495.90	1.48	0.03
1/2/3/5/8/9	8	-4739.91	9496.00	1.58	0.03
2/3/5/7/9	7	-4741.01	9496.16	1.74	0.03
2/3/4/5/9	7	-4741.04	9496.23	1.81	0.03
2/3/5/7/9/13	8	-4740.07	9496.34	1.92	0.03
Total edge					
2/3/4/5/6/9/10/11/12	11	-9742.98	19512.46	0.00	0.27
2/3/4/5/6/7/9/10/11/12	12	-9745.46	19513.27	0.81	0.18
1/2/3/4/5/6/9/10/11/12	12	-9744.88	19514.19	1.73	0.11
1/2/3/4/5/6/7/8/9/10/11/12	14	-9742.88	19514.34	1.88	0.11
Number of patches					
1/2/3/4/5/6/7/9/10/12	12	-4429.17	8882.77	0.00	0.14
1/2/3/5/6/7/9/12	10	-4431.64	8883.58	0.80	0.10
1/2/3/5/6/7/8/9/12	11	-4431.12	8884.60	1.83	0.06
1/2/3/4/5/6/7/8/9/10/12	13	-4429.10	8884.68	1.91	0.06
Euclidean nearest neighbour distance					
3/5/11	5	-3963.14	7936.39	0.00	0.04
1/3/5/11	6	-3962.37	7936.88	0.50	0.03
5	3	-3965.51	7937.06	0.67	0.03
1/3/4/5/11	7	-3961.59	7937.38	0.99	0.02
1/5	4	-3964.71	7937.50	1.11	0.02
3/4/5/11	6	-3962.80	7937.75	1.36	0.02
2/3/5/11	6	-3962.89	7937.92	1.54	0.02
1/4/5	5	-3964.01	7938.13	1.74	0.02
3/5/6/11	6	-3963.06	7938.26	1.87	0.01
Percentage of like-adjacencies					
1/3/4/5/7/8	8	-3062.71	6141.62	0.00	0.05
1/3/4/5/6/7/8/12	10	-3060.87	6142.04	0.42	0.04
1/3/4/5/7/8/10	9	-3062.22	6142.69	1.07	0.03
1/2/3/4/5/7/8	9	-3062.27	6142.78	1.16	0.03
1/3/4/5/7/8/13	9	-3062.34	6142.91	1.30	0.03
1/3/4/5/6/7/8/12/13	11	-3060.48	6143.32	1.70	0.02
1/2/3/4/5/6/7/8/12	11	-3060.53	6143.42	1.80	0.02
1/3/4/5/7/8/11	9	-3062.60	6143.45	1.83	0.02
1/3/4/5/6/7/8	9	-3062.65	6143.55	1.93	0.02
1/3/4/6/7/8/12	9	-3062.66	6143.56	1.94	0.02
Shannon diversity index					
1/4/6/7	6	-191.83	395.77	0.00	0.07
1/3/4/6/7	7	-191.51	397.17	1.40	0.03
1/2/4/6/7	7	-191.75	397.65	1.89	0.03
1/3/4/6/7/8	8	-190.75	397.70	1.93	0.03
1/4/5/6/7	7	-191.80	397.74	1.98	0.02

Table A1.4. Results of the relative variable importance from the *model.avg* function of the MuMin package (Barton and Barton 2019) for model selection for the general lineal models performed for each landscape metric. Highlighted in gray variables in the selected model. Variables code: Crop cover (1), Forest cover (2), Forest increase = FI (3), Latitude (4), Longitude (5), Elevation (6), Grassland/shrubland cover (7), Crop cover:FI (8), Forest cover:FI (9), Latitude:FI (10), Longitude:FI (11), Elevation:FI (12), Grassland/shrubland cover:FI (13).

Variables code:	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
Largest patch size model													
Importance:	0.49	1.00	1.00	0.39	0.43	0.38	0.38	0.30	1.00	0.15	0.13	0.12	0.15
Containing models:	518	518	729	518	518	518	518	248	234	243	243	243	243
Effective mesh size model													
Importance:	0.48	1.00	1.00	1.00	0.96	0.35	0.36	0.21	1.00	1.00	0.82	0.11	0.11
Containing models:	518	518	729	518	518	518	518	243	243	243	243	243	243
Mean patch area model													
Importance:	0.45	1.00	1.00	0.36	0.94	0.40	0.41	0.19	1.00	0.11	0.35	0.18	0.18
Containing models:	518	518	729	518	518	518	518	243	243	243	243	243	243
Total edge model													
Importance:	0.69	1.00	1.00	1.00	1.00	0.99	0.65	0.20	1.00	1.00	0.98	0.99	0.17
Containing models:	518	518	729	518	518	518	518	243	243	243	243	243	243
Number of patches model													
Importance:	1.00	1.00	1.00	0.56	1.00	0.98	1.00	0.32	1.00	0.39	0.30	0.84	0.30
Containing models:	518	518	729	518	518	518	518	243	243	243	243	243	243
Euclidean nearest neighbour distance model													
Importance:	056	0.37	0.76	0.47	0.97	0.35	0.34	0.14	0.09	0.11	0.57	0.08	0.07
Containing models:	518	518	729	518	518	518	518	243	243	243	243	243	243
Percentage of like adjacencies model													
Importance:	1.00	0.53	1.00	1.00	0.78	0.53	0.84	0.94	0.18	0.37	0.24	0.34	0.29
Containing models:	518	518	729	518	518	518	518	243	243	243	243	243	243
Shannon diversity index model													
Importance:	0.98	0.42	0.82	1.00	0.44	0.96	0.83	0.30	0.11	0.24	0.24	0.27	0.30
Containing models:	518	518	729	518	518	518	518	243	243	243	243	243	243

Appendix 2

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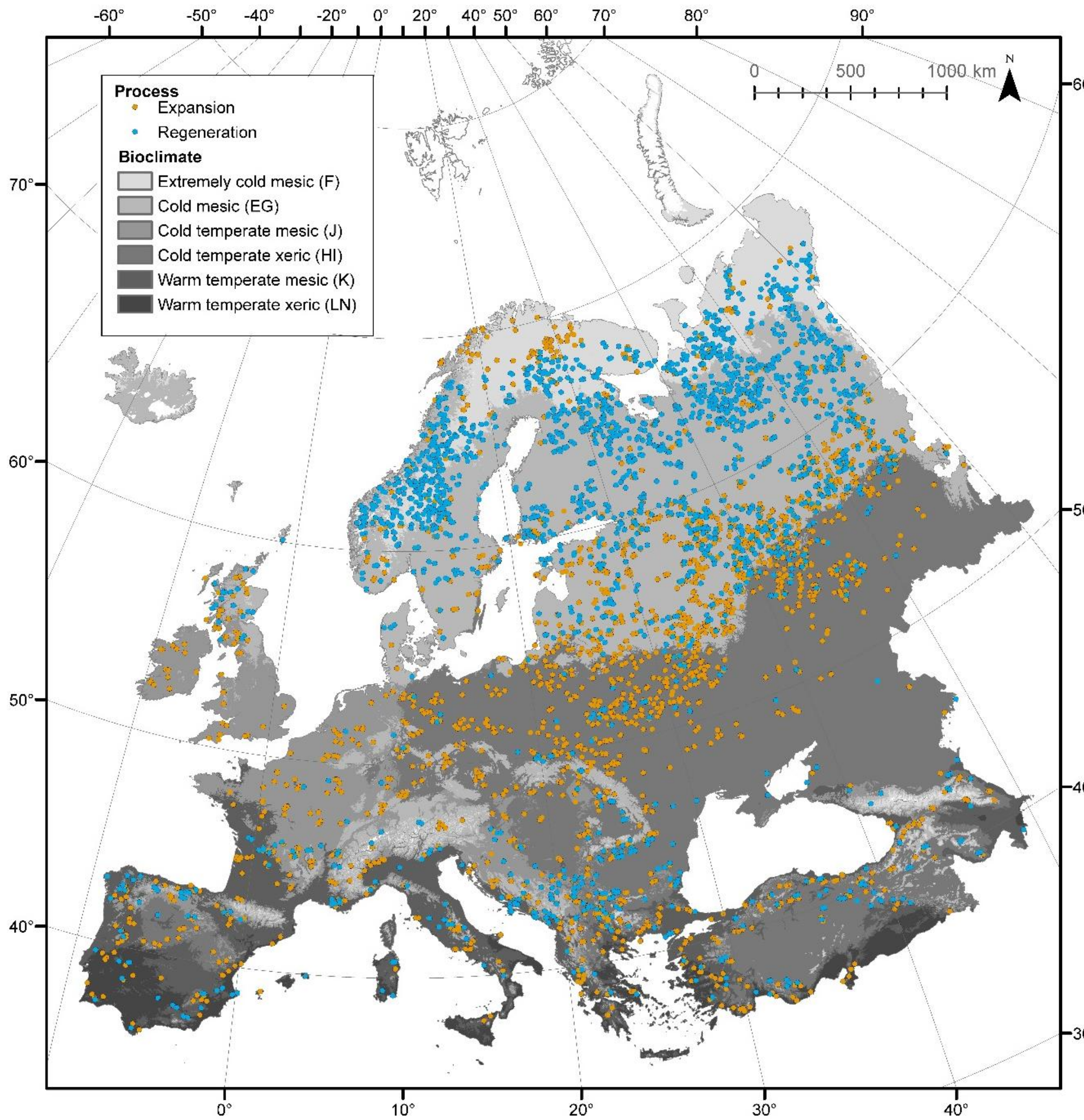

Figure A2.1. Forest expansion and forest regeneration points for the study of forest productivity (EVI values) on the different bioclimates (GEnZ described by Metzger et al. 2012).

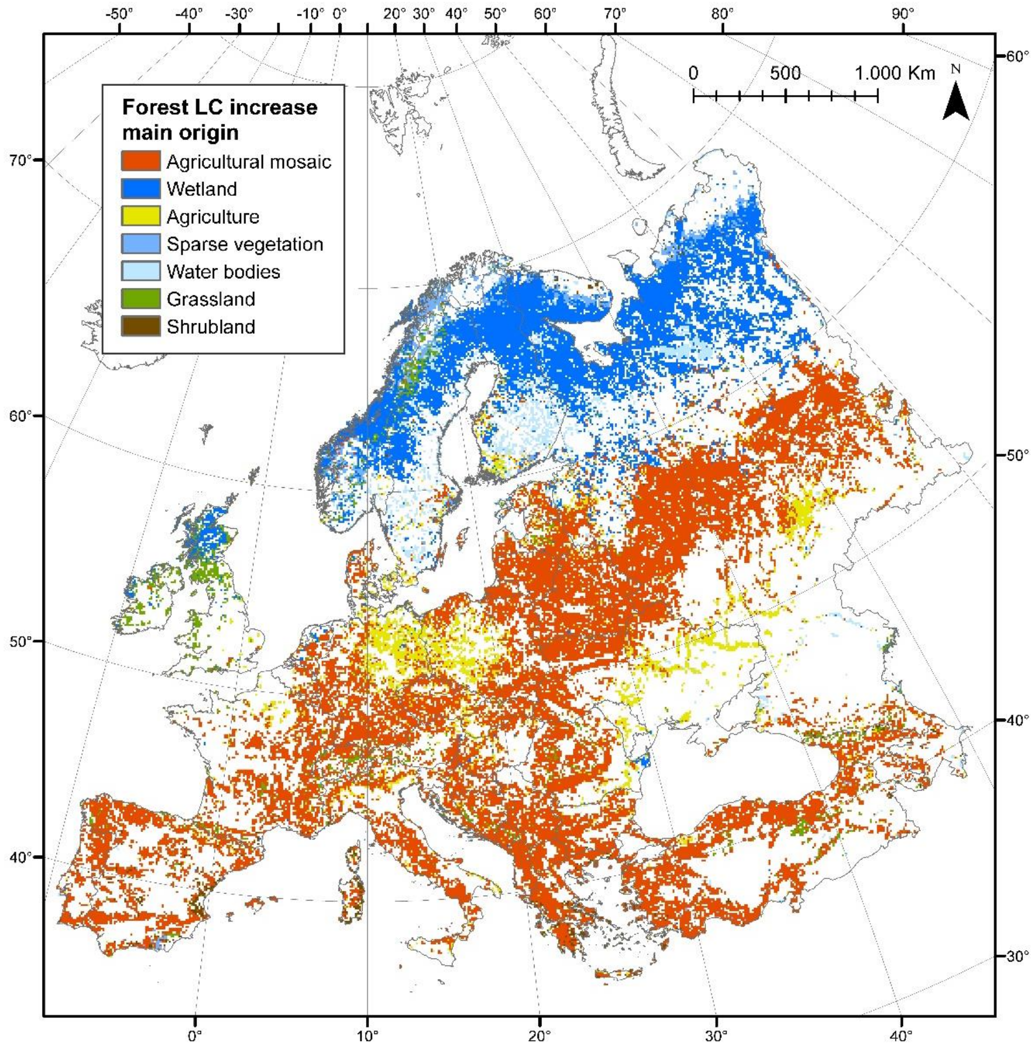

Figure A2.2. Forest area increase origin classes (land cover class in 1992 that become forest in 2015) in Europe. For each 10 km cell is shown the main land cover class that precedes forests appeared in 2015.

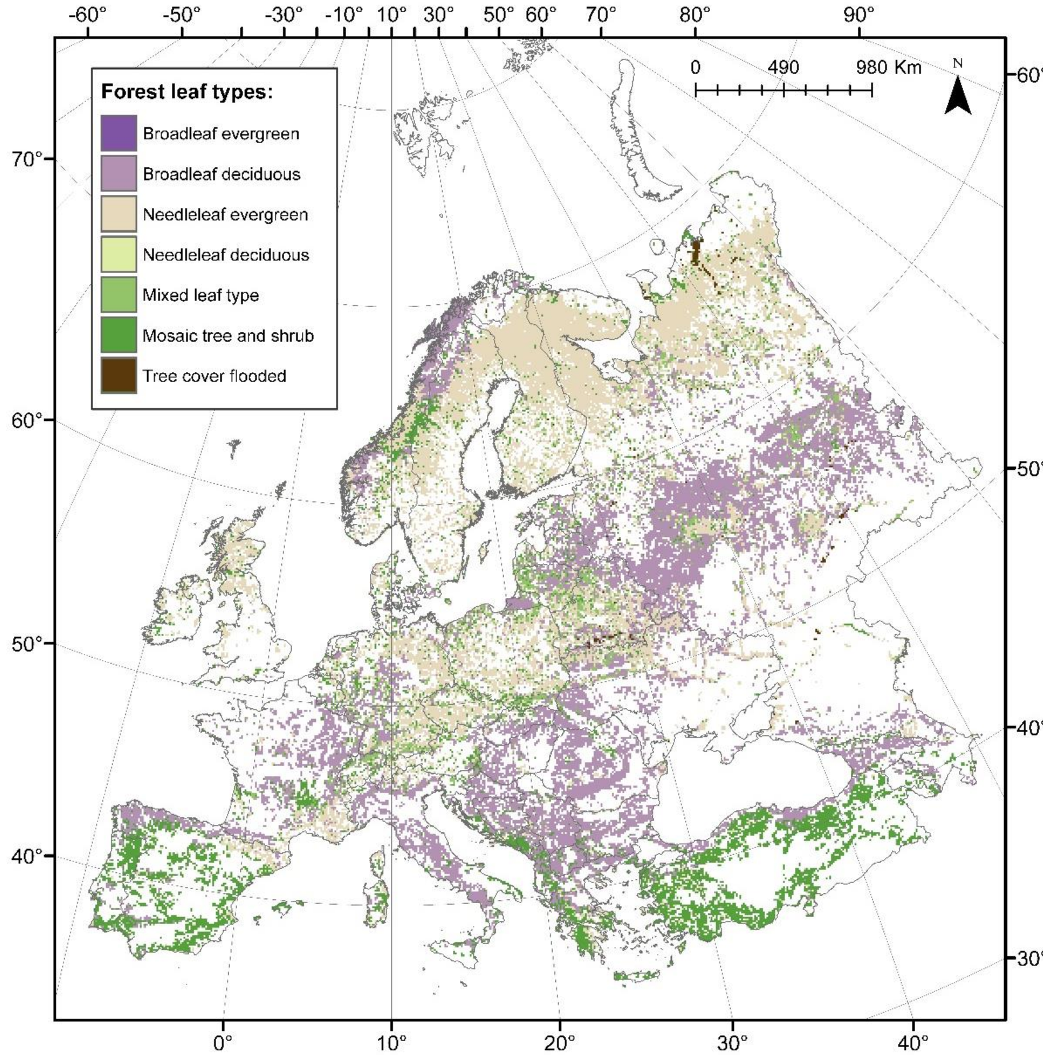

Figure A2.3. Forest area increase (land cover class in 1992 that become forest in 2015) according to the different leaf habit types in 2015 in Europe. For each 10 km cell is shown the main leaf habit types resulting from forest area increase between 1992 and 2015.

Table A2.1. Table of correspondence between the Climate Change Initiative (CCI) land cover (LC) classes (ESA, 2017) and the land cover classes (LCC) used in this study. *Forests were divided in 7 subclasses by forest leaf phenology and type as classified by ESA original CCI-LC classes.

ESA CCI-LC classes	LCC classes
10. Rainfed cropland 20. Irrigated cropland	1. Agriculture
30. Mosaic cropland (>50%) / natural vegetation (<50%) 40. Mosaic natural vegetation (>50%) / cropland (<50%)	2. Agricultural mosaic
50. Tree cover, broadleaved, evergreen, closed to open (>15%) 60. Tree cover, broadleaved, deciduous, closed to open (> 15%) 70. Tree cover, needleleaved, evergreen, closed to open (> 15%) 80. Tree cover, needleleaved, deciduous, closed to open (> 15%) 90. Tree cover, mixed leaf type (broadleaved and needleleaved) 100. Mosaic tree and shrub (>50%) / herbaceous cover (< 50%) 160. Tree cover, flooded, fresh or brakish water 170. Tree cover, flooded, saline water	3. Forest* 3.1. Broadleaved evergreen 3.2. Broadleaved deciduous 3.3. Needleleaved evergreen 3.4. Needleleaved deciduous 3.5. Mixed leaf type 3.6. Mosaic vegetation 3.7. Flooded (fresh or saline)
110. Grassland 130. Mosaic herbaceous cover (>50%) / tree and shrub (<50%)	4. Grassland
180. Shrub or herbaceous cover, flooded, fresh/saline/brakish water	5. Wetland
190. Urban areas	6. Settlement
120. Shrubland	7. Shrubland
140. Lichens and mosses 150. Sparse vegetation (tree, shrub, herbaceous cover) (<15%)	8. Sparse vegetation
210. Bare areas	9. Bare areas
200. Water bodies	10. Water bodies

Table A2.2. Spearman rank (r) correlation matrix for the socioenvironmental predictors included in this study.

	Forest % 1992	**LC diversity 1992 (Shannon Index)**	**Temperature seasonality**	**Growing degree days base 0**	**Aridity Index**	**PET seasonality**	**Slope**	**Elevation**	**Population in 1990**	**Road density**	**Mean annual temperature**	**Distance to urban areas**	**Distance to metropolitan areas**
Forest % 1992	1,00												
LC diversity 1992 (Shannon Index)	-0,23	1,00											
Temperature seasonality	0,08	-0,15	1,00										
Mean annual temperature0	-0,35	0,05	-0,09	1,00									
Aridity Index	0,14	0,15	-0,13	-0,51	1,00								
PET seasonality	-0,14	-0,16	0,28	0,55	-0,59	1,00							
Slope	0,08	0,31	-0,16	0,04	0,30	-0,21	1,00						
Elevation	0,03	0,21	-0,06	-0,04	0,12	-0,05	0,71	1,00					
Population in 1990	-0,12	0,13	-0,06	0,18	-0,06	0,02	-0,01	-0,05	1,00				
Road density	-0,20	0,12	-0,07	0,33	-0,14	0,13	-0,03	-0,08	0,33	1,00			
Gross domestic product	-0,10	0,13	-0,11	0,16	0,01	-0,08	0,01	-0,06	0,51	0,32	1,00		
Distance to urban areas	0,01	-0,09	-0,05	-0,41	0,21	-0,36	0,02	-0,02	-0,12	-0,28	-0,14	1,00	
Distance to metropolitan areas	0,04	-0,01	-0,01	-0,62	0,38	-0,51	-0,02	-0,11	-0,15	-0,35	-0,18	0,72	1,00

Table A2.3. Forest area increase grouped by land cover origin (LC class in 1992 that become forest in 2015) in Europe between years 1992 and 2015. Table shows forest land cover increase area, percentage of forest area increase, distribution (% of grid cells 10-km resolution related to total cells) and magnitude (average of percentage of cell 10-km resolution where land cover increase is detected).

Forest area increase				
Forest LC origin	**Area (km^2)**	**Area/Total area (%)**	**Distribution (% grid cells)**	**Magnitude (mean ± SE % increase per cell)**
Agricultural mosaic	136098	57.4	32.2	3.9 ± 0.02
Wetlands	53133	22.4	12.7	3.8 ± 0.02
Agriculture	20532	8.6	19.2	1.0 ± 0.01
Sparse Vegetation	8076	3.4	5.8	1.3 ± 0.01
Grassland	8006	3.4	11.2	0.6 ± 0.00
Water	7867	0.2	3.6	1.8 ± 0.01
Shrubland	3082	1.2	4.1	0.7 ± 0.00
Bare areas	303	0.1	1.0	0.3 ± 0.00
Settlement	0	0.0	0	0.0 ± 0.00

Table A2.4. Area of the different land cover classes and proportion related to Europe's surface in 1992 and 2015.

	Area 1992		**Area 2015**	
	km^2	**%**	**km^2**	**%**
Forest	4051036	37.5	4106392	38.0
Agriculture	3448752	31.9	3447212	31.9
Mosaic agriculture	910326	8.4	816527	7.6
Grassland	813226	7.5	826575	7.6
Wetland	351674	3.3	324991	3.0
Water	291410	2.9	292243	2.7
Sparse vegetation	282010	2.6	238042	2.2
Shrubland	219085	2.0	221591	2.0
Bare areas	137557	1.3	127736	1.2
Mosaic grassland	98564	0.9	104393	1.0
Settlement	97117	0.9	195057	1.8
Snow/ice	83116	0.8	83116	0.8
Lichens/Mosses	29328	0.3	29326	0.3

Table A2.5. Forest area increase, expansion and regeneration between years 1992 and 2015 in Europe subdivided by the forest leaf habit in 2015. Table shows area related to total forest area increase (expansion or regeneration), distribution (% of grid cells 10-km resolution) and magnitude (average of magnitude of cells 10-km resolution).

Forest leaf habit	Area (km^2)	Area/Total area (%)	Distribution (% of grid cells)	Magnitude (mean ± SE per cell)
Forest area increase				
Broadleaf deciduous	78910	33	29	2.5 ± 0.01
Broadleaf evergreen	0.3	0	0	0.1 ± 0.01
Needleleaf deciduous	78	0	0	0.2 ± 0.00
Needleleaf evergreen	83218	35	31	2.5 ± 0.01
Mixed	22649	10	20	1.0 ± 0.01
Mosaic	51763	22	32	1.5 ± 0.01
Flooded	1584	1	3	0.5 ± 0.01
Forest expansion				
Broadleaf deciduous	69955	45	25	2.5 ± 0.01
Broadleaf evergreen	0.2	0	0	0.0 ± 0.01
Needleleaf deciduous	20	0	0	0.2 ± 0.00
Needleleaf evergreen	32352	21	18	1.7 ± 0.01
Mixed	17636	11	15	1.1 ± 0.01
Mosaic	36773	23	23	1.5 ± 0.01
Flooded	349	0	1	0.5 ± 0.00
Forest regeneration				
Broadleaf deciduous	8956	11	11	0.7 ± 0.00
Broadleaf evergreen	0.1	0	0	0.0 ± 0.01
Needleleaf evergreen	50868	63	17	2.8 ± 0.01
Needleleaf deciduous	58	0	0	0.2 ± 0.00
Mixed	5013	6	7	0.7 ± 0.00
Mosaic	1990	19	16	0.9 ± 0.00
Flooded	1236	2	2	0.5 ± 0.01

Table A2.6. General linear mixed models (binomial family) exploring the association of forest area increase, expansion and regeneration between 1992 and 2015 with selected environmental and socioeconomic variables in the European boreal (A), temperate (B) and Mediterranean (C) regions. Models likelihood, effect estimate and significance of factors are shown. Significance: '*' = 0.05, '**' = 0.01, '***' = 0.001.

A) Boreal region (include the Extremely cold and mesic and Cold and mesic environmental zones)									
	Forest area increase			**Forest expansion**			**Forest regeneration**		
Fixed effect	**Estimate**	**SE**	**p value**	**Estimate**	**SE**	**p value**	**Estimate**	**SE**	**p value**
Intercept	0.66	0.02	**	0.01	0.21		-0.34	0.22	
Forest in 1992	0.73	0.02	***	0.22	0.02	***	1.18	0.03	***
LC diversity 1992	1.62	0.02	***	1.53	0.03	***	1.42	0.02	***
Distance to metropolitan areas	0.61	0.03	***	0.07	0.02	**	0.82	0.03	***
Altitude	0.11	0.02	***	0.34	0.03	***	0.00	0.02	
Temperature seasonality	1.19	0.03	***	1.12	0.04	***	0.67	0.03	***
Mean annual temperature	0.91	0.03	***	0.94	0.03	**	0.18	0.03	***
Aridity Index	0.16	0.02	***	-0.06	0.02	*	0.24	0.02	***
Random effect	**Variance**	**SD**	**ICC**	**Variance**	**SD**	**ICC**	**Variance**	**SD**	**ICC**
Country (groups 51)	2.16	1.47	0.40	1.49	1.22	0.31	1.83	1.35	0.36
Regression model accuracy metrics									
BIC	48161.29			30003.03			46231.20		
R^2 (fixed effect)	0.22			0.28			0.23		
R^2 (total)	0.53			0.51			0.51		
B) Temperate region (Cool temperate mesic and the Cool temperate xeric environmental zones)									
Fixed effect	**Estimate**	**SE**	**p value**	**Estimate**	**SE**	**p value**	**Estimate**	**SE**	**p value**
Intercept	-1.20	0.22	***	-1.43	0.29	***	-2.86	0.10	***
Forest in 1992	1.06	0.02	***	1.06	0.02	***	0.77	0.02	***
LC diversity 1992	1.40	0.02	***	1.35	0.02	***	1.23	0.02	***
Distance to metropolitan areas	-0.19	0.02	***	-0.20	0.02	***	0.06	0.02	**
Altitude	-0.17	0.02	***	-0.19	0.02	***	0.14	0.02	***
Temperature seasonality	-0.46	0.05	***	-0.61	0.05	***	-0.15	0.06	**
Mean annual temperature	-0.28	0.02	***	-0.39	0.03	***	-0.01	0.03	
Aridity Index	0.64	0.03	***	0.44	0.02	***	0.37	0.03	***
Random effect	**Variance**	**SD**	**ICC**	**Variance**	**SD**	**ICC**	**Variance**	**SD**	**ICC**
Country (groups 51)	1.79	1.34	0.35	3.13	1.77	0.48	0.27	0.52	0.08
Regression model accuracy metrics									
BIC	41005.23			39821.75			26447.60		
R^2 (fixed effect)	0.51			0.44			0.47		
R^2 (total)	0.68			0.71			0.51		
C) Mediterranean region (Warm temperate mesic and Warm temperate xeric environmental zones)									
Fixed effect	**Estimate**	**SE**	**p value**	**Estimate**	**SE**	**p value**	**Estimate**	**SE**	**p value**
Intercept	-0.31	0.19		-0.42	0.20	*	-1.84	0.21	***
Forest in 1992	0.88	0.03	***	0.88	0.03	***	0.67	0.04	***
LC diversity 1992	1.25	0.03	***	1.20	0.03	***	1.28	0.04	***
Distance to metropolitan areas	-0.09	0.02	**	-0.15	0.02	***	0.06	0.02	**
Altitude	0.04	0.03		0.02	0.03		0.33	0.03	***
Temperature seasonality	-0.39	0.04	***	-0.36	0.04	***	-0.07	0.05	
Growing degree days (GDD)	-0.19	0.03	***	-0.24	0.03	***	0.05	0.03	
Aridity Index	-0.10	0.03	**	-0.09	0.03	**	-0.18	0.04	***
Random effect	**Variance**	**SD**	**ICC**	**Variance**	**SD**	**ICC**	**Variance**	**SD**	**ICC**
Country (groups 51)	0.56	0.75	0.15	0.63	0.79	0.16	0.64	0.80	0.16
Regression model accuracy metrics									
BIC	12698.48			12709.82			9691.88		
R^2 (fixed effect)	0.44			0.43			0.42		
R^2 (total)	0.52			0.52			0.51		

Table A2.7. table showing effects of forest area increase process (process), bioclimate (bioclim), forest leaf habit (l_habit), EVI value in the year 2000 (EVI2000) and interactions on EVI maximum annual value increase from 1992 to 2015.

	DF	Sum Sq	Mean Sq	F-value	P-value
process	1	0.73	0.73	134,47	<0.001
bioclim	5	7.66	1.53	281,24	<0.001
l_habit	3	1.87	0.63	114,91	<0.001
EVI2000	1	57.35	20.45	10531,27	<0.001
process:bioclim	5	1.07	0.21	39,58	<0.001
process: l_habit	3	0.94	0.31	57,99	<0.001
bioclim: l_habit	14	3.79	0.27	49,70	<0.001
Residuals	34846	189.83	0.00		

Table A2.8. ANOVA table showing effects of forest area increase processes (process), bioclimate (bioclim), forest leaf habit (l_habit) and interactions on the EVI maximum annual value in the year 2015.

	Df	Sum Sq	Mean Sq	F-value	P-value
process	1	65,02	65,02	2129.45	<0.001
bioclim	5	43,53	8,71	223.11	<0.001
l_habit	3	94,53	31,51	3206.08	<0.001
process:bioclim	5	1,73	0,35	9.22	<0.001
process:l_habit	3	3,14	1,05	114.91	<0.001
bioclim: l_habit	14	11,69	0,84	21.97	<0.001
Residuals	34847	36.82	0.01		

Table A2.9. Estimated marginal means (EMMs) of the increase of Enhanced vegetation index (EVI) annual maximum between 1992 and 2015 and pairwise contrast between A) forest area increase process, B) forest area increase process and forest leaf habit and C) forest area increase process and bioclimate. BD= broadleaf deciduous, NE= needleleaf evergreen, MIX= mixed leaf type, MOS= mosaic forest/shrub, F= extremely cold mesic, EG= cold mesic, HI= cold temperate xeric, J= cold temperate mesic, K= warm temperate mesic, LN= warm temperate xeric.

	EMM ± SE	lower.CL-upper.CL	Estimate ± SE	t.ratio	p.value
A) Pairwise comparison (forest area increase process)					
Expansion	0.049 ± 0.002	0.046 – 0.053	0.024 ± 0.002	10.733	<0.001
Regeneration	0.025 ± 0.002	0.022 – 0.029			
B) Pairwise comparison (forest area increase process – forest leaf habit)					
Expansion - BD	0.074 ± 0.002	0.088 – 0.096	0.007 ± 0.005	2.858	0.091
Regeneration- BD	0.069 ± 0.005	0.073 – 0.092			
Expansion - NE	0.029 ± 0.005	0.012 – 0.048	0.031 ± 0.002	6.837	<0.001
Regeneration- NE	0.012 ± 0.003	0.008 – 0.019			
Expansion - MIX	0.068 ± 0.005	0.058 – 0.078	0.035 ± 0.05	7.152	<0.001
Regeneration - MIX	0.033 ± 0.005	0.022 – 0.043			
Expansion - MOS	0.036 ± 0.002	0.033 – 0.040	0.031 ± 0.05	13.37	<0.001
Regeneration- MOS	0.014 ± 0.002	0.008 – 0.017			
C) Pairwise comparison (forest area increase process – bioclimate)					
Expansion - F	0.061 ± 0.004	0.054 – 0.068	0.048 ± 0.004	12.433	<0.001
Regeneration- F	0.013 ± 0.002	0.010 – 0.016			
Expansion - EG	0.085 ± 0.001	0.083 – 0.088	0.029 ± 0.002	16.703	<0.001
Regeneration- EG	0.057 ± 0.001	0.055 – 0.059			
Expansion - J	0.065 ± 0.005	0.058 – 0.072	0.034 ± 0.004	8.329	<0.001
Regeneration- J	0.032 ± 0.004	0.023 – 0.042			
Expansion - HI	0.068 ± 0.005	0.065 – 0.071	0.037 ± 0.003	12.362	<0.001
Regeneration- HI	0.030 ± 0.003	0.024 – 0.036			
Expansion - K	0.023 ± 0.003	0.017 – 0.030	0.003 ± 0.003	1.226	0.986
Regeneration- K	0.019 ± 0.004	0.012 – 0.026			
Expansion - LN	0.013 ± 0.008	0.002 – 0.017	0.005 ± 0.009	1.146	0.992
Regeneration- LN	0.018 ± 0.007	0.008 – 0.023			

Table A2.10. Estimated marginal means (EMMs) of the Enhanced vegetation index (EVI) annual maximum of 2015 and pairwise contrast between A) forest area increase process, B) forest area increase process and forest leaf habit and C) forest area increase process and bioclimate. BD = broadleaf deciduous, NE= needleleaf evergreen, MIX=mixed leaf type, MOD= Mosaic forest/shrub, F= extremely cold mesic, EG= cold mesic, HI= cold temperate xeric, J= cold temperate mesic, K= warm temperate mesic, LN= warm temperate xeric.

	EMM ± SE	lower.CL- upper.CL	Estimate ± SE	t.ratio	p.value
A) Pairwise comparison (forest area increase process)					
Expansion	0.548 ± 0.002	0.544 – 0.552	0.055 ± 0.002	21.064	<0.001
Regeneration	0.493 ± 0.001	0.489 – 0.497			
B) Pairwise comparison (forest area increase process – forest leaf habit)					
Expansion - BD	0.599 ± 0.001	0596 – 0.602	0.014 ± 0.002	5.291	0.156
Regeneration - BD	0.584 ± 0.003	0.579 – 0.589			
Expansion - NE	0.499 ± 0.003	0.492 – 0.506	0.071 ± 0.004	19.018	<0.001
Regeneration - NE	0.428 ± 0.002	0.428 – 0.433			
Expansion - MIX	0.580 ± 0.006	0.568 – 0.592	0.062 ± 0.005	10.598	<0.001
Regeneration - MIX	0.518 ± 0.006	0.506 – 0.531			
Expansion – MOS	0.516 ± 0.002	0.512 – 0.520	0.072 ± 0.002	26.481	<0.001
Regeneration - MOS	0.443 ± 0.002	0.440 – 0.447			
C) Pairwise comparison (forest area increase process – bioclimate)					
Expansion - F	0.595 ± 0.004	0.587 – 0.603	0.108 ± 0.005	23.509	<0.001
Regeneration - F	0.487 ± 0.002	0.483 – 0.490			
Expansion - EG	0.601 ± 0.001	0.598 – 0.604	0.065 ± 0.002	32.627	<0.001
Regeneration - EG	0.535v± 0.001	0.538 – 0.538			
Expansion - J	0.597 ± 0.004	0.588 – 0.605	0.059 ± 0.004	12.307	<0.001
Regeneration- J	0.537 ± 0.005	0.525 – 0.548			
Expansion - HI	0.555 ± 0.001	0.551 – 0.558	0.069 ± 0.003	19.407	<0.001
Regeneration- HI	0.485 ± 0.003	0.478 – 0.492			
Expansion - K	0.506 ± 0.004	0.498 – 0.513	0.015 ± 0.004	3.996	0.003
Regeneration- K	0.490 ± 0.004	0.482 – 0.499			
Expansion - LN	0.436 ± 0.009	0.417 – 0.456	0.012 ± 0.011	1.119	1.000
Regeneration- LN	0.424 ± 0.008	0.409 – 0.439			

Appendix 3

Supplementary material - Chapter 4

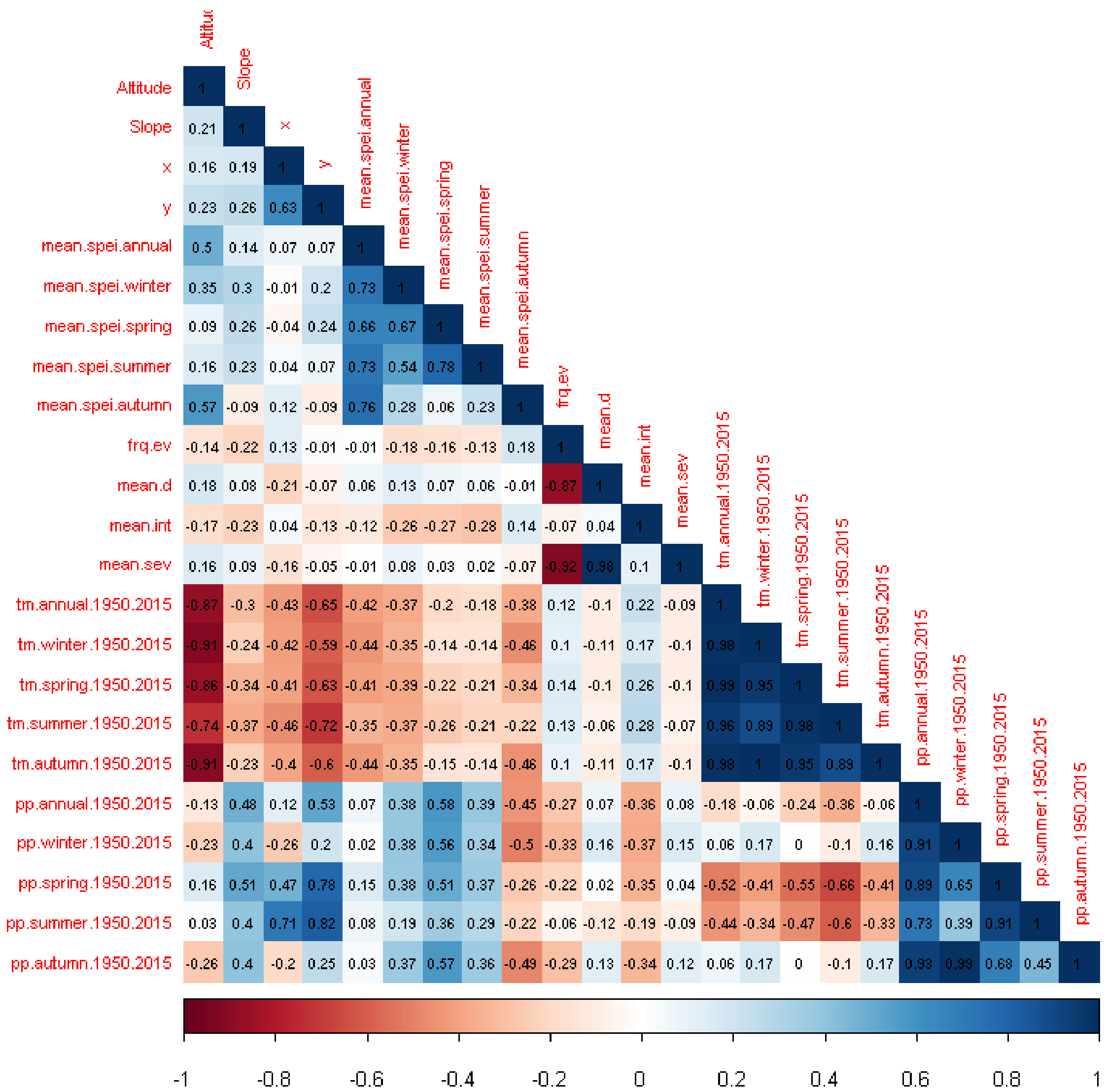

Figure A3.1. Correlation matrix with a Spearman rank test for the environmental predictors potentially included to study the changes of forest establishment over the time. X=longitude, y=latitude, Altitude =elevation, frq.ev=drought events frequency, mean.d= mean duration of drought events, mean.int= mean intensity of drought events, mean.sev= mean severity of drought events, tm=mean annual temperature, pp= annual precipitation. Climatic variables calculated for the period 1950-2015.

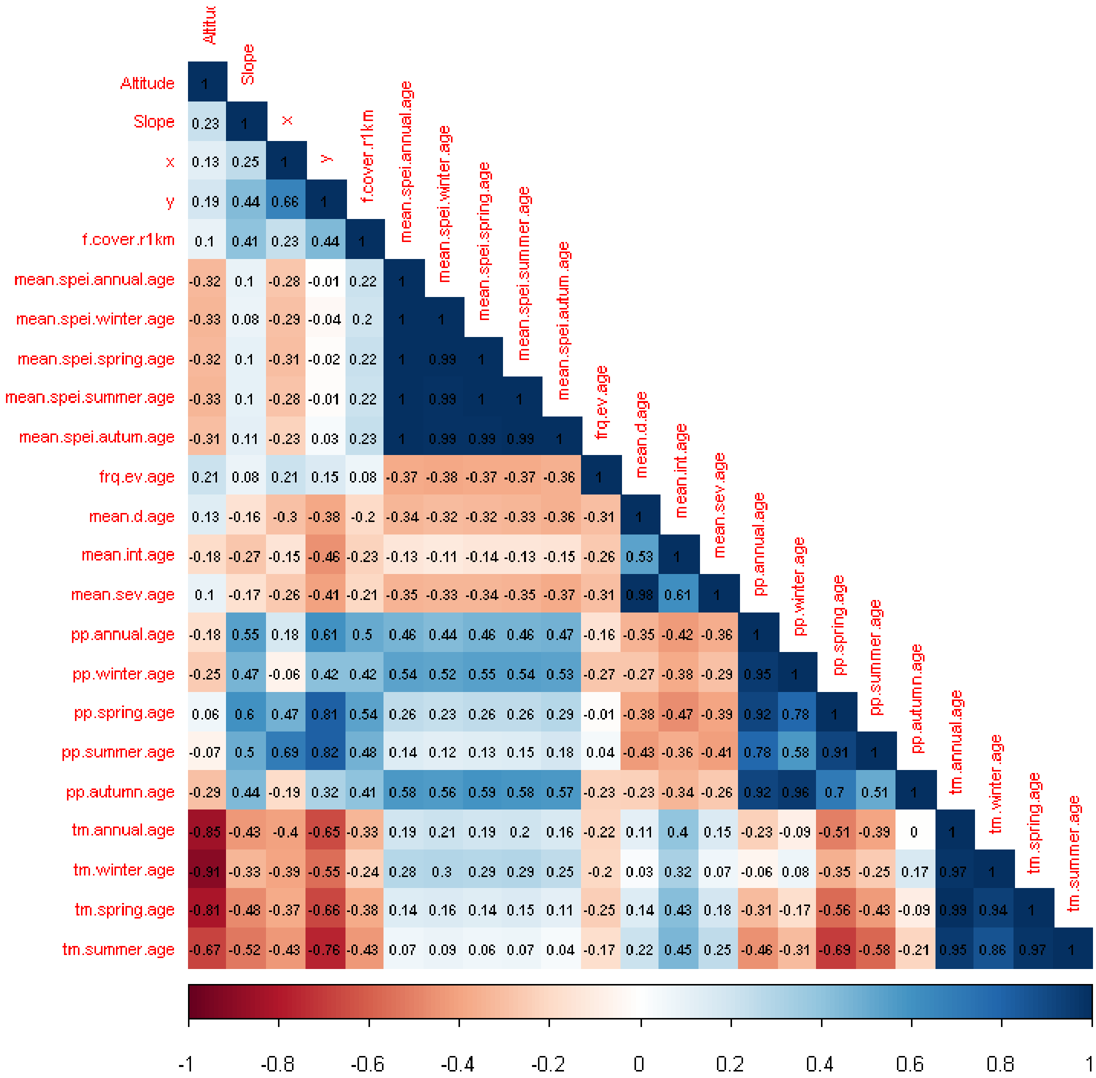

Figure A3.2. Correlation matrix with a Spearman rank test for the environmental predictors potentially included to study the impact on secondary forest biomass. x=longitude, y=latitude, Altitude =eleveation, frq.ev=drought events frequency, mean.d= mean duration of drought events, mean.int= mean intensity of drought events, mean.sev= mean severity of drought events, tm=mean annual temperature, pp= annual precipitation. Climatic variables calculated for the period of secondary forest growth (age).

Table A3.1. Classes of the Land cover maps for the analysis of global changes in the Iberian Peninsula developed by the Grumets Research Group of the Universitat Autònoma de Barcelona. Agriculture (C) and forest (F) general classes.

Land cover classes:	
1	Water
2	Rice crops (A)
3	Needleleaf forest (F)
4	Irrigated herbaceous cropland (A)
5	Rainfed herbaceous cropland (A)
6	Irrigated woody cropland (A)
7	Rainfed woody cropland (A)
8	Broadleaf deciduous forest (F)
9	Broadleaf evergreen forest (F)
10	Shrublands
11	Pastures (A)
12	Bare soil
13	Urban
14	Greenhouse
15	Recent wildfires

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