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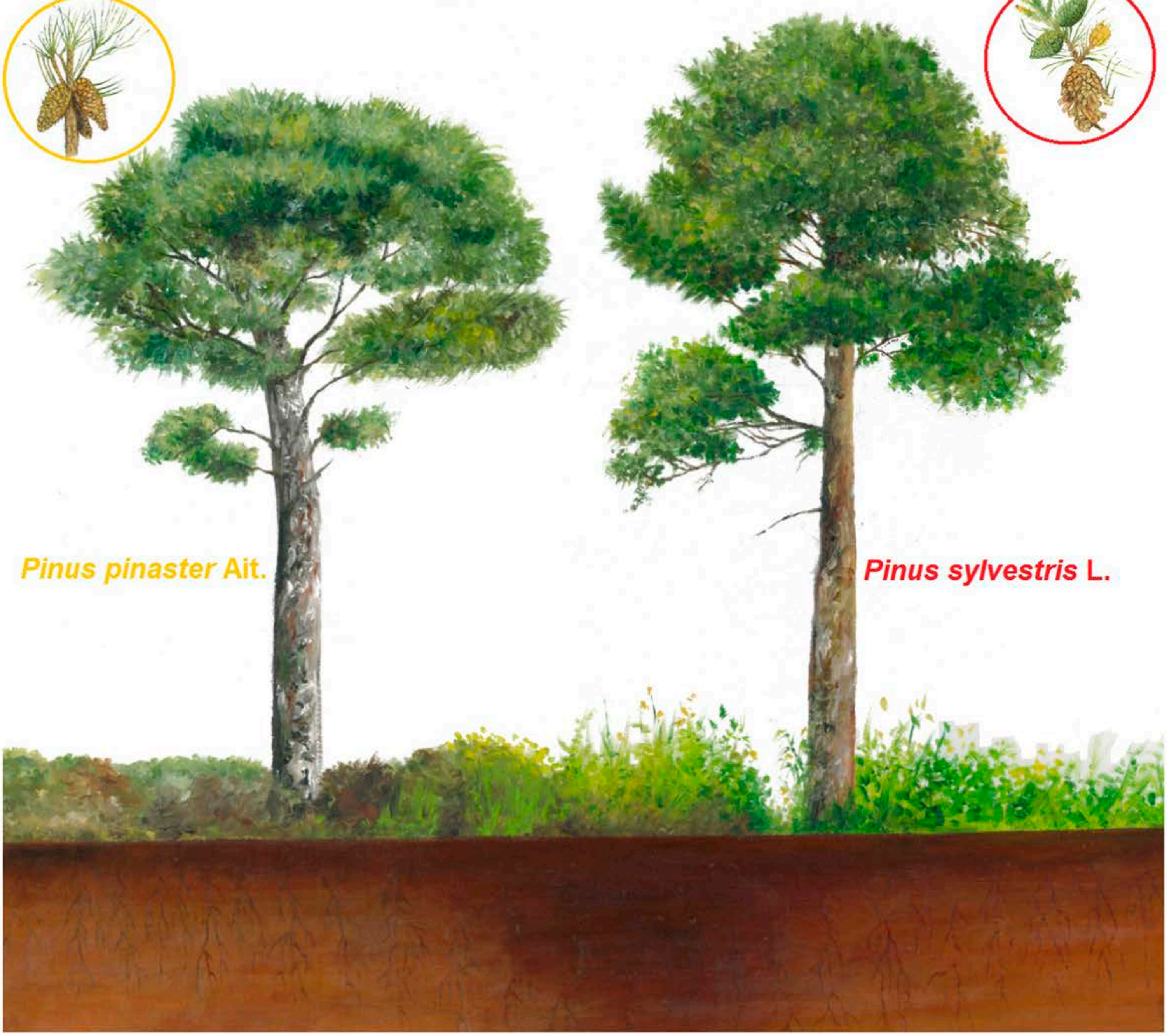
Ecosystem services of mixed stands of Scots pine and Maritime pine: biodiversity conservation and carbon sequestration

Daphne López Marcos

Ph.D. Thesis



Universidad de Valladolid

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PROGRAMA DE DOCTORADO EN CONSERVACIÓN Y USO SOSTENIBLE DE SISTEMAS FORESTALES

TESIS DOCTORAL:

Ecosystem services of mixed stands of Scots pine and Maritime pine: biodiversity conservation and carbon sequestration

SERVICIOS ECOSISTÉMICOS DE MASAS MIXTAS DE PINO ALBAR Y PINO RESINERO: CONSERVACIÓN DE LA BIODIVERSIDAD Y SECUESTRO DE CARBONO

Presentada por Daphne López Marcos
para optar al grado de
Doctora por la Universidad de Valladolid

Dirigida por:
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Dra. Mª Belén Turrión Nieves

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Ecosystem services of mixed stands of Scots pine and Maritime pine: biodiversity conservation and carbon sequestration

Servicios ecosistémicos de masas mixtas de pino albar y pino resinero: conservación de la biodiversidad y secuestro de carbono

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Un immense incendie ravage la jungle.
Affolés, les animaux fuient en tous sens.
Seul un colibri, sans relâche,
fait l'aller-retour de la rivière au brasier,
une minuscule goutte d'eau dans son bec,
pour l'y déposer sur le feu.
Un toucan à l'énorme bec l'interpelle
"tu es fou, colibri, tu vois bien que cela ne sert à rien".
"Oui, je sais" réponds le colibri, "mais je fais ma part"…

Agradecimientos

Sin duda este es uno de los apartados más complicados de escribir de la tesis, pues no hay estadística que ayude a expresar lo que un@ siente. Miro hacia atrás, y durante estos años han sido muchas las personas con las que he compartido buenos y malos momentos. Este ejercicio de retrospección no sólo se remonta al inicio del contrato que me ha permitido hacer esta tesis (2016), sino también a los años previos en los que conseguir financiación sólo traía una ilusión seguida de un gran disgusto (2012). Por ello, de antemano mis disculpas si a alguien he olvidado.

Quería expresar mi más sincero agradecimiento a todas aquellas personas que durante estos años han estado a mi lado:

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Contents

Note: Throughout this doctoral thesis will reference Chapter I as **(I)**, to Chapter II as **(II)**, to Chapter III as **(III)** and to Chapter IV as **(IV)**.

Abstract / Resumen

Abstract

Many studies highlight the role of mixed vs monospecific forests to supply ecosystem services. Most reports of positive mixture effects focus on mixtures that combine tree species with contrasting traits, but little is known on the effect of mixing species that are expected to behave quite similarly as they belong to the same genus. This thesis assessed the effect of mixed vs monospecific stands of Scots pine (*Pinus sylvestris* L.) and Maritime pine (*Pinus pinaster* Aiton.) **(I)** on the carbon storage and exchangeable cations along the soil profile; **(II)** on the understory richness and life-forms composition and its relationship with the soil status; **(III)** on the main tree species regeneration and understory species composition; and **(IV)** on the overstory productivity at two spatial scales (small-scale and stand-level), its relationship with soil moisture and fertility, and its repercussion on the understory.

The research of the overstory-understory-soil relationships was based on six triplets located in the northern Iberian Peninsula (Spain). Each triplet consisted of two plots dominated either by *P. sylvestris* or *P. pinaster* and one mixed plot that contained both species. In each plot, the **soil** was studied by one soil pit of at least 50 cm depth dug at each plot for organic and mineral horizons characterization. The **understory** was analyzed by ten square meter quadrats randomly located per plot, where the cover of every understory species and the number of individuals of the main regeneration trees was estimated visually. The understory species data were codified according to Raunkiær´s life-forms, and the understory richness was also calculated. The **overstory** study was developed at two scales (small-scale: plots of 4 m radius, and stand-level: plots of 15 m radius).

First of all, when the carbon storage and exchangeable cations along the soil profile were studied **(I),** two trends were found: in the topsoil, higher values of carbon stock and total organic carbon were found in *P. sylvestris* stands, lower in *P. pinaster* stands and intermediate in mixed stands; this pattern was related to the C:N ratio of the forest floor. In the intermediate soil layers, carbon stock and total organic carbon tended to be higher in mixed stands and it was related to the higher percentage of fine roots and greater thickness of the first mineral horizon. Differences in soil exchangeable cations among stands were related to the total organic carbon content.

Last, when the understory richness and composition and its relationship with the soil status were assessed **(II),** a water-stress gradient associated with the overstory composition indicated

that *P. pinaster* tolerates lower soil water content than *P. sylvestris*. Mixed stands were under greater water stress conditions than *P. sylvestris* monospecific stands but maintained the same level of understory richness. In addition, a soil fertility gradient defined by organic carbon and exchangeable-magnesium stocks was identified. Hemicryptophytes, whose abundance was greater in mixed stands, were the only understory life-form positively correlated to soil fertility.

Also, when the main tree species regeneration and understory species composition were analyzed **(III)**, the percentage of the basal area of both *Pinus* species was found to be the only characteristic of the stand that significantly influenced the understory composition and tree regeneration. Species characteristics of humid and temperate zones, including *P. sylvestris* regeneration, dominated in *P. sylvestris* monospecific stands, and typical species of well-drained Mediterranean areas, including *P. pinaster* regeneration, dominated in *P. pinaster* monospecific stands. In mixed stands, the highest regeneration of the native Pyrenean oak (*Quercus pyrenaica* Willd.) was accompanied by typical species that share the same regeneration niche.

Finally, when the effect of mixed vs monospecific stands of *P. sylvestris* and *P. pinaster* on productivity was assessed at two spatial scales, as well as the relationship between productivity and understory richness, and soil moisture and fertility **(IV)**, only a small-scale overyielding was found in mixed stands related to the more efficiency in the use of space by both *Pinus* species, thanks to soil water and fertility niche complementarity, which has no negative effect on the understory richness that was mantained in mixed stands thanks to hemicryptophytes. The fundamental role of scale in determining the relationship between species richness and ecosystem functioning in forests was emphasized.

The understanding of the mechanisms underlying the overstory-understory-soil relationships in the mixed forest is improved by these results. Thus, we postulated a competitive advantage of the mixed forests of Scots pine and Maritime pine over the respective monospecific stands in biodiversity conservation, carbon sequestration, fertility, and productivity. Additionally, bearing in mind that the mixture of Scots pine and Maritime pine is widely distributed in Spain, such a mixture should continue to be favored over pure stands in the study area because it helps to improve carbon accumulation in the subsoil, to achieve an overstory overyielding at small scale, to conserve the endemic Pyrenean oak forest regeneration and to maintain understory richness under greater water-stress conditions.

Keywords: *Pinus sylvestris, Pinus pinaster, Quercus pyrenaica,* mixed forest, ecosystem services, biodiversity conservation, carbon sequestration, fertility, productivity, subsoil carbon, soil exchangeable cations, Raunkiær's life-forms, water-stres gradient, richness maintenance, endemic pyrenean oak forest, niche complementarity, overyielding, overstory-understory-soil relationships.

Resumen

Muchos estudios destacan el papel de los bosques mixtos frente a los monoespecíficos en el suministro de servicios ecosistémicos. La mayoría de los estudios se centran en los efectos positivos de la mezcla de especies arbóreas con rasgos contrastables, pero poco se sabe sobre el efecto de la mezcla de especies de las que se espera un comportamiento similar por pertenecer al mismo género. En esta tesis se evalúa el efecto de rodales mixtos frente a los monoespecíficos de pino albar (*Pinus sylvestris* L.) y resinero (*Pinus pinaster* Aiton.) **(I)** sobre el almacenamiento de carbono y cationes intercambiables a lo largo del perfil edáfico; **(II)** sobre la riqueza y composición del sotobosque (formas de vida de Raunkiær) y su relación con el estado del suelo; **(III)** sobre la regeneración de las principales especies arbóreas y la composición de especies del sotobosque; y **(IV)** sobre la productividad del arbolado a dos escalas espaciales (pequeña escala y nivel de rodal), su relación con el suelo y su repercusión sobre la riqueza del sotobosque.

Se realizó una investigación de la relación arbolado-sotobosque-suelo en seis tripletes ubicados en el norte de la Península Ibérica (España). Cada triplete consta de dos parcelas dominadas por *P. sylvestris* o *P. pinaster* y una parcela mezcla de ambas especies. En cada parcela, se estudió el **suelo** de una calicata de al menos 50 cm de profundidad, caracterizando los horizontes tanto orgánicos como minerales. El **sotobosque** se inventarió mediante diez cuadrados de un metro de lado distribuidos aleatoriamente dentro de cada parcela, en los que se estimó visualmente la cobertura de cada especie de sotobosque y el número individuos regenerados de las principales especies arboreas. Las especies del sotobosque se clasificaron por formas de vida de Raunkiær (riqueza y cobertura), y también se calculó la riqueza total del sotobosque. El estudio del **arbolado** se desarrolló a dos escalas espaciales (pequeña escala: parcelas de radio 4 m, y a nivel de rodal: parcelas de radio 15 m).

En primer lugar, cuando se estimaron el almacenamiento de carbono y los cationes intercambiables en el perfil del suelo **(I)**, se encontraron dos tendencias: en la capa superior del suelo, los valores más altos del carbono almacenado y carbono orgánico total se dieron en los rodales de *P. sylvestris,* los más bajos en los de *P. pinaster* e intermedios en los mixtos; este patrón se relacionó con la proporción C/N de la hojarasca. En capas inferiores, ambos parámetros fueron más altos en los rodales mixtos y se relacionó con el mayor porcentaje de raíces finas y espesor del primer horizonte mineral. Las diferencias en los cationes intercambiables del suelo entre rodales se relacionaron con el contenido total de carbono orgánico.

Después, cuando se evaluó la riqueza y composición del sotobosque y su relación con el estado del suelo **(II)**, un gradiente de estrés hídrico asociado a la composición del arbolado indicó que *P. pinaster* toleraba menor contenido de agua en el suelo que *P. sylvestris*. Los rodales mixtos se encoentraban bajo mayor estrés hídrico que los monoespecíficos de *P. sylvestris* pero

mantenían el mismo nivel de riqueza en el sotobosque. Además, se identificó un gradiente de fertilidad edáfico definido por el carbono orgánico y reservas de magnesio intercambiable. Los hemicroptófitos, cuya abundancia fue mayor en los rodales mixtos, fue la única forma de vida del sotobosque que se correlacionó positivamente con la fertilidad del suelo.

Además, cuando se analizó la regeneración de las principales especies arbóreas y la composición de las especies del sotobosque **(III)**, el porcentaje de área basal de ambas especies de *Pinus* fue la única característica del rodal que influyó significativamente en la composición del sotobosque y en la regeneración de los árboles. Especies características de zonas húmedas y templadas, incluido el regenerado de *P. sylvestris*, dominaban en los rodales monoespecíficos de *P. sylvestris*, y especies típicas de áreas mediterráneas bien drenadas, incluido el regenerado de *P. pinaster*, dominaban en los rodales monoespecíficos de *P. pinaster*. En los rodales mixtos, la regeneración del roble melojo nativo fue mayor y estuvo acompañada por especies típicas del sotobosque que comparten su mismo nicho de regeneración.

Finalmente, cuando se estudió la productividad del arbolado a dos escalas espaciales, se relacionó con el suelo y se analizó su repercusión en el sotobosque **(IV)**, se encontró en los rodales mixtos un sobre-rendimiento del arbolado a pequeña escala espacial, que se relacionó con la mayor eficiencia en el uso del espacio por ambas especies de pinos, gracias a la complementariedad de nicho edáfico (uso del agua y fertilidad). Además, no se encontró un efecto negativo del sobre-rendimiento del arbolado sobre la riqueza del sotobosque que se mantiene en los rodales mixtos gracias a la contribución de los hemicriptófitos. Se destaca la importancia de la escala para determinar la relación diversidad-productividad en bosques.

Estos resultados contribuyen a comprender mejor algunos de los mecanismos subyacentes a la relación arbolado-sotobosque-suelo en bosques mixtos. Parece que la mezcla de *P. sylvestris* y *P. pinaster* supone una ventaja competitiva sobre las masas monoespecíficas en cuanto a la conservación de la biodiversidad, secuestro de carbono, fertilidad y productividad. Teniendo en cuenta, además, que estas mezclas están ampliamente distribuidas en España, parece adecuado proponer que se sigan potenciando en el área de estudio porque contribuyen a incrementar la acumulación de carbono en el subsuelo, proporcionar un sobre-rendimiento del arbolado, conservar el regenerado de especies endémicas como el roble melojo y mantener la riqueza del sotobosque en suelos con menor contenido hídrico.

Palabras clave: *Pinus sylvestris*, *Pinus pinaster*, *Quercus pyrenaica*, bosque mixto, servicios ecosistémicos, conservación de la biodiversidad, secuestro de carbono, fertilidad, productividad, carbono del subsuelo, cationes intercambiables del suelo, formas de vida de Raunkiær, gradiente hídrico, mantenimiento de la riqueza, melojar endémico, complementariedad de nicho, sobre-rendimiento, relación arbolado-sotobosque-suelo.

Outline of the thesis

This thesis comprises four studies focused on increasing the knowledge of the dynamics and the functioning of mixed vs. monospecific stands of Scots pine (*Pinus sylvestris* L.) and Maritime pine (*Pinus pinaster* Ait.) in relation to the provision of ecosystem services such as biodiversity conservation and carbon sequestration. For that, the relationships between different components of forest ecosystem (i.e. overstory, understory and soil) are addressed in the different chapters (see Figure 1).

Chapter **(I)**, the first article of the compendium, addresses the study of soil profile by depths, including organic and mineral horizons, and its relationship with the overstory composition at the stand level (see Figure 19). The aim of this study is to quantify the differences among stand types in carbon storage along the soil profile and its relationship with exchangeable cations in mixed vs. monospecific stands of Scots pine and Maritime pine.

Chapter **(II)**, the second article of the compendium, addresses the characterization of the understory (Raunkiær´s life-forms richness and composition) and its relationship with the overstory composition and soil properties (of the whole soil profile) at the stand level (see Figure 25). The aim of this study is to assess the effect of the overstory on the understory richness and life-forms composition and its relation to soil status.

Chapter **(III)**, the third article of the compendium, also addresses the characterization of the understory, but now at the species level (species richness and composition) and including main tree species regeneration, and its relationship with overstory composition and stand characteristics (see Figure 30). The aim of this study is to relate the understory richness and tree regeneration to significant stand characteristics, responsible for the niche segregation of the main understory species.

Chapter **(IV)**, the fourth article of the compendium, addresses the fundamental role of scale in determining the relationship between species richness and ecosystem functioning in forests (Figure 37). The aim of this study is to assess the effect of the mixture of *Pinus sylvestris* and *P. pinaster* on productivity at two spatial scales, the relation of overyielding found in mixed stands with soil moisture and fertility, and its effect on the understory richness.

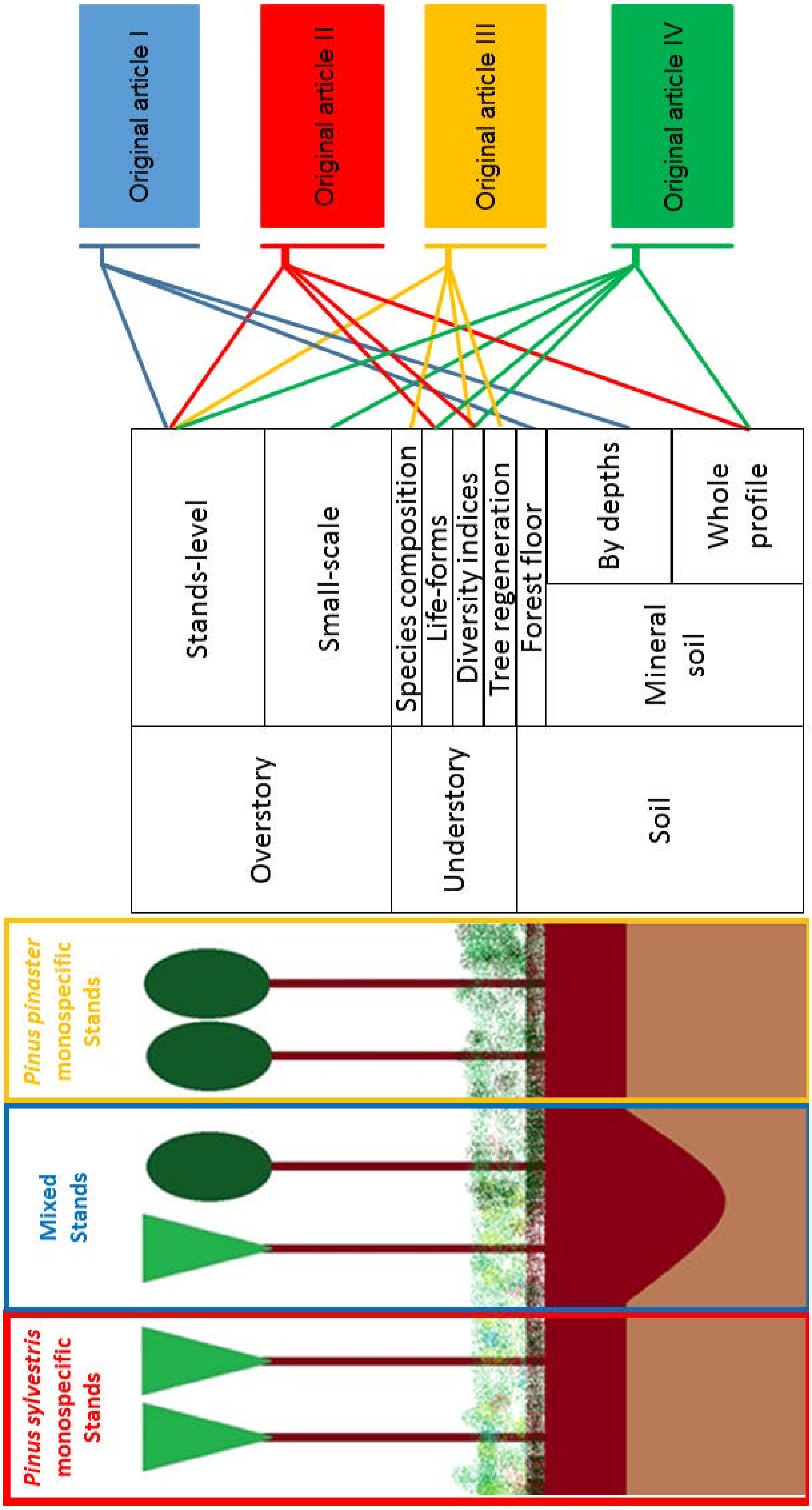

Figure 1. Thesis synthesis. Illustration of a triplet with the three stand types (monospecifics stands of *Pinus sylvestris* or *P. pinaster*, and mixed stand) and their ecosystem components, overstory, understory, and soil. Also, the relationships between different ecosystem components assesed in each original article are indicated.

List of Original Articles

This thesis has generated four original articles published or under consideration for publication in SCI journals. The firt two have already been published, and the third one has been accepted for publication. The fourth paper is under revision. Each article gives rise to a chapter of this thesis.

Chapter I

López-Marcos D, Martínez-Ruiz C,Turrión MB, Jonard M, Titeux H, Ponette Q, Bravo F (2018). **Soil carbon stocks and exchangeable cations in monospecific and mixed pine forests**. European Journal of Forest Research 137: 31–84. doi:10.1007/s10342-018-1143-y

Q1 Journal of "Forestry" category with an impact factor of **2.629** in the last 5 years.

Chapter II

López-Marcos D, Turrión MB, Bravo F, Martínez-Ruiz C (2019). **Understory response to overstory and soil gradients in mixed vs. monospecific Mediterranean pine forests**. European Journal of Forest Research 138: 939–955. doi:10.1007/s10342-019-01215-0

Q1 Journal of "Forestry" category with an impact factor of **2.629** in the last 5 years.

Chapter III

López-Marcos D, Turrión MB, Bravo, F, Martínez-Ruiz C (2020a). **Can mixed pine forests conserve understory richness by improving the establishment of understory species typical of native oak forests?** Annals of Forest Science doi: 10.1007/s13595-020-0919-7

Q1 Journal of "Forestry" category with an impact factor of **2.555** in the last 5 years.

Chapter IV

López-Marcos D, Turrión MB, Bravo F, Martínez-Ruiz C (2020b). **Overyielding at a small spatial scale in mixed pine forests as result of belowground resources complementarity: implications for understory richness conservation**. Ambio (under revision)

Q1 Journal of "Enviromental Sciences" category with an impact factor of **4.674** in the last 5 years.

Note: Citation styles in each original article are standardised through the Thesis. Numeration of tables and figures is correlative throughout the thesis.

Ecosystem services

Westman (1977) wondered for the first time how much nature's services cost and coined the term “nature’s services”, and years after Ehrlich and Mooney (1983) mention for the first time the term “ecosystem services”. However, related ideas had been brewing in the academic literature for decades (Costanza et al. 2017). What changed in the second half of the 20th century was that the loss of these ecosystem services became much more apparent, as natural capital was quickly being depleted (Beddoe et al. 2009).

A key event in the history of ecosystem services was a meeting in October 1995 of Pew Scholars in Conservation and the Environment in New Hampshire (Costanza et al. 2017). During the meeting, the idea to synthesize all the information being assembled into a quantitative global assessment of the value of ecosystem services was proposed and it was concluded that quantity was significantly larger than the global gross domestic product at the time (Costanza et al. 2017). Thus was demonstrated that ecosystem services were much more important to human wellbeing than conventional economic thinking had given them credit for (Costanza et al. 2017).

An important milestone of ecosystem services research was the Millennium Ecosystem Assessment (MEA; La Notte et al. 2017), a monumental work involving over 1300 scientists (Fisher et al. 2009). MEA classified the ecosystem services in four categories: supporting, regulating, provisioning and cultural services (Table 1; MEA 2005), and defined the “ecosystem services” as the ecological characteristics, functions, or processes that directly or indirectly contribute to human wellbeing: that is, the benefits that people derive from functioning ecosystems (MEA 2005).

MEA (2005), in their reports, evaluates the ecosystem services of different systems as Marine Fisheries Systems, Coastal Systems, Inland Water Systems, Forest and Woodland Systems, Dryland Systems, Island Systems, Mountain Systems, Polar Systems, Cultivated Systems, and Urban Systems.

Table 1. Ecosystem services categories (MEA 2005; Wallace 2007).

Ecosystem services	Definition	Examples
Provisioning services	The products obtained from ecosystems	Food, fiber, genetic resources, bio-chemicals, natural medicines, ornamental resources, and freshwater
Regulating services	The benefits obtained from the regulation of ecosystem processes	Air quality regulation, climate regulation, water regulation, erosion regulation, disease regulation, pest regulation and pollination
Cultural services	The non-material benefits people obtain from ecosystems through spiritual enrichment, cognitive development, reflection, recreation, and aesthetic experience	Cultural diversity, spiritual and religious values, recreation and ecotourism, aesthetic values, knowledge systems, and educational values
Supporting services	The ecosystem services that are necessary for the production of all other ecosystem services	Soil formation, photosynthesis, primary production, nutrient cycling, and water cycling

Since the world's forests cover thirty percent of the earth's surface and provide critical and diverse services and values to human society the formally measuring and accounting for forest ecosystem services is a necessary first step toward properly valuing them (Jenkins and Schaap 2018). MEA (2005) examined the state of forest ecosystem services worldwide and concluded that the combined economic value of 'nonmarket' (social and ecological) forest services may exceed the recorded market value of timber, although these values are rarely taken into account in forest management decisions.

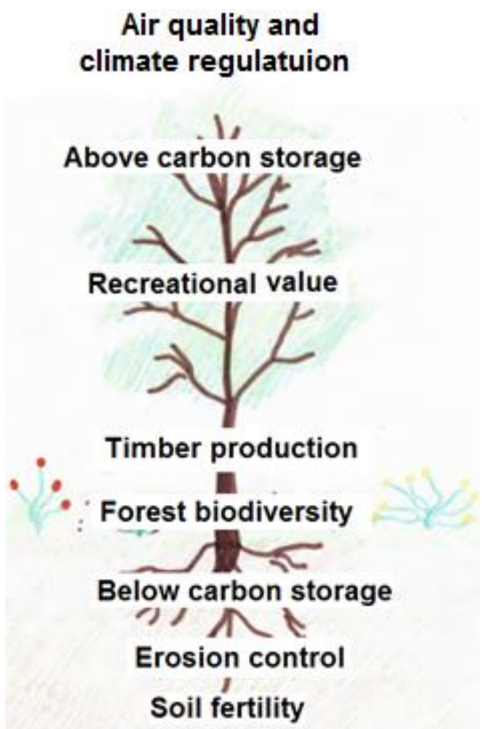

Figure 2. Forest ecosystem services (Illustration by Daphne López-Marcos based on Lambini et al. 2018)

MEA (2005) mentions as Major Classes of Forest Services the biodiversity conservation and the carbon sequestration (Figure 2). On the one hand, the forest functions as a primary habitat for a wide range of species supporting biodiversity maintenance and conservation (Jenkins and Schaap 2018). But also, the forest growth sequesters and stores carbon from the atmosphere, contributing to the regulation of the global carbon cycle and climate change mitigation (Jenkins and Schaap 2018). Thus, the analysis of biodiversity conservation and carbon sequestration in a forest type (i.e. mixed stands of Scots pine and Maritime pine) will be the target of this thesis.

Biodiversity conservation

The biodiversity concept is in constant evolution because it continues to be a topic of great interest since the end of the 19th century when Ecology emerges as a science (Martínez-Ruiz 2009). Magurran (1988, 2004) dedicates several chapters to its importance and measurement.

At the Rio Earth Summit in 1992, one of the most widely accepted definitions of biodiversity emerged: *"the variability among living organisms, including terrestrial, marine and other aquatic ecosystems, and the ecological complexes of which they are part: this includes diversity within species, between species, and of ecosystems"* (UNEP 1992).

Unfortunately, such important processes as interspecific interactions, natural disturbances, and nutrient cycles are left to mention. Biodiversity is not simply the number of genes, species, ecosystems in a defined area (Noos 1990). To complete this definition is necessary to recognize the three primaries attributes of ecosystems that constitute the biodiversity of an area, i.e. composition, structure, and function. The composition is the total number of species (Noos 1990; MEA 2005); the structure is a measure of their heterogeneity and complexity through the study of their patterns (Noos 1990; MEA 2005); and the function tries to understand the impact of processes in the ecosystem (Noos 1990; MEA 2005).

The importance of forest biodiversity for both its existence value as a major component of global biodiversity and its utilitarian value as the source of innumerable biological resources used by people has been recognized by the Convention on Biological Diversity and numerous other agreements and studies. Understory vegetation represents the largest component of plant biodiversity in most forest ecosystems (Mestre et al. 2017) and is a key element in the forest ecosystem because of its high compositional, structural and functional diversity, its numerous interactions with different trophic levels, and its important role in ecosystem functioning (Aubin et al. 2008; Liu et al. 2017). Thus, the understory biodiversity should be also considered to know the potential of mixed vs. monospecific stand of Scots pine and Maritime pine in the provision of ecosystem services.

Accordingly, this thesis addresses the analysis of first, diversity composition through the study of the richness **(II) (III) (IV)**, composition and niche amplitude **(III)** of the plant species of the understory; second, biodiversity structure through the study of the understory Raunkiær's life-forms composition **(II)** and the tree species mixture proportion **(II) (III)** and third, diversity function through the study of the overstory and understory relationships with soil carbon sequestration **(I) (II)** and soil water and fertility **(II) (IV).**

Carbon sequestration

Warming in the climate system is unequivocal and the human influence on the climate system is clear (IPCC 2014). Global warming has its origin in increasing the atmospheric concentration of greenhouse gases (Herrero de Aza 2010), such as carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O).

The term "carbon sequestration" is defined as the transfer and secure storage of atmospheric CO_2 into other long-lived pools that would otherwise be emitted or remain in the atmosphere (Lal 2008). These pools are located in the ocean, biosphere, pedosphere, and geosphere (Lorenz and Lal 2010).

Forest ecosystems can sequestrate the atmospheric CO_2 during photosynthesis and stored the fixed carbon in the vegetation biomass (Ruiz-Peinado 2013). Also, forest ecosystems can sequester carbon in the soil for secure carbon storage (Lorenz and Lal 2010). Thus, forests play an important role in the global carbon cycle as an Earth's terrestrial carbon sink (Andivia et al. 2016). Carbon sequestration is necessary to reduce CO_2 concentrations and promote the mitigation of the effects of warming on the planet (Herrero de Aza 2010) and is considered one of the most cost-effective climate change mitigation strategies in the sustainable forest management (Figure 3; IPCC 2014), being also a forest ecosystem service.

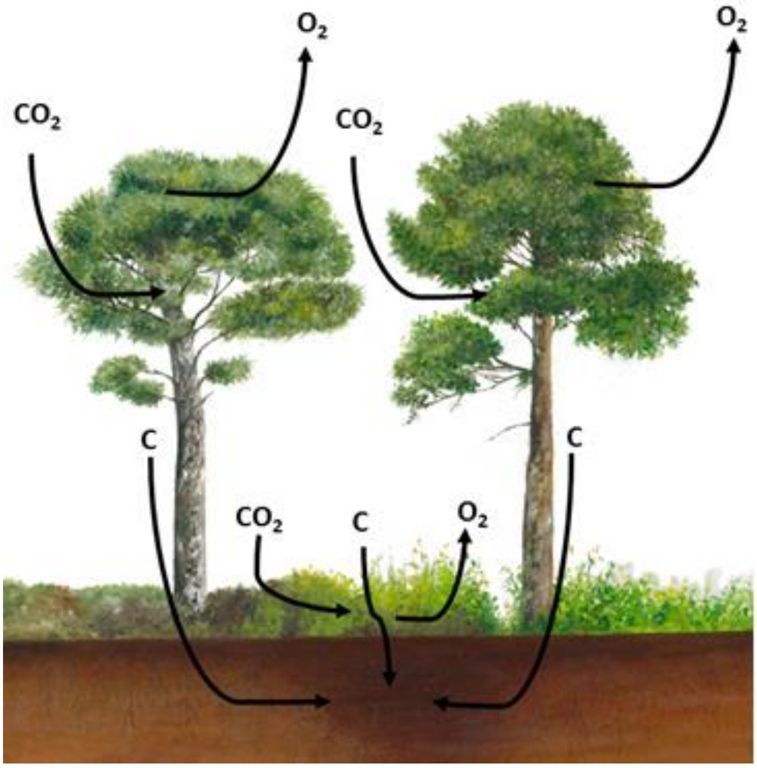

Figure 3. Carbon and oxygen fluxes associated with the photosynthesis in mixed forests of Scots pine and Maritime pine. CO_2 = carbon dioxide, O_2 = oxigen; C = carbon. Illustration by Carmen Calvo-Mañero.

Although the carbon input inthe vegetation (overstory and understory) is considerable, the more important carbon inputs are below ground. About two-thirds of the carbon stored by forest ecosystems are contained in the forest soil (Table 2; Pan et al. 2011).

Table 2. Stored carbon in vegetation and soil in diferent biomes (Pardos 2010).

Bioma	Distribution	Stored carbon (Gt)		
		Vegetation	Soil	Total
Temperate forests	USA, Europe, China, Australia	59	100	159
Boreal forests	Rusia, Canada, Alaska	88	471	559
Tropical forests	Asia, Africa, South America	66	264	330

The mechanisms of carbon storage vary depending on climate, vegetation, soil texture and mineralogical composition (Almendros 2004). Therefore, the species composition (Augusto et al. 2015) and the identity of the dominant species (Ruiz-Peinado et al. 2017) besides the climate, type of soil, and geomorphology affect both the accumulation and the distribution of the carbon along the soil profile (Chapin 2003) including the forest floor (Ruiz-Peinado et al. 2017). Consequently, the carbon stock of the upper mineral horizon is not a useful estimator of the total carbon set of the soil, since a substantial fraction of this carbon can be stored in the subsoil (Jandl et al. 2014). Although the carbon stock in the subsoil is less dynamic, it can contribute to changes in the total soil carbon set (Jandl et al. 2014). Thus, the study of the soil profile **(I)** **(II)** and the forest floor **(I)** is of great relevance.

On the other hand, the soil nutrient status could be an indirect consequence of the organic matter contribution to the soil (Cremer and Prietzel 2017), since the decomposition of plant tissues in terrestrial ecosystems regulates the transfer of carbon and nutrients to the soil (Wang et al. 2014a,b). But also the soil nutrient status could be an indirect consequence of the forest management through the tree species selection (Jandl et al. 2014; Cremer and Prietzel 2017). Thus, it is necessary to clarify the relationships of soil nutrients, as soil exchangeable cations, with soil organic matter **(I)** and vegetation **(II)** **(IV)**.

The indirect benefits of soil carbon sequestration are reflected in the improvement of other soil features, such as water retention capacity or nutrient availability (Almendros 2004). All these characteristics are associated with the potential of organic matter to regulate soil composition (Almendros 2004). Thus, it is relevant to study not only the soil organic matter but also other soil features, as water or fertility, to better understand this process.

Mixed forests

The definition of the mixed forest has been widely debated (Bravo-Oviedo et al. 2014), and there is not yet a common definition valid across Europe (Bravo-Oviedo et al. 2013). The large climatic variability and types of admixtures in the continent has lead to local definitions (Bravo-Oviedo et al. 2013). Thus, in the Cost European Cooperation in science and technology framework, the European Network on Mixed Forests (EuMIXFOR) has been created to establish a long-lasting network of mixed forests (Bravo-Oviedo et al. 2013).

The proposed definition by EuMIXFOR sais that *"A mixed forest is a forest unit of at least 0.5 ha, excluding linear formations, where at least two tree species coexist at any developmental stage sharing common resources (light, water, and/or soil nutrients). The presence of each of the component species is normally assessed as a proportion of the number of stems or basal area, although volume, biomass and canopy cover may be used for specific objectives. A variety of structures and patterns of mixtures can be perceived to occur, while the interactions between the component species and their relative proportions may change over time"* (Bravo-Oviedo et al. 2013).

Toumey and Korstian (1947) clarified what species proportion must have a mixed forest. They defined the pure stands as those where 80 percent or more of the overstorey is of a single species. Thus, a mixed forest must have less of the 80 percent of the overstorey of each species.

The overlapping of ecological niches is the first requirement that allows the coexistence of the species in the mixture (Pretzsch 2009). Mixing can occur only in areas where there is overlap, in terms of resource availability and environmental conditions (Pretzsch 2009).

The European Commission and EuroStat (2013) calculated that 180.2 million ha of the pan-European region is cover by forests and 23% of this land is covered by mixed forests (Forest Europe et al. 2011). Also, the gradual decrease in the area of single-species forests in Europe and a steady evolution towards mixtures of species have been verified (Forest Europe et al. 2011)

On the other hand, the management of mixed-species forests has taken on greater relevance over the last decades as a result of the growing evidence that mixtures can supply numerous ecosystem services more efficiently than monospecific forests (Gamfeldt et al. 2013). Thus the need for monitoring this portfolio of mixed forest ecosystem services is acknowledged within the Pan-European region with the adoption of a framework of criteria and indicators of sustainable forest management (Bravo-Oviedo et al. 2014).

Until recently, pure stands were believed to ameliorate the timber yield both in quantitative and qualitative terms, and that had an impact on the quality of the forest ecosystem and its biodiversity. Nowadays, the way of managing natural resources is changing towards multi-functional management because the provision of goods is not anymore the only objective that forest managers should achieve (Grilli et al. 2016). After the introduction of the concept of ecosystem services, multifunctional management gained even more consensus (Grilli et al. 2016).

Recent studies have highlighted the benefits provided by mixed forests. They have higher growth rates (Piotto 2008) and, under certain conditions, mixed forests can produce a higher yield than monocultures (Saetre et al. 1997; Pretzsch et al. 2010). The improvement in soil conditions (Davidson et al. 1998; Brandtberg et al. 2000) and the carbon sequestration increment (European Commission 2010; Andivia et al. 2016; López-Marcos et al. 2018) have also been recorded. They can create a better habitat for wildlife (Carnus et al. 2006) as well as participate in biodiversity conservation (Felton et al. 2010; López-Marcos et al. 2019, 2020a). Mixed forests are also more resilient, being less affected by damages from hunting and pathogens and less sensitive to the wind and fire outbreak (González et al., 2006). The mixture of tree species also performs as a measurement of adaptive management to climate change, increasing the resilience of forest ecosystems and improving their adaptability (Temperli et al. 2012). Finally, in some cases, socio-economic studies highlighted that mixed forests have a higher recreational value for tourists (Norman et al. 2010; Grilli et al. 2014).

In Spain, 19% of the total forest surface is mixed forests (MAGRAMA 2012) and they are mainly formed by combinations of broadleaf-broadleaf or broadleaf-conifer species (Riofrío 2018). However, forests with coexisting pine species are also common in Spain, covering almost 0.5 million ha (Montero and Serrada 2013). Some of the mixed pine forests in Spain are composed by *P. sylvestris–P. nigra* J.F.Arnold (Trasobares et al. 2004), or *P. halepensis* Mill.–*P. nigra–P. sylvestris* (Granda et al. 2018) in the northeast; *P. halepensis–P. pinea* L. (Cattaneo et al. 2018), or *P. pinaster–P. pinea* (Ledo et al. 2014) in the northern plateau; *P. sylvestris–P. nigra* in the Southern Iberian Range (Jucker et al. 2014), or *P. pinaster–P. sylvestris* in the "Sierra de la Demanda" (Riofrío et al. 2017a, b, 2019; Cattaneo 2018; López-Marcos et al. 2018, 2019, 2020a, b). The admixtures of *Pinus pinaster-Pinus sylvestris* being the object of this thesis.

Mixed stands of Scots pine and Maritime pine

Scots pine and Maritime pine are two of the main forest species in Spain. They grow in pure and mixed stands (see Figures 4, 5 and 6) either naturally or as a result of species selection for afforestation (Serrada et al. 2008). Both species coexist on moderate slopes mainly in the Iberian and Central Mountain Range in approximately 120,000 ha when their natural ecological distributions overlap: in the colder and higher areas of Maritime pine distribution and close to the southern latitudinal limit of Eurasian distribution for Scots pine (Riofrío 2018).

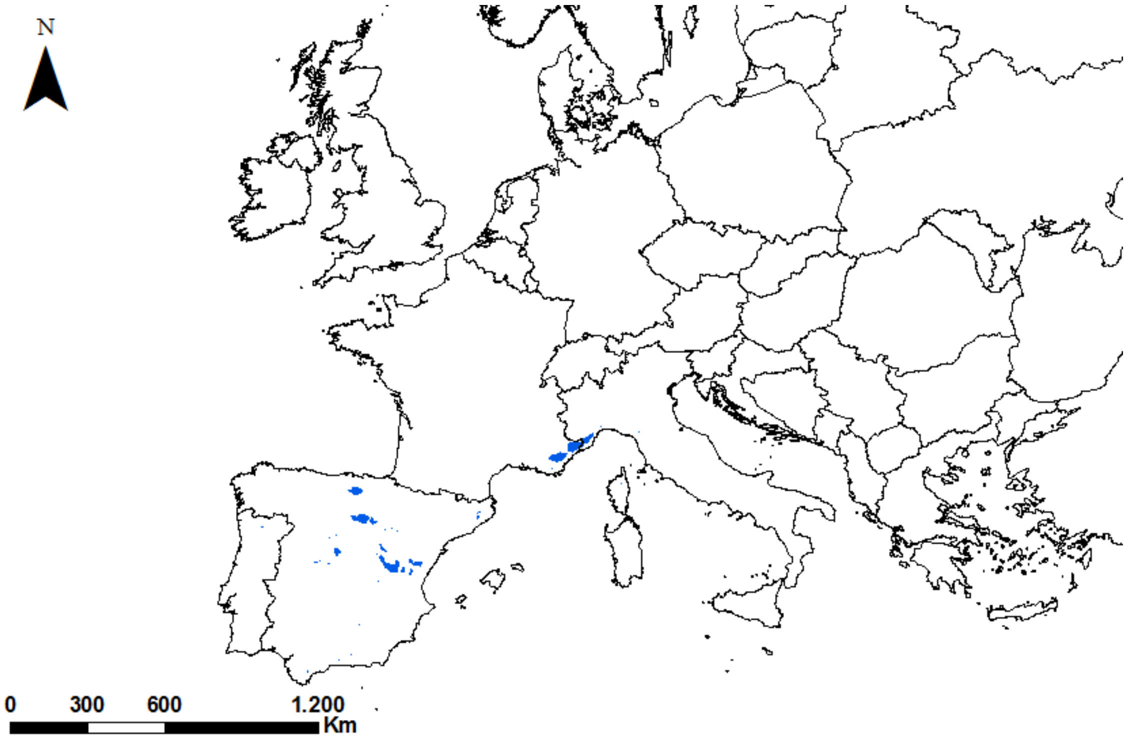

Figure 4. Distribution map of admixtures of Scots pine (*Pinus sylvestris* L.) and Maritime pine (*Pinus pinaster* Ait.) elaborated by crossing the data of the EUFORGEN (2009) programme of both natural and naturalized occurrences of *Pinus pinaster* and *Pinus sylvestris*.

These mixed stands are particularly interesting because of their location at the edges of the Scots pine range distribution, where ecological conditions (high temperatures, frequent droughts) approach the species tolerance limit and the most drastic effects of climate change are expected (Matías and Jump 2012). Meanwhile, Maritime pine in a dynamic and continuous process expands into the natural distribution areas of Scots pine, especially in more xeric site conditions (García-Güemes and Calama 2015).

Both *Pinus* species show similar crown architecture and slight differences in shade tolerance (Riofrío et al. 2017a), but differ in leaf traits (more recalcitrant leaf litter (Herrero et al.

2016) and longer needles (Amaral Franco 1986) for Maritime pine), and water-stress tolerance (*P. pinaster* tolerates lower soil water content than *P. sylvestris*; López-Marcos et al. 2019).

The mixed pine forests of Maritime pine (*Pinus pinaster*) and Scots pine (*Pinus sylvestris*) in the "Sierra de la Demanda" will be the object of this thesis due to the high ecological and economic value of both species in that area. The "Sierra de la Demanda" is a place with a high ecological value and one of the areas with most tradition in forest management in Spain. The population is strongly linked to forests, which have been the basis of the economy for centuries. In this frame, monitoring the biodiversity and carbon sequestration of mixed vs monospecific stands of Scots pine and Maritime pine in the "Sierra de la Demanda" will be an opportunity to value these forests in the field of ecosystem services.

In the "Sierra de la Demanda" the Sustainable Forest Management Research Institute (iuFOR) has a network of 36 permanent plots established in 2014. Productivity (Riofrío et al. 2017b), grow efficiency (Riofrío et al. 2017a), changes in the crowns (Cattaneo 2018) and the allometric changes (Riofrío et al. 2019) in mixed vs monospecific stands of Maritime pine and Scots pine have been studied there. Nevertheless, the provision of ecosystem services of this admixture such as carbon sequestration and biodiversity conservation have not been studied yet.

<u>Scots pine</u>

Scots pine (*Pinus sylvestris* L.) is the most widely distributed *Pinus* species in the world. This species presents great ecological amplitude (Bueis et al. 2016) cross the whole Eurasian continent (Mátyás et al. 2004; see Figure 5). At the boreal forest limit, it survives with 300 mm annual rainfall, and towards the steppe plains of Central Asia, its occurrence is limited by the length of the drought period (Mátyás et al. 2004). In southern Europe and Asia Minor, isolated occurrences are confined to the montane zone (Mátyás et al. 2004). Spanish stands constitute the southern limit of its distribution, where it occupies 1.28 million hectares (Serrada et al. 2008). The genetic variety is immense and several different subspecies exist across its distribution (Mátyás et al. 2004).

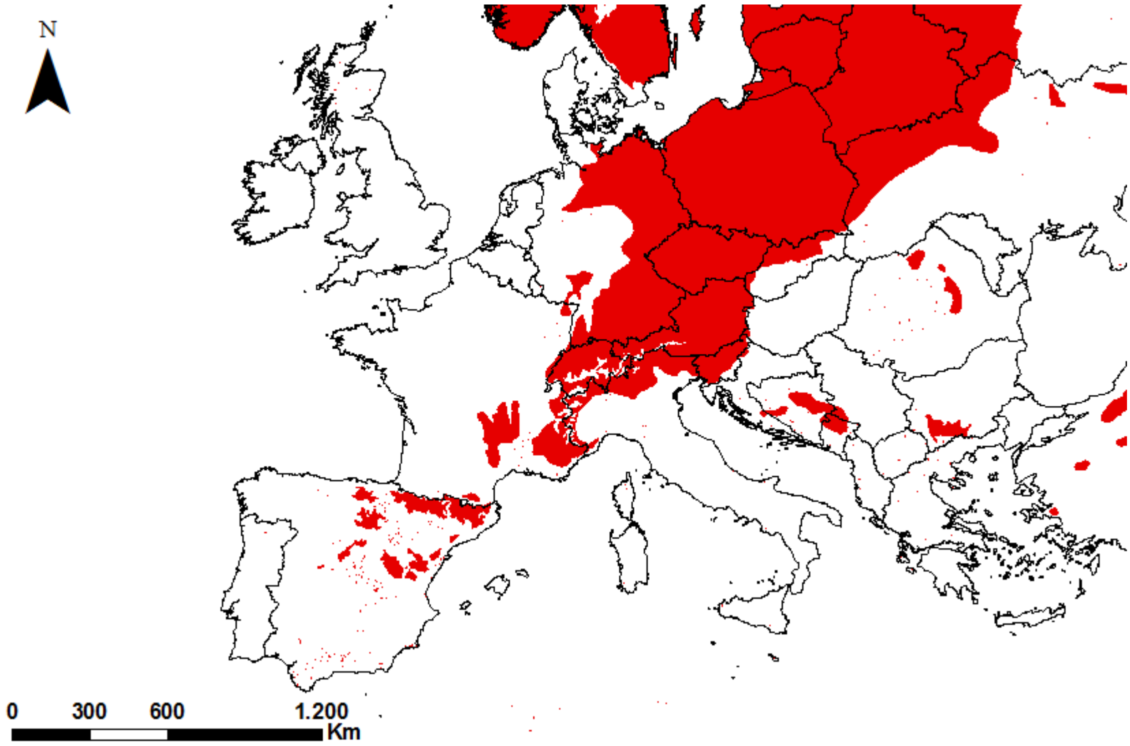

Figure 5. Distribution map of Scots pine (*Pinus sylvestris* L.) elaborated by crossing the data of the EUFORGEN (2009) programme of both natural and naturalized occurrences of *Pinus sylvestris*

Scots pine is a pioneer species that readily regenerate after major natural or human disturbances if weed competition and grazing pressure are low (Mátyás et al. 2004). That *Pinus* species demands a lot of light but tolerates partially shaded sites, tolerates frost and drought relatively well (Cattaneo 2018), has a xeric-mesophilic character and develops in soils with a frank texture. It has a powerful radical system, with a generally long main root and an oblique and long secondary radical system (Bravo-Oviedo and Montero 2008).

Scots pine is a commercially important tree species in Europe (Mátyás et al. 2004). Its moderate ecological demands render Scots pine an ideal species for artificial regeneration, thus its seeds have been traded and used across Europe for centuries (Mátyás et al. 2004).

Maritime pine

Maritime pine (*Pinus pinaster* Ait.) is a broadly distributed conifer in the western Mediterranean Basin, Southern Europe and Africa, and the Atlantic coast of Portugal, Spain, and France (Alía and Martín 2003; Figure 6) but not continuously due to geographic isolation and human activity since ancient times (Serrada et al. 2008). The Spanish stands occupy 0.68 million ha (Serrada et al. 2008).

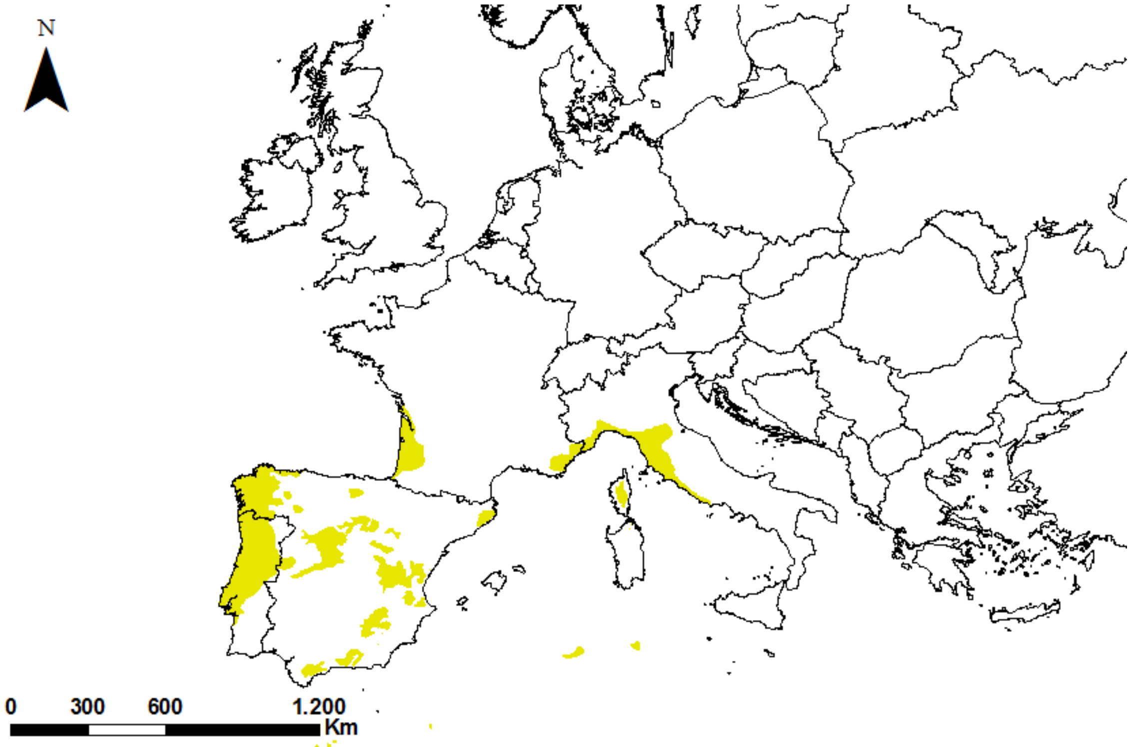

Figure 6. Distribution map of Maritime pine (*Pinus pinaster* Ait.) elaborated by crossing the data of the EUFORGEN (2009) programme of both natural and naturalized occurrences of *Pinus pinaster*

Maritime pine is a light-demanding, shade-intolerant, fast-growing species that occupy very diverse sites, showing high genetic diversity within populations (Riofrío 2018). It is also frost-resistant and tolerant to summer drought, which favors adaptation to local ecological conditions (Riofrío 2018). That pine has a xerophytic character with a potent radical system: a very deep main root and horizontal secondary radical system (Bravo-Oviedo and Montero 2008). The ability of the species to grow in very poor soils and under prolonged drought is one of the reasons for its use in afforestation programs for wood production or soil protection (Alía and Martín 2003b).

The Maritime pine's wood is used for construction, furniture, and poles, while its resin is tapped to make rosin and turpentine. Other uses include stabilization of dunes and slopes, as shelterbelts near coastal areas and for the production of plant nursery substrates (Alía and Martín 2003b).

Objectives and hypothesis

General objective

The purpose of this thesis is to increase the knowledge on the dynamics and the functioning of mixed vs. monospecific stands of Scots pine and Maritime pine concerning the provision of ecosystem services such as the conservation of biodiversity and carbon sequestration. For that, we relate the different components of the forest ecosystem such as overstory, understory, and soil (see Figure1).

Our general hypothesis is that mixed stands of Scots pine and Maritime pine can supply ecosystem services more efficiently than the respective monospecific forests.

Specific objectives

The specific objectives and the hypotheses are structured by chapters:

I. To quantify the differences among stand types in carbon storage along the soil profile (every 10 cm depth) and its relationship with the exchangeable cations, and to investigate the possible causes of these observed differences.

   We hypothesize that the stand type influences the C storage and, indirectly, the exchangeable base cations of the mineral soil by the organic matter decomposition effect. Thus, differences in the topsoil among stand types are expected to be found, as well as a positive interactive effect of the admixture of both pine species on the accumulation of carbon in the soil profile in comparison with monospecific stands.

II. To assess the effect of the overstory on the understory richness and Raunkiær's life-forms composition and its relationship with soil properties.

   We hypothesize that the admixture of both pine species has a positive interactive effect on the understory richness in comparison with monospecific stands and that the understory composition and richness are positively correlated with (and can be derived from) the availability of nutrients and water.

III. To relate the understory richness and tree regeneration to significant stand characteristics, responsible for the niche segregation of the main understory species.

We hypothesize that the proportion of both *Pinus* species in the overstory is the most influential characteristic of the stands on the understory composition and tree regeneration and that the mixture of both pine species favors the native tree regeneration and associated understory species that contribute to conserving a high understory species richness in mixed stands.

IV. To assess the effect of the spatial scale on overstory yield in mixed forests, to understand the mechanisms involved, and to analyze the overstory yield effect on the understory richness.

We hypothesize that there is an overstory overyielding in the mixed stand, only detected at a small spatial scale, caused by soil niche complementarity.

Study area

The experimental device is located in the "Sierra de la Demanda" between the Burgos and Soria regions, in North-Central Spain (41° 47' 35'' N and 41° 53' 41'' N latitude, and 2° 56' 12'' W and 3° 20' 46" W longitude). It consists of eighteen forest plots distributed in six triplets located on an east-west axis of about 33 km and on a north-south axis of about 11 km (Figure 7). For further details about the location of the triplets, see Figure 45, 47, 48, 49, 50 and 51 in Suplementary material 'Location').

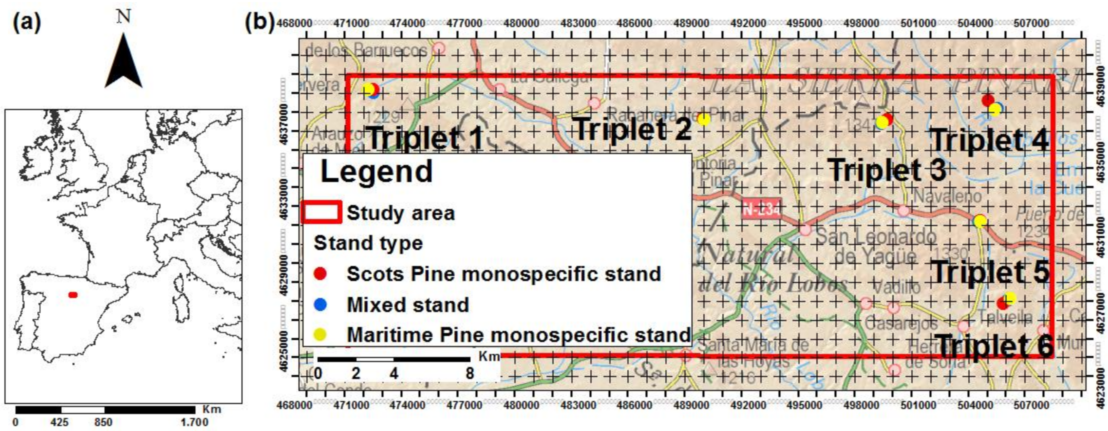

Figure 7. (a) Location the study area in Europe. (b) Location of the triplets in the 'Sierra de la Demanda' in the North-Central Spain and location of the plots in each triplet. *Pinus sylvestris* monospecific stands: red circles; *Pinus pinaster* monospecific stand: yellow circles; Mixed stand of *P. sylvestris* and *P. pinaster*: blue circles.

The climate of the study area is Temperate (mainly temperate with dry summer, Csb, and in a minor extent temperate without a dry season and warm summer, Cfb) according to the Köppen classification (1936) for the Iberian Peninsula. The mean annual temperature ranges from 8.7 to 9.8 °C and the annual rainfall ranges from 684 to 833 mm. The altitude varies from 1093 to 1277 m a.s.l and the slope from 0.9 to 20%. The geological parent materials are sandstones and marls from the Mesozoic era (IGME 2015). The soils are Inceptisols with a xeric soil moisture regime and a mesic temperature regime and they are classified as Dystroxerept Typic or Typic Humixerept (sensu Soil-Survey-Staff 2014). The sandy soil texture was dominant and the pH varies from extremely acidic to very acidic (López-Marcos et al. 2018). The natural vegetation surrounding the study area, highly degraded by anthropogenic action, is characterized by Pyrenean oak (*Quercus pyrenaica* Willd.) forests or communities dominated by junipers.

In 'Supplementary material', a description of the climate (Figure 52), including the mean annual temperature (Figure 53) and the annual rainfall (Figure 54) is shown, as well as information on the geological materials (Figure 55), the soils (Figure 56), and the potential (Figure 57) and current (Table 34) vegetation of the study area. A detail description of the pit soil profile of each plot is also provided (Tables 35-88).

Experimental design

The experimental device has 18 plots distributed in six triplets (Figure 8). Each triplet consists of three circular plots of 15 m radius, including two plots dominated either by *P. sylvestris* (PS) or *P. pinaster* (PP) and one mixed plot that contained both species (MM). Plots within triplet are located less than 1 km from each other (Figure 9) so that the environmental conditions are homogeneous within the triplet, although they can differ among distinct triplets (see in Suplementary material 'Climate', 'Soils' and 'Vegetation').

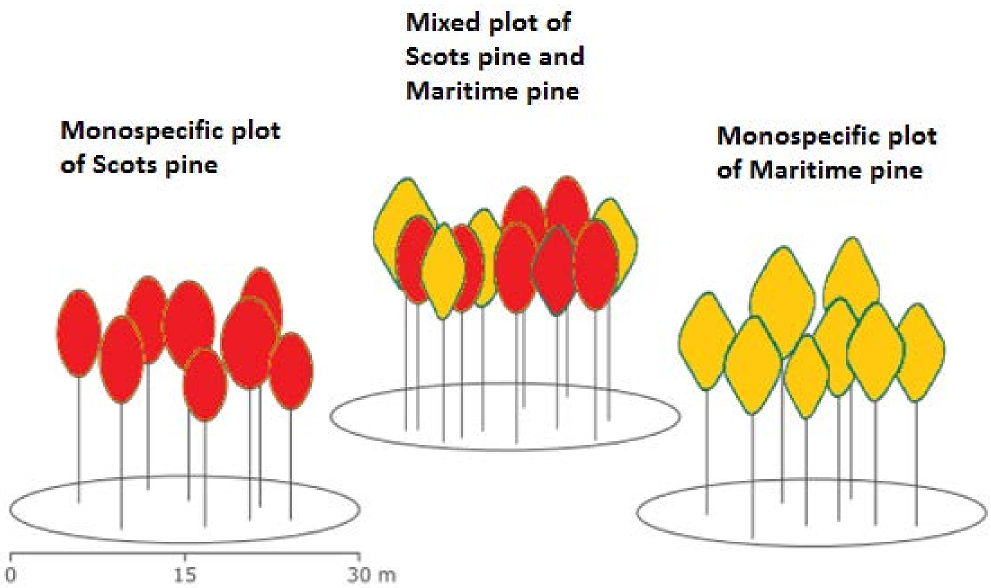

Figure 8. Ilustration of a triplet. Modified of Cattaneo (2018).

The sampling design in triplets is well balanced for stand composition (six repetitions per stand type) but not necessarily balanced for other stand characteristics (i.e. density, total basal area, dominant height, mean quadratic diameter, age). Stand characteristics are intended to be similar within the triplet (avoiding biases in the sampling design) but differed between triplets (see Table 34 in 'Suplementary material') facilitating a pair-wise plausible comparison of mixed versus monospecific stands (Riofrío 2018).

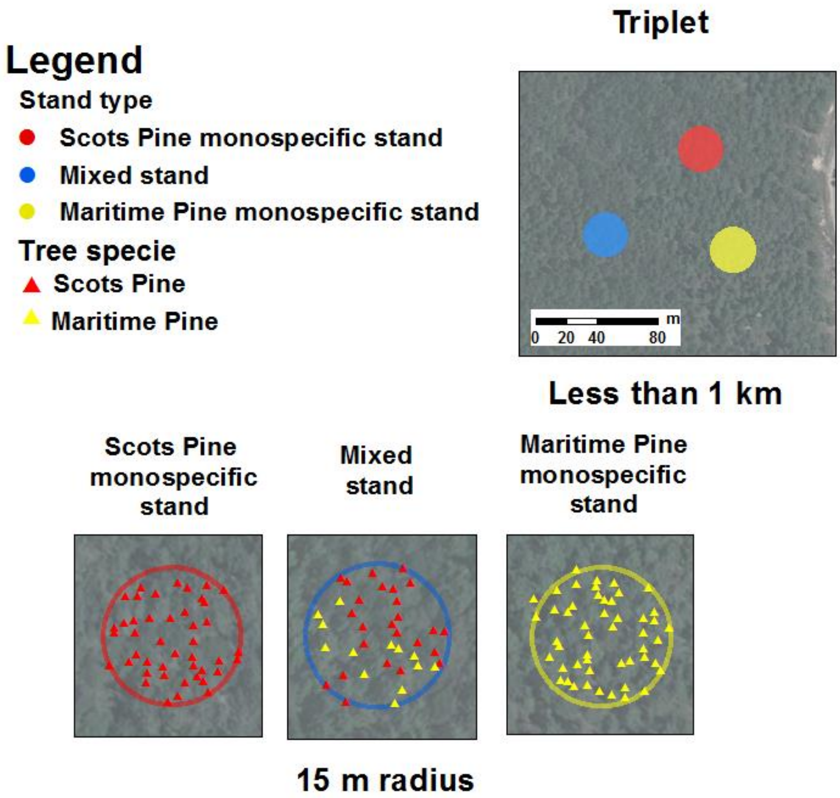

Figure 9. Map of triplet 5 as an example.

Traditionally, forest management has consisted of strip clear-cutting with soil movement and planting or sowing when necessary, and moderate thinning from below (Riofrío et al. 2019) benefiting *P. sylvestris* (López-Marcos et al. 2019c). The stands have had no silvicultural intervention or damage in the last ten years in an attempt to minimize the effect of the thinning or another type of intervention in what is intended to study, either growth, floristic richness or soil nutrients. Triplets belong to the network of permanent plots of the Sustainable Forest Management Research Institute UVa-INIA (iuFOR) and they have been previously used in a series of recent studies (Riofrío et al. 2017a, b, 2019; Cattaneo 2018; López-Marcos et al. 2018, 2019, 2020a).

The plots were selected to rely on species composition. In monospecific plots of Scots pine and Maritime pine, the target species constitutes at least 80% of the total basal area. Plots are defined as mixed when the combined basal area of both species represents at least the 90%, and the basal area of each target species is higher than 15%. Thus, the proportion of other species remained lower than 10% (Riofrío 2018). The plots have approximately a full-cover, with densities above 60% (Cattaneo 2018). Therefore, the percentage of the basal area of the dominant species in the monospecific plots of *P. sylvestris* was greater than 83%, the percentage of the basal area of the dominant species in the monospecific plots of *P. pinaster* was greater than 95%, and the basal area percentage of both species in the mixed plots ranged from 33 to 67%.

The age of the selected plots ranged between 44 and 151 years, the stand density between 509 and 1429 trees ha^{-1}, the basal area between 33.3 and 70.30 and m^2 ha^{-1} and the dominant height between 15.60 and 25.04 m (see Table 34 in 'Supplementary material').

Soil sampling and laboratory analyses

One soil pit of at least 50 cm depth was dug at each plot (eighteen in total) for organic (Forest floor, FF) and mineral soil horizons characterization.

Forest floor

A 25x25 cm quadrant (Figure 10) placed at the top of the pit was used to collect the forest floor or organic horizon. Coarse woody materials, such as large branches, were carefully removed from the forest floor before sampling (Andivia et al. 2016). The forest floor was separated into three fractions according to van Delft et al. (2006): almost undecomposed litter or fresh fraction (FsL), partially decomposed litter or fragmented fraction (FgL) and mostly decomposed organic matter or humified fraction (HmL).

Figure 10. Forest floor sampling and handling procedure.

The three fractions of leaf litter were dried separately at 60 °C during 48 h and weighed (±0.01 g) to determine the amount of biomass of each litter fraction per hectare (B_{FsL}, $B_{FgL,}$ B_{HmL}). A representative portion of each sample was ground up and analyzed with a LECO-CHN 2000 elemental analyzer to determine total organic carbon (TOC) and total nitrogen (TN) concentrations.

The total forest floor biomass (B_{FF}) was calculated as the sum of B_{FsL}, B_{FgL} and B_{HmL}. The total organic carbon stock (Cstocks) of FsL, FgL and HmL litter fractions were calculated by multiplying TOC concentration by the biomass of each fraction (Andivia et al. 2016) to obtain C $stock_{FsL}$, C $stock_{FgL}$, $Cstock_{HmL}$, respectively. Cstock of the FF ($Cstock_{FF}$) was the sum of $Cstock_{FsL}$, $Cstock_{FgL}$ and $Cstock_{HmL}$. The C/N ratio was calculated for the fresh (CN_{FgL}), fragmented (CN_{FgL}), and humified litter (CN_{HmL}). C/N of the FF was calculated as the weighted average of C/N of three decomposition fractions (Equation 1).

$$\mathrm{CN_{FF}} = \left[\left(\frac{\mathrm{B_{FsL}}}{\mathrm{B_{FF}}}\right)\mathrm{CN_{FsL}}\right] + \left[\left(\frac{\mathrm{B_{FgL}}}{\mathrm{B_{FF}}}\right)\mathrm{CN_{FgL}}\right] + \left[\left(\frac{\mathrm{B_{HmL}}}{\mathrm{B_{FF}}}\right)\mathrm{CN_{HmL}}\right]$$

Mineral soil

Two undisturbed soil samples were collected from each mineral horizon of each pit with steel cylinders (98.18 cm^3) keeping their original structure in order to determine the bulk density of each horizon. One disturbed sample was also taken from each mineral horizon of each pit (ca. 2.5 kg; see Figure 11).

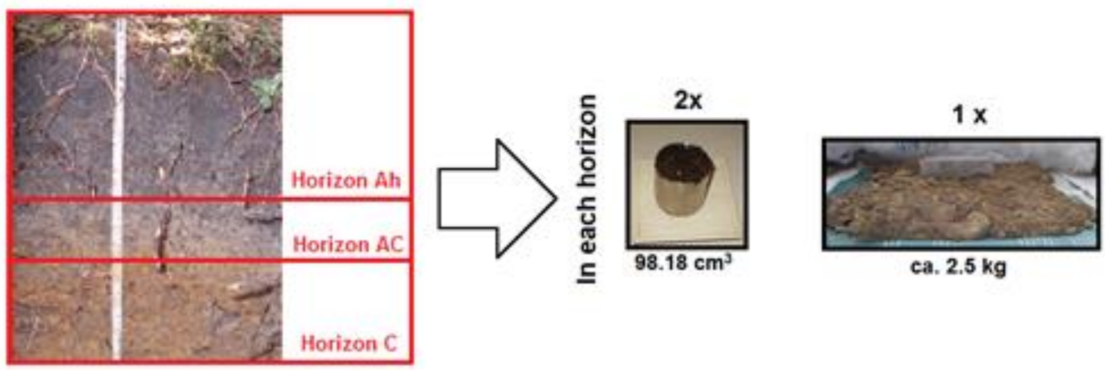

Figure 11. Mineral soil sampling procedure.

The percentages of fine (%FR) and coarse (%CR) roots were estimated visually in each horizon at the time of digging the soil pit, i.e. many, normal, few, very few or no roots cover in the cross-section of the soil profile classified as 80%, 50%, 30%, 10% and 0% respectively. The roots with a diameter below 5 mm were considered fine roots and those with a diameter above 5 mm as coarse roots.

Both undisturbed and disturbed mineral soil samples were dried at 105 °C during 24 h before analyses. Undisturbed mineral soil samples were weighed (± 0.001 g) and used to calculate the soil bulk density (bD). Disturbed mineral soil samples were sieved (2 mm) before physical and chemical analyses.

Physical analyses included percentage by weight of coarse fraction (> 2 mm; stones) and earth fraction (< 2 mm; EF), particle distribution determined by the pipette method (MAPA 1994) and subsequent determination of clay (%clay), sand (%sand) and silt (%silt) contents, and classification according to USDA criteria. Available water (AW) was determined by the MAPA (1994) method as the difference between water content at field capacity (water remaining in a soil after it has been thoroughly saturated for 2 days and allowed to drain freely) and the permanent wilting point (soil water content retained at 1500 kPa using Eijkelkamp pF Equipment).

Chemical parameters analyzed for each mineral horizon included: exchangeable cations (Ca^{+2}, Mg^{+2}, K^{+}, Na^{+}) extracted with 1 M ammonium acetate at pH = 7 (Schollenberger and Simon 1945) and determined using an atomic absorption/emission spectrometer; total organic carbon (TOC) and total nitrogen (TN) quantified by dry combustion using a Leco CHN 2000 elemental analyzer; easily oxidizable carbon (oxC) analyzed using the K-dichromate oxidation method (Walkley 1947); and available phosphorus using the Olsen method (Olsen and Sommers 1982).

Then the information from chemical and physical analyses of soil from mineral horizons was converted by depths (every 10 cm) and estimated for the whole profile as follows (Figure 12):

- By depths. The mineral soil horizon data were converted into five different depths (every 10 cm) calculating weighted averages between the horizons (Figure 12b; see also Appendix Ic).

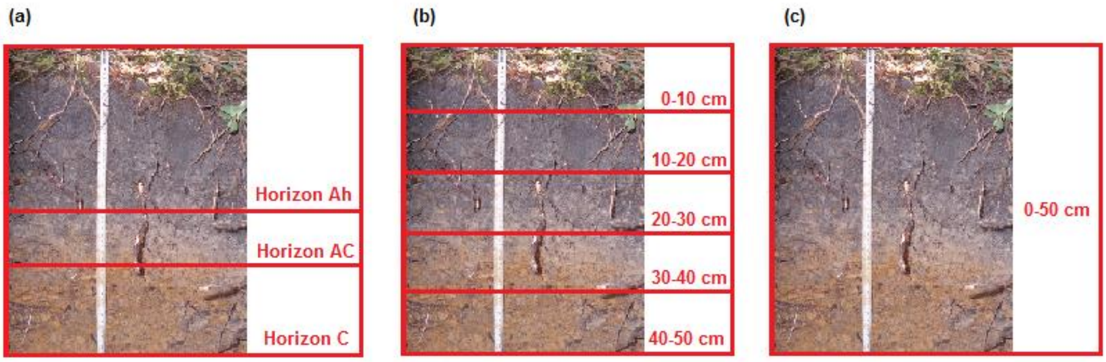

Figure 12. Mineral soil profile by horizons (a), by depths (b) and as a whole (c) in the Maritime pine monospecific stand of triplet 5, as an example.

- For the whole profile. The mineral soil horizon data were used to calculate the stocks of different soil properties and the soil water content in the whole profile (Figure 12c). First, in each horizon, the water holding capacity (WHC) and the stock of different soil properties were calculated as indicated in Appendix IIb. After, the water holding capacity and the stocks of different soil properties in the soil profile (0–50 cm) were calculated as the sum of the values of each horizon (see Appendix IIb). In addition, the sum of bases (SB) was the sum of the Ca^{+2}, Mg^{+2}, K^{+} and Na^{+} concentrations ($cmol^{+}$ kg^{-1}).

Overstory sampling and data analyses

In order to assess the role of scale in determining the relationship between species richness and productivity, the overstory composition and structure were characterized at two different spatial scales: 1) at the stand level (Figure13), i.e. within each circular plot of 15 m radius; and 2) at a smaller scale (Figure 14), i.e. within each circular 4 m radius subplot centered in each quadrat of understory sampling according to Rodríguez-Calcerrada et al. (2011).

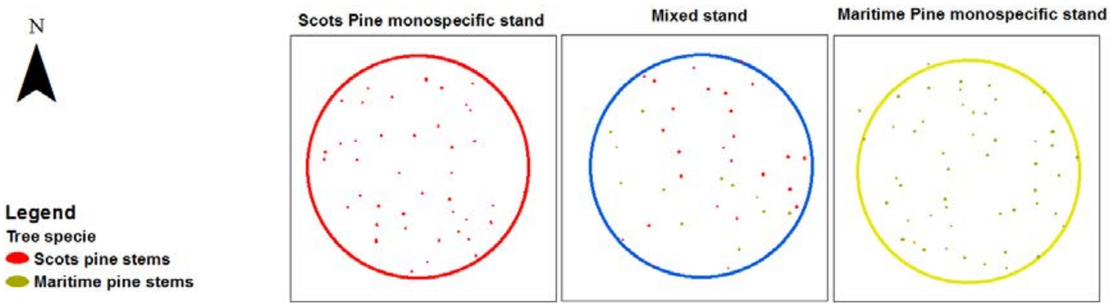

Figure 13. Illustration of overstory study at stand level of triplet 5 as an example. Red circles: Scots pine stems; Yellow circles: Maritime pine stems. The diameter of each circle represents the basal area.

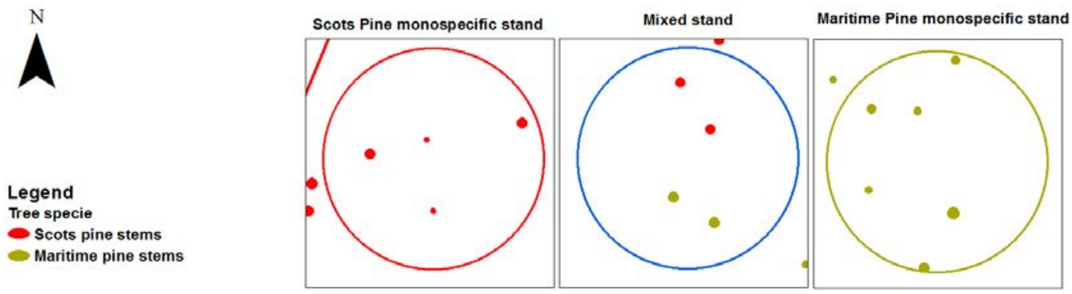

Figure 14. Illustration of overstory study at the smaller spatial scale in the sub-plot number 5 of each stand type in triplet 5. Red circles: Scots pine stems; Yellow circles: Maritime pine stems. The diameter of each circle represents the basal area.

The number and diameter of all stems > 7.5 cm DBH (diameter at the breist height) for every *Pinus* species in each plot were computed at both spatial scales. Tree density (N), total basal area (GT), and the basal area of each *Pinus* species (GPS: *P. sylvestris* basal area; GPP: *P. pinaster* basal area) were calculated at both spatial scales; GT, GPS and GPP as indicated in Appendix IVa.

At the smaller scale, the average of the ten circular 4 m radius subplots was made within each plot. The percentages of *P. pinaster* basal area (%PP) or *P. sylvestris* basal area (%PS) were calculated as the ratio between the basal area of *P. pinasteror* or *P. sylvestris* and the total basal area of each plot.

In addition, in order to assess the 'randomness' of the spatial distribution pattern of trees (Byth and Ripley 1980), both without differentiating species (*P. sylvestris* + *P. pinaster*) and for each species separately (*P. sylvestris* or *P. pinaster*), two different distances were measured within each plot following Hopkins (1954): 1) the distance from a random point (the quadrat for understory sampling) to the nearest tree (piD), and 2) the distance from that tree to its nearest neighbor (iiD); see Figure 15.

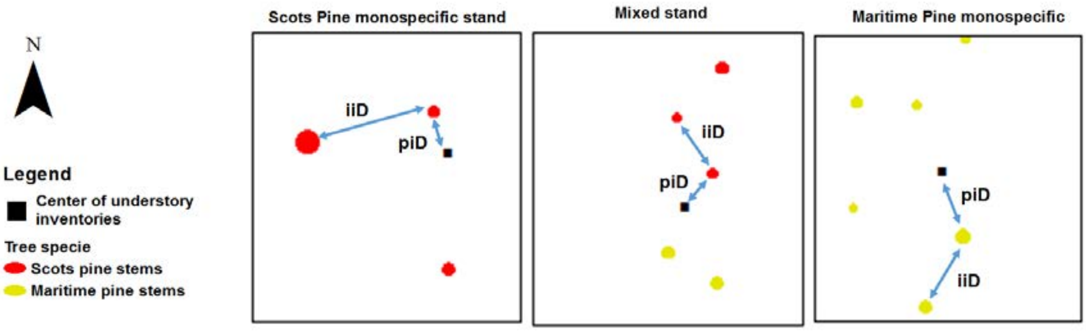

Figure 15. Ilustration of the distances mesurement within each plot of 15 m radius following the Hopkins`s (1954) methodology. The distance from a random point (the quadrat for understory sampling) to the nearest tree (piD), and the distance from that tree to its nearest neighbor (iiD). Black square: understory inventories; Red circles: Scots pine stems; Yellow circles: Maritime pine stems. The diameter of each circle represents the basal area. This methodolody was applied for each species separately (*P. sylvestris* or *P. pinaster*), and without differentiating species (*P. sylvestris* + *P. pinaster*).

Understory sampling and data analyses

In each plot of 15 m radius, 10 quadrats of 1m×1m were randomly located to record the understory vegetation and tree regeneration (Figure 16).

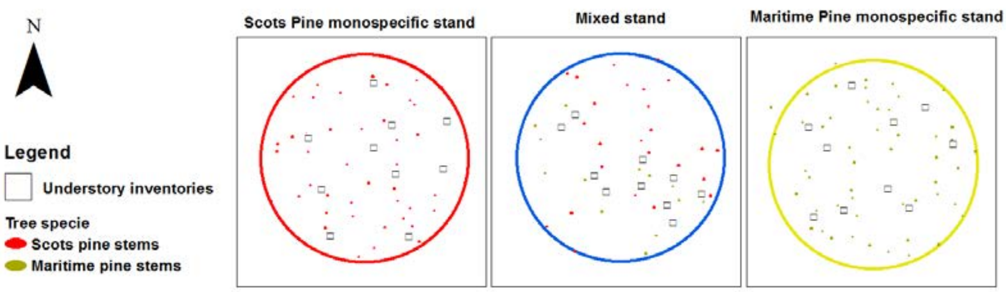

Figure 16. Distribution of square inventories for the understory sampling in triplet 5.

In each quadrat the percentage cover of bare soil, stoniness, leaf litter, vascular plant species (including tree regeneration), and bryophytes were recorded (Figure 17a). The number of individuals (stems) of the tree regeneration was also counted within each quadrat (Figure 17b). The sampling was carried out in June 2016 by the same observer to encompass and better identify the maximum number of vascular plant species (Martínez-Ruiz and Fernández Santos 2005; Alday et al. 2010).

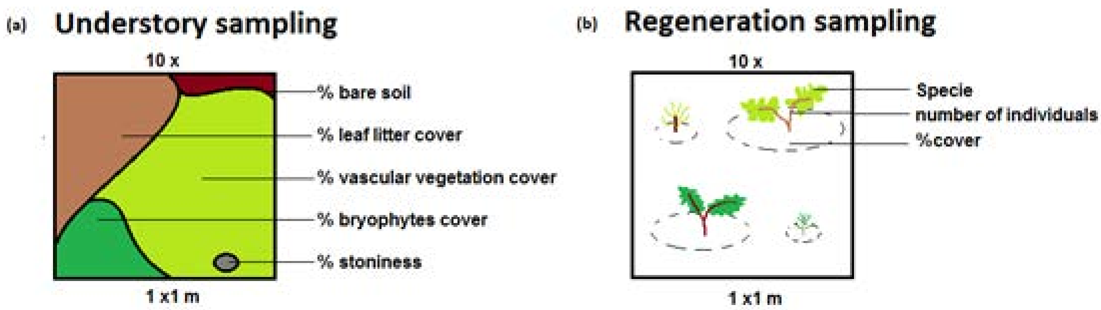

Figure 17. Ilustration of the understory sampling (a) and the regeneration sampling (b) in each inventory.

The cover percentage of every vascular plant species and bryophytes in each quadrat was estimated visually "in situ" whenever possible. Specimens of the unknown or doubtful species were collected for later identification in the laboratory with the help of botanical keys such as Aizpiru et al. (2007) and Castroviejo et al. (1986-2012). Vascular plant species nomenclature follows Tutin et al. (1964-1980) and bryophytes nomenclature follows Crosby et al. (1992).

Tree regeneration included the main tree species found in seedlings/saplings stages (i.e. *P. sylvestris*, *P. pinaster*, *Q. pyrenaica* and *Q. faginea*) because no old regeneration was found (it had probably cleared by management). In these stands, there are no subordinate tree species. Only two layers of vegetation can be distinguished (overstory and understory): the overstory measuring c.a. 20 m in height, and the understory being only c.a. 20 cm in height, and never higher than 1 m.

In addition, the legal protection status at local, regional and national level in Spain according to the Anthos (2017) project (http://www.anthos.es/), as well as the conservation status according to the International Union for Conservation Nature (UICN 2012) criteria were recorded for vascular plants (see Appendix IIa).

Vascular plant species were classified according to the Raunkiær's life-forms classification (1934) following Aizpiru et al. (2007); see Appendix IIa. The cover (%) of each Raunkiær's life-form in each plot was calculated as the average of the 10 vegetation sampling quadrats per plot (see López-Marcos et al. 2019). The Raunkiær's life-forms are defined by Rivas-Martínez (2005) as follows (see Figure 18):

- Therophytes: annual plants whose shoot and root systems die after seed production and which complete their whole life cycle within one year.
- Geophytes: plants with subterranean resting buds (i.e. bulbs, rhizomes…).
- Hemicryptophytes: perennial herbaceous plants with periodic shoot reduction to a remnant shoot system that lies relatively flat on the ground surface.
- Chamaephytes: woody plants whose natural branch or shoot system remains perennially between 25 and 50 cm above ground surface (dwarf shrubs).
- Phanerophytes: woody plants that grow taller than 25-50 cm (tree regeneration and shrubs).

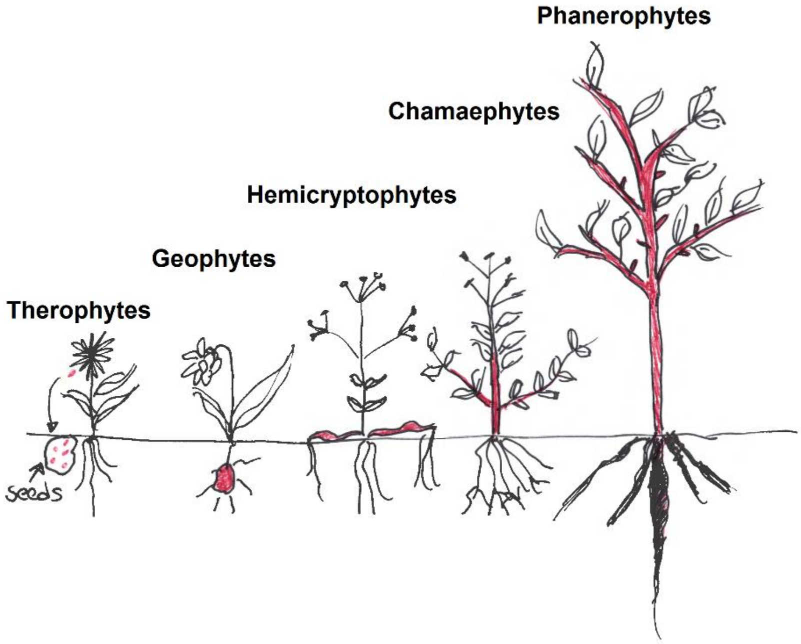

Figure 18. Life-forms of vascular plants according to Raunkiær (1934). Buds in red colour. (Illustration of Daphne López-Marcos)

Finally, richness was calculated as total cumulative number of plant species in the 10 quadrats per plot (Colwell 2009), including understory vegetation and tree regeneration (see López-Marcos et al. 2019). Although several indices of diversity were tested, only the number of species showed any difference among stand types and thus is shown in results.

Chapter I

Reservas de carbono y cationes intercambiables del suelo en pinares mixtos y monoespecíficos

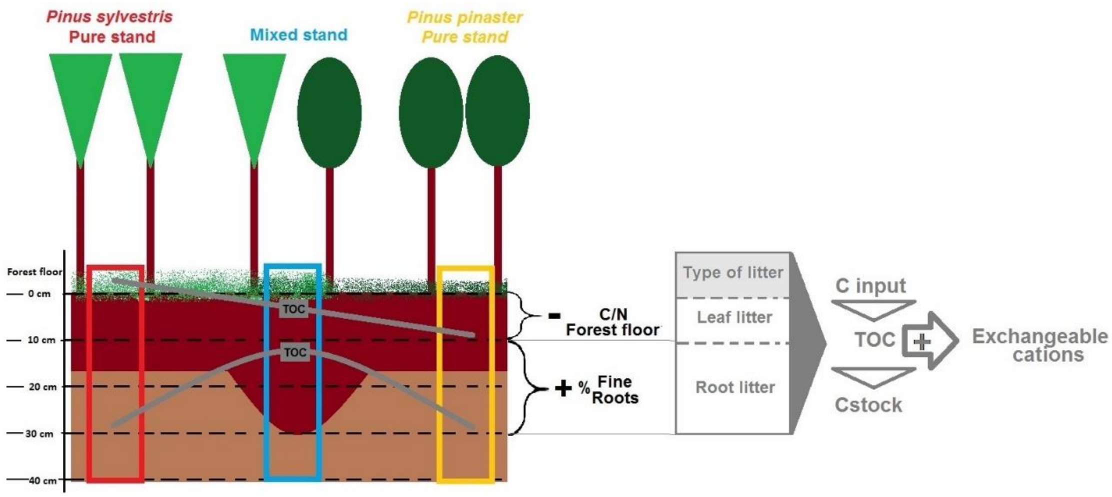

Figure 19. Graphical abstract of the article that gives rise to chapter I of the thesis (López-Marcos et al. 2018).

This chapter has been published as:

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Soil carbon stocks and exchangeable cations in monospecific and mixed pine forests

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Abstract

Many studies highlight the role of mixed versus monospecific forests to supply numerous ecosystem services. Most reports of positive mixture effects on carbon storage focus on mixtures that combine tree species with contrasting traits, but little is known on the effect of mixing species that are expected to behave quite similarly as they belong to the same genus. In this study, we assessed the effect of mixed versus monospecific stands of *Pinus sylvestris* and *P. pinaster* on carbon storage and exchangeable cations along the soil profile, based on research with six triplets in the northern Iberian Peninsula (Spain). One soil pit of at least 40 cm depth was dug at each plot for organic and mineral horizons characterization. Two trends were found: in the topsoil, higher values of carbon stock and total organic carbon were found in *P. sylvestris* stands, lower in *P. pinaster* stands and intermediate in mixed stands; this pattern was related to the C:N ratio of the forest floor; In the intermediate soil layers, its tends to be higher in mixed stands and is related to percentage of fine roots and to the greater thickness of the first mineral horizon. Differences in soil exchangeable cations among stands were related to the total organic carbon content. These results improve our understanding of the mechanisms underlying soil carbon accumulation in mixed stands and emphasize the use of mixtures as a strategy to combat climate change, due to the advantage in the accumulation of carbon in the subsoil layers.

Keywords: *Pinus sylvestris* L., *Pinus pinaster* Ait., soil profile, C stock, exchangeable cations.

Introduction

Over the last decades, the management of mixed-species forests has taken on greater relevance as a result of the growing evidence that they can supply numerous ecological, economic and socio-cultural goods and services more efficiently than monospecific forests (Gamfeldt et al. 2013a). Taking into account that 23% of the land is covered by mixed forests in the pan-European region (FAO 2011), mixed forests management is becoming a new paradigm (Bravo-Oviedo et al. 2014) in order to increase the provision of many high-value goods and ecosystem services (Stenger et al. 2009), including biodiversity conservation or carbon sequestration (European Commission 2010).

Forests play an important role in the global carbon cycle and in the Earth's terrestrial carbon sink (Andivia et al. 2016). Forest ecosystems contain approximately 1725 Pg of carbon and about two-thirds are contained in the forest soil (Pan et al. 2011). However, there is still great uncertainty regarding best management strategies to promote soil organic carbon sequestration (Andivia et al. 2016), including the mixture of different species of trees (Jandl et al. 2007).

Carbon accumulation mechanisms may vary depending on the dominant species (Augusto et al. 2015) and the different layers of the soil (Vesterdal et al. 2013) since the aboveground litter and the root litter are the responsible for soil C input (Rasse et al. 2005). Therefore, the mixture of tree species can affect both the accumulation and the distribution of the carbon along the soil profile (Chapin 2003). Although a general understanding of the effect of tree species across site types have not yet been reached (Jandl et al. 2007), many authors suggest that the impact on the forest floor or mineral soil depends on the identity of the species, species richness, and kind of mixture (Ruiz-Peinado et al. 2017). In fact, Dawud et al. (2016) revealed that forests with greater diversity had higher soil carbon stocks in deeper layers. However, most reports of positive mixture effects on C storage focus on mixtures that combine species with contrasting traits, such as the mixing of European beech and Norway spruce (Andivia et al. 2016), the mixing of European beech, Douglas fir and Norway spruce (Cremer et al. 2016), or even in plantations of mixed stand vs monocultures in a chronosequence of *Pinus massoniana*-*Cinnamomum camphora* (Liu et al. 2017).

The effect of mixing for species that are expected to behave quite similarly as they belong to the same genus is still unknown, despite being frequent in many environments, such as the admixtures of Scots pine (*Pinus sylvestris* L.) and Maritime pine (*Pinus pinaster* Ait.) in Spain. Both *Pinus* species show similar crown architecture and slight differences in shade tolerance (Riofrío et al. 2017a), but clearly differ in leaf traits (e.g. more recalcitrant leaf litter for *P. pinaster*; Herrero et al. 2016; longer *P. pinaster* needles; Amaral Franco 1986), whereas the information on root distribution is not clear, since rooting depth may vary depending on the moisture conditions (Bakker et al. 2006). Maritime pine is an important species of Mediterranean forests and Scots pine is the most widely distributed species of pine in the world (Bogino and Bravo 2014). They are two of the main forest species in Spain (Scots pine: 1.20 million ha; Maritime pine: 0.68 million ha) and grow in monospecific and mixed stands, either naturally or as a result of species selection for afforestation (Serrada et al. 2008). In addition to their wide distribution and forest area, they hold great ecological and socio-economic value (Riofrío et al. 2017b). Mixed stands where these two species coexist are particularly interesting because of their location at the rear-edges for *P. sylvestris* forests, where ecological conditions (high temperatures, frequent droughts) approach the species tolerance limit and the most drastic effects of climate change are predicted (Matías and Jump 2012).

Forest management in general and tree species selection, in particular, have various impacts on soil biological, physical and chemical processes and characteristics (Jandl et al. 2007; Cremer and Prietzel 2017). With regard to the soil chemical properties, soil exchangeable cation concentrations may be affected by tree species composition (Cremer and Prietzel 2017). Different tree species growing under similar conditions, such as climate, soil type, and land use history differ substantially from each other with respect to foliage nutrient content, root and litter chemistry, all of them having a large impact on soil nutrient input, output, and cycling (Augusto et al. 2015; Cremer and Prietzel 2017). Also, the soil nutrient input could be an indirect consequence of the organic matter contributions to soil (Cremer and Prietzel 2017), since the decomposition of plant tissues in terrestrial ecosystems regulates the transfer of carbon and nutrients to the soil (Wang et al. 2014).

Differences in the concentration of cations in the soil may depend on differences between tree species in biomass accumulation rates and/or biomass cation concentrations (Brandtberg et al. 2000). The amount and composition of litter produced also vary between species, and these two factors can, in turn, influence the rate of accumulation of organic matter and properties of the forest floor (Brandtberg et al. 2000). Whether species differ in the depth at which nutrient uptake is concentrated and/or in the rate of biocycling, the result may appear in subsoil mineral horizons (Brandtberg et al. 2000).

The forest management practices must be used as a mitigation tool as regards the carbon sequestration because the type of tree species affects forest growth, carbon and nutrient cycling (Augusto et al. 2015). That is why we investigated the impact of the mixture of tree species of the same genus with a wide distribution in Spain (*Pinus sylvestris* and *P. pinaster*) on C storage along the soil profile in comparison with monospecific stands. We hypothesize that: (1) the stand type influences the C storage and, indirectly, the exchangeable base cations of the mineral soil by the organic matter decomposition effect; (2) differences in the topsoil among stand types are expected to be found; and (3) the admixture of both pine species might have a positive interactive effect on the accumulation of carbon in the soil profile in comparison with monospecific stands. Therefore, the aims of this study were: (i) to quantify the differences among stand types in C storage, including both total accumulation in soil and distribution in the soil profile; (ii) to investigate the possible causes of the observed differences; and (iii) to explore how the difference in C accumulation might affect the exchangeable cation concentrations.

Material and methods

Study sites

The research was carried out in eighteen forest plots (6 triplets) located in the 'Sierra de la Demanda' between the Burgos and Soria regions, in North-Central Spain (41°47'35'' N and 41°53'41''N latitude and 2°56'12''W and 3°20'46''W longitude; Figure 20). The climate is Temperate Type Cfb and Csb, i.e. temperate with dry or temperate summer and atlantic respectively, according to the Köppen classification (1936) for the Iberian Peninsula. The mean annual temperature ranges between 8.7 and 9.8 °C and the annual precipitation ranges between 684 and 833 mm (Nafría-García et al. 2013). Altitude varies from 1093 to 1277 m a.s.l., and the slope from 0.9 to 20%. The geological parent materials are sandstones and marl of Mesozoic age (IGME 2015). The soils are Inceptisols with a xeric soil moisture regime and mesic soil temperature regime and they are classified as Typic Dystroxerept or Typic Humixerept (sensu Soil-Survey-Staff 2014). The sandy soil texture was dominant and the pH varies from extremely acid to strongly acid (Appendix Ia). The natural dominant vegetation in the study area, highly degraded by anthropogenic action, is characterised by Pyrenean oak forests or communities dominated by junipers.

Each triplet consisted of two plots dominated either by *Pinus sylvestris* (PS) or *Pinus pinaster* (PP) and one plot with a mixture of both species (MM) located less than 1 km from each other. Plots were circular of radius 15 m and the tree species composition was the main varying factor. The percentage of the basal area of the dominant species in the monospecific plots was greater than 83% or 95% for *P. sylvestris* or *P. pinaster* respectively, whereas the basal area percentage of both species in the mixed plots ranged from 33 to 67%. Historically, the area has been occupied by forests and it has been traditionally managed for decades through selective thinning, being *P. sylvestris* benefited. The stands had no silvicultural intervention or damage in the last ten years. The age of the selected plots ranged between 44 and 151 years, the stand density between 509 and 1429 trees ha^{-1}, the basal area between 33.3 and 70.30 and m^{2} ha^{-1} and the dominant height between 15.60 and 25.04 m (Appendix Ib). These plots belong to the network of permanent plots of iuFOR-UVa.

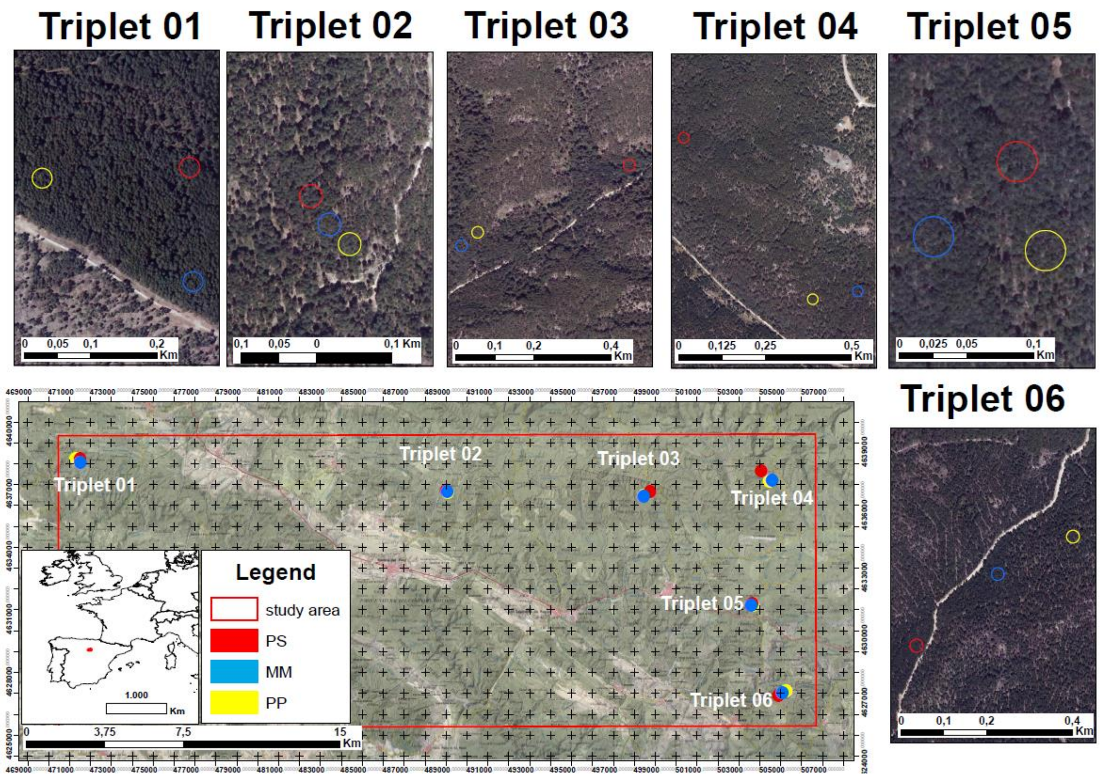

Figure 20. Location of the triplets in the 'Sierra de la Demanda' in the North-Central Spain and location of the plots in each triplet. *Pinus sylvestris* monospecific stands (PS): red circles; *Pinus pinaster* monospecific stand (PP): yellow circles; Mixed stand of *P. sylvestris* and *P. pinaster* (MM): blue circles.

<u>Soil sampling</u>

One soil pit of at least 40 cm depth was dug at each plot (eighteen in total) for organic and mineral soil horizons characterization and sampling (Appendix Ic). A 25x25 cm quadrant placed at the top of the pit was used to collect the forest floor or organic horizon. Coarse woody materials, such as large branches, were carefully removed from the forest floor before sampling (Andivia et al. 2016). The forest floor (FF) was separated into three fractions according to Van Delft et al. (2006): almost undecomposed litter or fresh fraction (FsL), partially decomposed litter or fragmented fraction (FgL) and mostly decomposed organic matter or humified fraction (HmL).

Two undisturbed soil samples were collected from each mineral horizon of each pit with steel cylinders (98.18 cm^{3}) to keep their original structure (Appendix Ic). One disturbed sample was also taken from each mineral horizon of each pit (ca. 2.5 kg). The percentages of fine (%FR) and coarse (%CR) roots were estimated visually in each horizon at the time of digging the soil pit, i.e. many, normal, few, very few or no roots coverage in the cross-section of the soil profile classified as 80%, 50%, 30%, 10% and 0% respectively. The roots with a diameter below 5 mm were considered fine roots and those with a diameter above 5 mm as coarse roots.

Laboratory analyses

The three fractions of leaf litter were dried separately at 60°C during 48 h and weighed (±0.01 g) to determine the amount of biomass of each litter fraction per hectare (B_{FsL}, B_{FgL}, B_{HmL}). A representative portion of each sample was ground up and analyzed with a LECO-CHN 2000 elemental analyzer to determine total organic carbon and total nitrogen concentrations (TOC and N, respectively).

Both undisturbed and disturbed mineral soil samples were dried at 105°C during 24 h before analyses. Undisturbed mineral soil samples were weighed (±0.001 g) and used to calculate the soil bulk density (bD). Disturbed mineral soil samples were sieved (2 mm) before physical and chemical analyses. Physical analyses included percentage by weight of coarse fraction (>2 mm; stones) and earth fraction (<2 mm; EF), particle distribution determined by the pipette method (MAPA 1994) and subsequent determination of clay (%clay), sand (%sand) and silt (%silt) contents, and classification according to USDA criteria.

Chemical parameters analyzed for each mineral horizon included: exchangeable cations (Ca^{+2}, Mg^{+2}, K^{+}, Na^{+}) were extracted with 1N ammonium acetate at pH=7 (Schollenberger and Simon 1945) and determined using an atomic absorption/emission spectrometer; TOC was quantified by dry combustion using a Leco CHN 2000 elemental analyzer.

Data analyses

The percentage of *Pinus pinaster* basal area (% PP) was calculated as the ratio between the basal area of *P. pinaster* and the total basal area of each plot. Total FF biomass (B_{FF}) was calculated as the sum of B_{FsL}, B_{FgL} and B_{HmL}. C stocks of FsL, FgL and HmL litter fractions were calculated by multiplying TOC concentration by the biomass of each fraction (Andivia et al. 2016) to obtain C $stock_{FsL}$, C $stock_{FgL}$, C $stock_{HmL}$ respectively. C stock of the FF (C $stock_{FF}$) was the sum of C $stock_{FsL}$, C $stock_{FgL}$ and C $stock_{HmL}$. The C:N ratio was calculated for the fresh (CN_{FgL}), fragmented (CN_{FgL}), and humified litter (CN_{HmL}). C:N of the FF was calculated as the weighted average of C:N of three decomposition fractions.

$$CN_{FF} = \left[\left(\frac{B_{FsL}}{B_{FF}}\right) CN_{FsL}\right] + \left[\left(\frac{B_{FgL}}{B_{FF}}\right) CN_{FgL}\right] + \left[\left(\frac{B_{HmL}}{B_{FF}}\right) CN_{HmL}\right]$$

C stock in the mineral soil (C $stock_{SOIL}$) was calculated as: C $stock_{SOIL}$ = TOCi · bDi · %EFi Ti, being TOCi the total organic carbon concentration, bDi the measured bulk density, %EFi the percentage of earth fraction and Ti the thickness of the soil horizon. The C stock in the whole mineral soil profile (C $stock_{0\text{-}40cm}$) was calculated as the sum of the C stock of all soil horizons. The sum of bases (SB) was the sum of the Ca^{+2}, Mg^{+2}, K^{+} and Na^{+} concentrations ($cmol^{+}$ kg^{-1}).

The mineral soil horizon data were converted into four different depths (every 10 cm) calculating weighted averages between the horizons. Some variables were transformed (lnx or 1/x) before statistical analysis to achieve residual normality and homoscedasticity.

While soil texture is not expected to be affected by stand species composition, it may have a large impact on C sequestration in the mineral soil (Jandl et al. 2007). In order to remove the effect of the soil texture variability within a triplet, texture variables (sand, silt, clay) were therefore tested as additional fixed effects in the alternative models; based on AIC values, only the sand content was included in the final model.

The possible effects of the type of stand on the C $stock_{FF}$ (C $stock_{FF}$, C $stock_{FsL}$, C $stock_{FgL}$ and C $stock_{HmL}$) as well as on TOC, C $stock_{SOIL}$, exchangeable cations (Na^{+}, K^{+}, Ca^{+2}, Mg^{+2}), and SB in different mineral soil layers were analyzed using Linear Mixed Models (LMM) with the Restricted Maximum Likelihood method (REML; Richards 2005). The type of stand was considered as a categorical variable with three levels: PS, PP and MM. In all cases, a null model considering the random effect of triplet was tested with the alternative model that included the fixed effects of the type of stand plus the soil sand content (%sand). The Akaike Information Criterion (AIC; Akaike 1973) was used to verify whether the alternative model was more parsimonious, i.e. smaller values of AIC, and the ANOVA was applied to test the significant differences between the null and the alternative models (see Appendix Id). One monodominant plot of *P. sylvestris* was considered an outlier and excluded from all analyses because it was the only one that presented aquic conditions (Soil-Survey-Staff 2014; see Appendix Ia).

Finally, linear correlations between some variables of interest were investigated, using the Pearson's coefficient ($p<0.05$). In order to test the influence of the type of stand on the nature of the leaf litter and to verify whether the TOC comes from the leaf litter and/or the roots decomposition at different mineral soil layers. Also the relationships between TOC and either the exchangeable cations or SB were tested. All statistical analyses were implemented in the R environment (version 3.3.3, R-Core-Team 2015) using LME4 package for LMM (Bates et al. 2015).

Results

Forest floor quantity and quality

The biomass of the fresh (B_{FsL}) and fragmented (B_{FgL}) leaf litter showed the same trend ($p<0.05$ for B_{FgL}; $p<0.10$ for B_{FsL}) when comparing among stand types (Figure 21A), being higher in PS, lower in PP and intermediate in MM; no significant trend was found for B_{HmL}. An opposite significant trend ($p<0.05$) was found for the C:N ratio of the fresh litter (CN_{FsL}), being higher in PP, lower in PS and intermediate in MM; no clear trend was observed for CN_{FgL} and CN_{HmL} (Figure 21B). In addition, %PP was positively correlated with CN_{FsL} ($r = 0.64$, $p<0.005$) and negatively with B_{FsL} ($r = -0.45$; $p<0.05$), B_{FgL} ($r = -0.54$; $p<0.025$) and B_{FF} ($r = -0.46$; $p<0.05$).

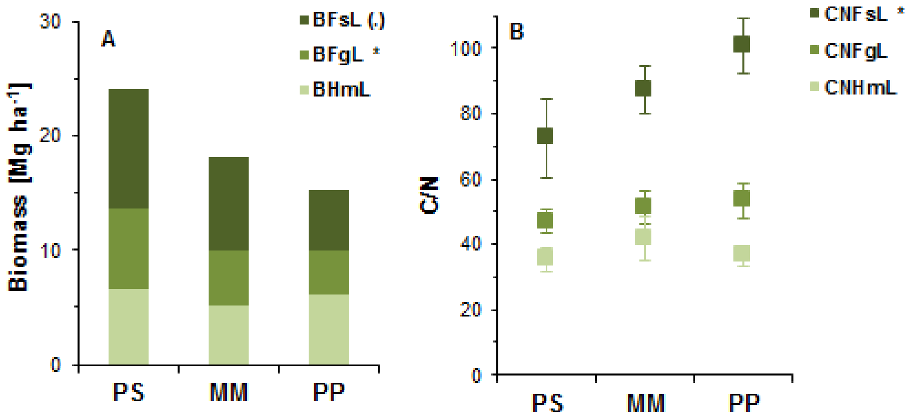

Figure 21. (A) Biomass (B, mean value, Mg ha-1) and (B) C:N ratio (CN, mean±SE) of the different fractions of leaf litter (FsL, FgL, HmL: fresh, fragmented and humidified, respectively) according to the type of stand. PS (n=5): *Pinus sylvestris* monodominant stands; PP (n=6): *P. pinaster* monodominant stand. MM (n=6): mixed stands of both species. Signification level: * p<0.05; (•) p<0.1.

TOC in the mineral soil

The total organic carbon concentration (TOC) decreased according to the depth in the three types of stand, as expected (Figure 22). It differed significantly ($p<0.05$) among stands in the topsoil (0-10 cm), and almost significantly at the third depth (20-30 cm, $p<0.10$). In the same way as for the C stockSOIL, two different trends were found for TOC: $TOC_{0\text{-}10cm}$ was higher in PS, lower in PP and intermediate in MM, while $TOC_{20\text{-}30cm}$ was higher in MM. This latter tendency, yet not significant, was also found at the second depth (10-20 cm). In addition, $TOC_{0\text{-}10cm}$ was negatively correlated with CN_{FF} ($r = -0.46$; $p<0.05$), and TOC at intermediate depths (10-20 cm and 20-30 cm) was positively correlated with %FR ($TOC_{10\text{-}20cm}$: $r = 0.66$, $p<0.005$; $TOC_{20\text{-}30cm}$: 20-30 cm: $r = 0.76$, $p<0.005$).

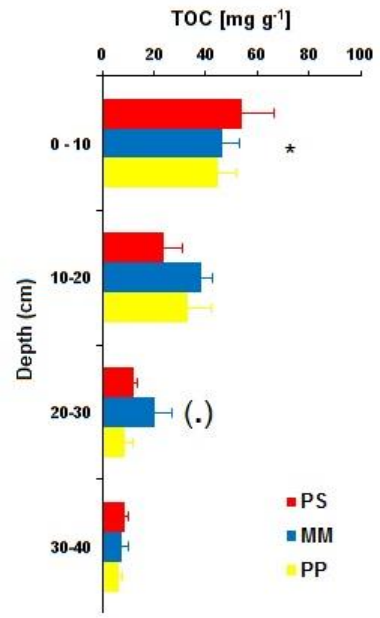

Figure 22. Mean±SE of total organic carbon (TOC mg g^{-1}) at four different depths of the mineral soil profile according to the type of stand. Other abbreviations as in Figure 21. Signification level: * $p<0.05$; (•) $p<0.1$.

<u>C stock in the soil profile</u>

The carbon stock in the forest floor (C $stock_{FF}$) differed almost significantly among stands ($p<0.1$), being higher in PS (8.41±1.43 Mg TOC ha^{-1}), lower in PP (4.87±0.89 Mg TOC ha^{-1}) and intermediate in MM (6.67±1.09 Mg TOC ha^{-1}). The same pattern was observed for the three fractions of the litter (Figure 23), being statistically significant only for the fragmented litter (C $stock_{FgL}$, $p<0.05$) and almost significant for the fresh one (C $stock_{FsL}$, $p<0.10$).

The carbon stock in the mineral soil (C $stock_{SOIL}$) decreased with depth in the three types of stand, as expected (Figure 23), but the differences among stands were only almost significant ($p<0.10$) at 0-10 cm, 20-30 cm, and 30-40 cm. Two different trends were found: C $stock_{0\text{-}10cm}$ and C $stock_{30\text{-}40cm}$ were higher in PS, lower in PP and intermediate in MM; by contrast, C $stock_{10\text{-}30cm}$ was the highest in MM. $Cstock_{0\text{-}40cm}$ was also higher in MM (93.70±13.63 Mg TOC ha^{-1}), lower in PP (70.94±10.20 Mg TOC ha^{-1}) and intermediate in PS (81.62±11.37 Mg TOC ha^{-1}), but these differences were not statistically significant ($p=0.18$).

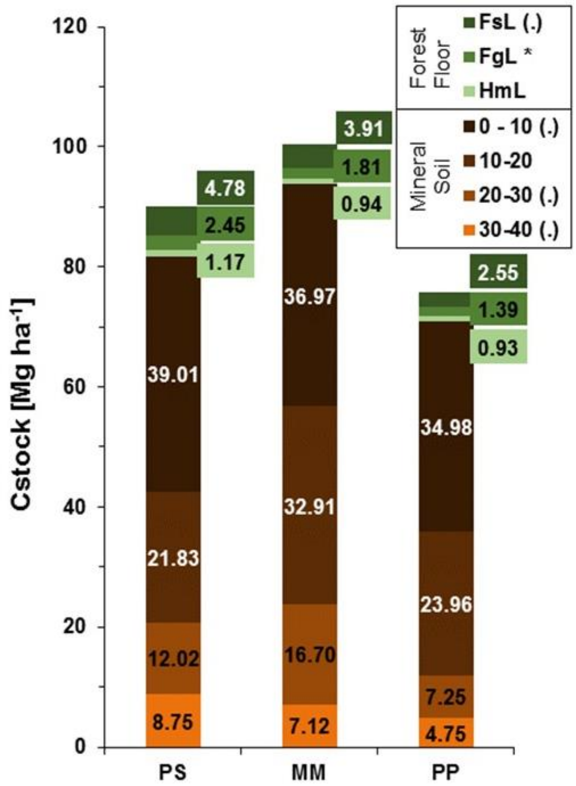

Figure 23. Carbon stock (C stock, mean value, Mg ha^{-1}) in the forest floor (green tones) for the organic layers (FsL, FgL, HmL: fresh, fragmented and humidified litter, respectively), and in the mineral soil profile (brown tones) at four different depths according to the type of stand. Signification level: * $p<0.05$; (•) $p<0.1$.

<u>Sum of bases and exchangeable cations in the mineral soil</u>

The same two trends found for TOC and C stock in the mineral soil were observed for the exchangeable cations and the sum of bases (Table 3). In the topsoil (0-10 cm), exchangeable cations (K^+, Ca^{+2}, Mg^{+2}) and the sum of bases (SB) differ significantly ($p<0.05$) among stands, being higher in PS, lower in PP and intermediate in MM (Table 3). In addition, K^+ ($r = 0.61$, $p<0.005$), Ca^{+2} ($r = 0.74$, $p<0.005$), Mg^{+2} ($r = 0.57$, $p<0.01$) and SB ($r = 0.71$, $p<0.005$) correlated positively with TOC at this depth. However, in the 10-20 cm soil layer, K^+ and Mg^{+2} reached significantly higher values in MM ($p<0.05$), and a similar trend but not significant ($p>0.10$) was found for Ca^{+2} and SB. Again, K^+ ($r = 0.53$, $p<0.025$), Ca^{+2} ($r = 0.73$, $p<0.005$), Mg^{+2} ($r = 0.56$, $p<0.01$) and SB ($r = 0.70$, $p<0.005$) correlated positively with TOC at this depth. The same pattern was observed at the third soil depth (20-30 cm), where MM showed significantly higher values for Mg^{+2} ($p<0.05$) and almost significantly ($p<0.1$) for Ca^{+2} and SB. At this depth, only Ca^{+2} ($r = 0.91$, $p<0.005$), Mg^{+2} ($r = 0.81$, $p<0.005$) and SB ($r = 0.90$, $p<0.005$) correlated positively with TOC.

Table 3. Mean±SE of exchangeable cations concentration and sum of bases (cmol+ kg^{-1}) at four different depths of the mineral soil profile according to the type of stand. Other abbreviations as in Figure 21. Signification level: * p<0.05; (•) p<0.1.

	Depth (cm)	PS	MM	PP	p
Na^+	0-10	0.86 ± 0.04	0.87 ± 0.03	0.80 ± 0.03	*
	10-20	0.84 ± 0.03	0.87 ± 0.02	0.80 ± 0.02	*
	20-30	0.82 ± 0.04	0.85 ± 0.03	0.81 ± 0.04	
	30-40	0.80 ± 0.05	0.87 ± 0.04	0.85 ± 0.06	*
K^+	0-10	0.24 ± 0.05	0.21 ± 0.02	0.16 ± 0.03	*
	10-20	0.18 ± 0.06	0.20 ± 0.02	0.14 ± 0.02	*
	20-30	0.19 ± 0.07	0.15 ± 0.04	0.13 ± 0.04	(•)
	30-40	0.19 ± 0.07	0.12 ± 0.03	0.14 ± 0.04	*
Ca^{+2}	0-10	4.03 ± 0.63	3.35 ± 0.48	3.06 ± 0.49	*
	10-20	2.29 ± 0.12	2.95 ± 0.51	2.62 ± 0.53	
	20-30	1.70 ± 0.28	2.25 ± 0.65	1.45 ± 0.46	(•)
	30-40	1.47 ± 0.22	1.50 ± 0.38	1.65 ± 0.68	*
Mg^{+2}	0-10	0.83 ± 0.16	0.80 ± 0.12	0.79 ± 0.13	*
	10-20	0.56 ± 0.04	0.74 ± 0.13	0.70 ± 0.13	*
	20-30	0.49 ± 0.07	0.62 ± 0.15	0.47 ± 0.12	*
	30-40	0.53 ± 0.10	0.52 ± 0.13	0.55 ± 0.21	*
SB	0-10	6.00 ± 0.84	5.22 ± 0.62	4.81 ± 0.66	*
	10-20	3.87 ± 0.17	4.76 ± 0.66	4.29 ± 0.69	
	20-30	3.20 ± 0.34	3.87 ± 0.84	2.86 ± 0.59	(•)
	30-40	2.99 ± 0.30	3.00 ± 0.56	3.18 ± 0.96	*

In the deepest soil layer (30-40 cm), a different pattern was observed: Ca^{+2}, Mg^{+2} and SB were significantly (p<0.05) higher in PP, whereas K^+ was significantly higher (p<0.10) in PS. Only K^+ correlated positively with TOC at this depth (r = 0.53; p<0.025). Na^+ showed significantly higher values in MM (p<0.05) at 0-10 cm, 10-20 cm and 30-40 cm, and did not correlate with TOC at any depth.

Discussion

Our results show, that when comparing monospecific and mixed pine forests in central Spain, the carbon stocks and exchangeable cations in the first 30 cm of the mineral soil profile respond in a similar way to the influence of the type of stand within the same soil layer, although patterns differ considerably when comparing between layers. At the topsoil (0-10cm), C stock and cations reach higher values in PS, lower in PP and intermediate in MM, whereas at the subsoil layers (10-30 cm) it reaches higher values in MM than in monospecific stands.

These different trends could be a consequence of the different mechanisms of soil carbon accumulation caused by the type of litter deposited in each soil layer. In our study, the % PP was positively correlated with CN_{FL} while CN_{FF} and the topsoil TOC were negatively correlated, while subsoil layers TOC are positively correlated to %FR. In the same way, TOC and exchangeable cations were positively correlated in all soil layer, so it seems the organic matter could be the responsible of the exchangeable cations values. The higher exchangeable cations at the MM subsoil layers could be related to the higher productivity described by other authors in the same study area. In addition, the higher C stock soil confers to the mixed stands a competitive advantage if the forestry goal encourages the climate change mitigation potential of the forests.

<u>Carbon accumulation as a function of stand type</u>

Our results showed that the response of TOC and C stock to tree species composition in the 0-30 cm layer depends on the soil layer, with higher C stocks under PS in the 0-10 cm and greater C accumulation under MM in the 10-30 cm. Below 30 cm, there was only limited evidence of any tree species effect.

We postulate that the different trends between the 0-10 and 10-30 cm layers are mainly related to the type of litter input since the decomposition of plant tissues in terrestrial ecosystems regulates the transfer of carbon and nutrients to the soil (Wang et al. 2014). C inputs to forest soils are related to leaf litter type (Berg 2000; Andivia et al. 2016) and roots (Rasse et al. 2005; Andivia et al. 2016). Possibly, the decomposition of the organic matter of the leaf litter brings the greater content of carbon to the topsoil (0-10 cm), whereas in deeper layers the greatest contribution comes from the roots (Andivia et al. 2016).

Regarding the upper mineral soil layer, we found a significant negative correlation between CN_{FF} and $TOC_{0\text{-}10cm}$. Our results indicate that the monospecific stands of *Pinus pinaster* accumulate less leaf litter (%PP and B_{FF} correlate negatively) than those of *P. sylvestris*. In addition, the *Pinus pinaster* leaf litter appears to be more recalcitrant than that of *Pinus sylvestris* since it has a significantly higher C:N ratio in the fresh fraction as also found by Herrero et al. (2016). In fact, CN_{FsL} and %PP correlate positively. Augusto et al. (2015) found that the species with more sclerophyllous foliage have higher lignin content and higher C:N ratio. The presence of more chemically recalcitrant compounds such as lignin could explain the lower decomposition rate of litter (Wang et al. 2016), and in turn the lower C input into the soil as humic substances. As a result, at the topsoil (0-10 cm) the TOC and C stock were higher in PS, lower in PP and intermediate in MM. Gallardo et al. (1991) also found lower carbon content in the first soil horizon in *P. pinaster* stands in relation to *P. sylvestris* stands.

At intermediate depths (10-30 cm), we found a significant positive correlation between TOC and %FR, suggesting that at deeper soil layers the greatest C input to the soil mainly comes from the decomposition of the organic matter from the fine roots, as found by other authors (Andivia et al. 2016). According to this, the higher TOC and $Cstock_{SOIL}$ values in MM at intermediate depths (10-30 cm) could be related to a higher %FR that, in turn, correlates positively with the richness of the understory vegetation (unpublished data). The higher richness of the understory vegetation due to plant community composition in mixtures may also influence storage of soil carbon through species–specific differences in plant detritus chemical composition and input rates (Ahmed et al. 2016). In plant communities where root litter is composed of inputs of many species, more complex organic forms are formed compared to the root litter of monospecific forests (Ahmed et al. 2016). It has been demonstrated that the highly complex and heterogeneous organic residues found in the soil organic matter of mixed communities alter the residence times of these compounds in the soil due to differences in biodegradability (Ahmed et al. 2016), even it was reported that high diversity of leaf litter promoted the rate of decomposition (King et al. 2002). On the other hand, a positive correlation between the tree species diversity, fine root biomass and C stock in deeper layers of the soil (30-40 cm) has been previously described by Dawud et al. (2016). They comment that the greater inputs of root litter cause higher accumulation of soil carbon stocks and relate the belowground niche complementarity with the mixed forests higher carbon accumulation in deeper layers, i.e. the stratification of roots of different tree species to top and subsoil in different stands (Dawud et al. 2016). In mixed forests also species interactions may increase productivity through the resource use complementarity (Ahmed et al. 2016). Tree species may behave differently in a mixture compared with their behaviour in monospecific stands (Brandtberg et al. 2000). In some cases, it has been shown to change towards a deeper rooting in admixtures (Brandtberg et al. 2000). In addition, different rooting depths and root turnover rates among species impact soil organic carbon distribution (Cremer and Prietzel 2017).

Next to a higher contribution of C inputs from roots in the 10-30 cm layer, higher values of TOC and C stock at intermediate depths could also be related to a greater thickness of the first mineral horizon in mixed stands in relation to monospecific stands (MM=22.8±3.5 cm, PS=14.7±3.5 cm, PP=15.3±1.9 cm; see Appendix Ia). Schleuß et al. (2014) have already reported the higher thickness of the A horizon in mixed stands in relation to monospecific stands, studying a tree diversity gradient with European beech being increasingly diluted by other species (dominance of 1, 3 or 5 species). Under 30 cm depth, the trends are confusing because TOC was less than 1% and the observed effects of stand type are limited. In the same way, Ahmed et al. (2016) confirmed the lack of differences between treatments for 40-100 cm depth when comparing admixtures vs. monospecific stands of *Betula pendula*, *Alnus glutinosa* and *Fagus sylvatica*.

Some authors have reported that the mixture of tree species significantly affect soil organic carbon stocks (Andivia et al. 2016; Cremer et al. 2016). This effect was reported not only for the topsoil (Andivia et al. 2016) but also for deeper layers of the mineral soil (Jandl et al. 2007), even in plantations (Liu et al. 2017). These authors highlight the positive effect of mixed stands in carbon accumulation (Jandl et al. 2007; Andivia et al. 2016; Cremer et al. 2016), more pronounced along time (Liu et al. 2017), but always when the mixtures combined species with contrasting traits, such as broadleaf–conifer. Despite the effect of admixture on soil C stock and TOC was limited in our study, probably because both tree species belongs to the same genus, a relatively strong tree species identity effect was observed in the FF and 0-10 cm layer.

<u>Exchangeable cations</u>

An indirect effect of exchangeable cations and sum of bases was also reported due to the different carbon amounts. It is likely that the effect of tree species composition on exchangeable cations and SB is mediated by their effect on the carbon (Cremer and Prietzel 2017). Soil organic matter improves the soil capacity to retain nutrients including exchangeable cations (Beldin et al. 2007), but also litter decomposition returns nutrients bound in organic material to mineral form in the soil (Gartner and Cardon 2004). In fact, we found a positive correlation between TOC and exchangeable cations from 0 to 30 cm depth, because soil organic matter plays an essential role in retaining soil base cations especially in sandy soils (Wang et al. 2017). As a result, exchangeable cations and SB describe the same two tendencies found for the carbon storage: higher values in PS, lower in PP and intermediate in MM, at the topsoil, but higher values in MM at intermediate soil layers.

Also it should be mentioned that in mixed forests composed by species with different rooting depth, deep system species absorbed nutrients from deeper soil horizons and redistributed the basic cations to the upper layers of the soil (Brandtberg et al. 2000). This fact could not be contrasted since there is no agreement in the literature on the rooting depth of the two species under study. According to Bravo-Oviedo and Montero (2008), *Pinus sylvestris* has a xeric-mesophilic character with a powerful root system: long main root and oblique secondary radical system, and *Pinus pinaster* has a xerophytic character with a potent radical system: very deep main root and horizontal secondary radical system. Other authors describe the highest density of roots for *P. sylvestris* (Finér et al. 2007), and for *P. pinaster* (Sudmeyer et al. 2004) at the first 50 cm, and Montero et al. (2005) mention that the 21.4% of the total biomass in *P. sylvestris* is root biomass and the 22.1% for *P. pinaster*.

Implications for forest management

We would like to point out that our results have important implications for forest management in the context of adaptation and mitigation to climate change through carbon sequestration or at least soil carbon preservation (Schleuß et al. 2014).

Even though the differences in TOC and C stock between stands at the intermediate layers of mineral soil were not statistically significant, the significant higher values of some exchangeable cations at intermediate soil layers in MM should make us reflect on the management strategies of Scots and Maritime pine stands in Spain. First, because Scots and Maritime pine forests occupy an important area in Spain, growing in monospecific and mixed stands (Serrada et al. 2008). Second, because the subsoil carbon is known to be more effectively stabilized as compared to topsoil or litter layer carbon (Rumpel and Kögel-Knabner 2011); therefore, potential losses of soil carbon from subsoil induced by warming will lag in time and provide a temporal buffer (Schleuß et al. 2014). Third, because exchangeable cations serve as good indicators of soil fertility and are critical nutrients for both plant and microbial metabolism; in fact, the lack of exchangeable cations availability constraints net primary productivity (Wang et al. 2017). And, fourth, because in mixed species communities, species interactions may either increase productivity through resource use complementarity (Ahmed et al. 2016). Some authors have reported a positive effect of species mixing by light use efficiency, in mixtures of *P. sylvestris* and *P. nigra* (Jucker et al. 2014), by water use efficiency, in Mediterranean areas (Vilà et al. 2007), or by growth efficiency, in admixtures of *Pinus sylvestris* and *P. pinaster* at the same study area (Riofrío et al. 2017b; Ruiz-Peinado et al. 2017), although the effect of mixing on productivity varies with stand development stage, stand density and site conditions (Ruiz-Peinado et al. 2017). In the same study area, (Riofrío et al. 2017a) have found a canopy vertical stratification by the complementarity of the crown in the mixed stand of Scots and Maritime pines in relation to monocultures that could affect productivity.

Conclusions

Despite the effect of the studied admixture on soil C stock and TOC is limited, probably because both tree species belong to the same genus, a relatively strong tree species identity effect is observed in the FF and 0-10 cm layer. Moreover, the influence of stand type on the first 30 cm of the mineral soil shows different patterns when comparing between layers: in the topsoil (0-10 cm) C stock is higher in monospecific Scots pine stands whereas in the subsoil C stock is higher in the mixed pine stand. These different patterns could be related to the amount and type of litter deposited in each soil layer (leaf and/or root litter) and to the different thickness of the first mineral soil horizon. Finally, these influences of the stand type on carbon of the mineral soil profile are reflected in differences in the exchangeable cations.

The positive effects on goods and services, such as carbon sequestration, in mixed stands in relation to monospecific stands of the same genus species should make us to reflect on: (1) the use of mixtures as a strategy to combat climate change, due to the advantage in the accumulation of carbon in the subsoil layers where it is protected from external disturbance; and (2) the implementation of the adaptive forest management that includes a non-monetary good and services (carbon sequestration or biodiversity conservation) as is demanded in a new climate change scenery.

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Appendix Ia

Table4. General soil properties of the soil profiles excavated under the monospecific stands of Scots pine (*Pinus sylvestris)*. Soil: soil classification according to Soil-Survey-Staff (2014); Colour: dry and wet matrix colour (Hue Value/Chroma); Thickness: thickness of each horizon; Soil texture: textural class according to Soil-Survey-Staff (2014); Sand/Silt/Clay: % of sand, silt and clay determined by the pipette method (MAPA 1994); Stones: coarse soil material (>2mm); pH (H_2O): pH according to MAPA (1994).

Stand type		*Pinus sylvestris*-monospecific stands					
Triplet		01	02	03	04	05	06
Soil type		Typic Dystroxerept	Typic Dystroxerept	Aquic Humixerept	Typic Dystroxerept	Typic Humixerept	Typic Dystroxerept
Horizon		Ah	Ah	Ah	Ah	Ah	Ah
Colour	Dry	10YR 4/2	10YR 4/2	10YR 4/1	10YR 5/2	10YR 4/2	10YR 7/2
	Wet	10YR 2/2	10YR 3/2	10YR 2/1	10YR 3/1	10YR 2/1	10YR 6/3
Thickness (cm)		0-10	0-15	0-12	0-8	0-15	0-28
Soil texture		Sandy Loam	Loamy Fine Sand	Loam	Sandy Loam	Sandy Loam	Sandy Loam
Sand/Silt/Clay		51/36/10	75/15/6	44/30/18	56/21/14	55/21/13	81/9/8
Stones (%)		2.25	7.90	6.11	9.04	2.68	13.03
pH (H_2O)		4.22	3.95	4.35	4.63	4.05	4.45
Horizon		AB	AC	AC	AB	AB	C
Colour	Dry	10YR 6/4	10YR 7/3	10YR 6/1	10YR 6/6	10YR 6/3	10YR 4/1
	Wet	7.5YR 4/6	10 YR 5/4	10YR 4/1	10YR 3/2	10YR 5/3	10YR 5/6
Thickness (cm)		10-40	15-35	12-30	08-30	15-40	28-65+
Soil texture		Loam	Loamy Fine Sand	Sandy Loam	Loam	Sandy Loam	Loamy Fine Sand
Sand/Silt/Clay		35/39/17	79/10/8	58/26//12	48/41/12	53/23/12	74/12/11
Stones(%)		24.61	11.83	20.24	25.68	11.68	5.53
pH (H_2O)		4.79	4.22	4.77	5.37	4.75	4.60
Horizon		Bw	C	Cg	C	C	-
Colour	Dry	7.5 YR 5/6	10 YR 6/6	10YR 8/1	10 YR 7/4	10 YR 7/4	-
	Wet	5 YR 4/6	10 YR 4/6	10YR 6/1	10YR 5/8	10YR 5/8	-
Thickness (cm)		40-60+	35-65+	30-60+	30-60+	40-60+	-
Soil texture		Loam	Sandy Loam	Sandy Loam	Loam	Sandy Loam	-
Sand/Silt/Clay		34/31/23	77/10/10	60/21/11	35/35/22	49/26/16	
Stones (%)		33.20	8.39	22.27	25.56	16.09	-
pH (H_2O)		4.82	4.76	4.69	4.98	5.31	-

Table 5. General soil properties of the soil profiles excavated under the monospecific stands of Maritime pine (*Pinus pinaster)*. Soil: soil classification according to Soil-Survey-Staff (2014); Colour: dry and wet matrix colour (Value/Chroma); Thickness: thickness of each horizon; Soil texture: textural class according to Soil-Survey-Staff (2014); Sand/Silt/Clay: % of sand, silt and clay determined by the pipette method (MAPA 1994); stones: coarse soil material (>2mm); pH (H_2O): pH according to MAPA (1994).

Stand type		*Pinus pinaster* monospecific stands					
Triplet		01	02	03	04	05	06
Soil type		Typic Dystroxerept	Typic Humixerept	Typic Humixerept	Typic Dystroxerept	Typic Humixerept	Typic Dystroxerept
Horizon		Ah	Ah	Ah	Ah	Ah	Ah
Colour	Dry	10YR 5/3	10YR 4/1	10YR 5/2	10YR 6/2	10YR 5/1	10YR 6/2
	Wet	10YR 3/2	10YR 2/1	10YR 3/1	10YR 3/1	10YR 2/1	10YR 4/1
Thickness (cm)		0-15	0-20	0-17	0-8	0-20	0-12
Soil texture		Loam	Sandy Loam	Sandy Loam	Sandy Loam	Sandy Loam	Loamy Fine Sand
Sand/Silt/Clay		52/34/13	64/16/11	66/18/8	80/12/5	65/16/11	85/9/5
Stones (%)		3.14	31.84	59.50	5.62	12.01	6.44
pH (H2O)		4.67	3.98	5.04	4.75	4.45	4.90
Horizon		AB	C	C	AC	AC	C
Colour	Dry	10YR 6/4	10YR 7/4	10YR 6/6	10YR 6/6	10YR 6/2	10YR 7/3
	Wet	10YR 4/4	10YR 5/6	10YR 4/6	10YR 3/2	10YR 4/2	10YR 6/4
Thickness (cm)		15-30	20-60+	17-57+	08-34	20-30	12-50+
Soil texture		Loam	Sandy Loam	Sandy Loam	Sandy Loam	Sandy Loam	Loamy Fine Sand
Sand/Silt/Clay		48/37/14	72/10/13/	68/15/10	74/13/8	59/24/11	84/8/6
Stones (%)		34.12	21.66	58.56	9.29	52.86	9.07
pH (H2O)		5.23	4.72	4.80	5.15	4.91	5.16
Horizon		Bw	-	-	C	C	-
Colour	Dry	5YR 5/6	-	-	10YR 7/4	10YR 6/4	-
	Wet	5YR 4/6	-	-	10YR 5/8	10YR 4/4	-
Thickness (cm)		30-60+	-	-	34-60+	30-52+	-
Soil texture		Clay	-	-	Loam	Sandy Loam	-
Sand/Silt/Clay		15/31/52			64/16/14	61/23/8	
Stones (%)		38.09	-	-	12.75	65.63	-
pH (H2O)		4.78	-	-	5.01	4.41	-

Table 6. General soil properties of the soil profiles excavated under the mixed stands of Scots (*Pinus sylvestris*) and Maritime (*Pinus pinaster*) pines. Soil: soil classification according to Soil-Survey-Staff (2014); Colour: wet matrix colour (Value/Chroma); Thickness: thickness of each horizon; Soil texture: textural class according to Soil-Survey-Staff (2014); Sand/Silt/Clay: % of sand, silt and clay determined by the pipette method (MAPA 1994); Stones: coarse soil material (>2mm); pH (H_2O): pH according to MAPA (1994).

Stand type		Mixed Stands					
Triplet		01	02	03	04	05	06
Soil type		Typic Humixerept	Typic Humixerept	Typic Humixerept	Typic Dystroxerept	Typic Dystroxerept	Typic Dystroxerept
Horizon		Ah	Ah	Ah	Ah	Ah	Ah
Colour	Dry	10YR 5/3	10 YR 5/2	10 YR 4/1	10 YR 6/2	10 YR 4/1	10 YR 6/1
	Wet	10 YR 3/2	10 YR 3/1	10 YR 2/2	10 YR 4/1	10 YR 2/1	10 YR 3/1
Thickness (cm)		0-35	0-23	0-17	0-20	0-12	0-30
Soil texture		Loam	Sandy loam	Sandy loam	Loamy Fine Sand	Sandy loam	Sandy loam
Sand/Silt/Clay		43/46/11	66/11/13	53/23/15	77/14/5	51/24/18	72/14/9
Stones (%)		15.79	5.21	15.02	15.12	11.70	47.93
pH (H_2O)		5.30	3.97	4.42	5.16	4.38	4.56
Horizon		Bw	C	C	C	AC	C
Colour	Dry	7.5 YR 6/6	10 YR 7/4	10 YR 6/3	10 YR 6/6	10 YR 6/3	10 YR 8/3
	Wet	5 YR 5/8	10 YR 6/6	10 YR 5/3	10YR 5/8	10 YR 4/4	10 YR 5/6
Thickness (cm)		35-75+	32-60+	17-54+	20-50	12-24	30-70+
Soil texture		Clay loam	Sandy loam	Sandy loam	Sandy loam	Sandy loam	Loamy Fine Sand
Sand/Silt/Clay		24/33/31	69/14/15	72/12/11	71/14/11	47/22/17	78/14/5
Stones (%)		34.80	8.33	60.57	35.15	15.27	11.88
pH (H_2O)		4.77	5.16	4.72	5.20	4.47	5.02
Horizon		-	-	-	-	C	-
Colour	Dry	-	-	-	-	10 YR 6/6	-
	Wet	-	-	-	-	10 YR 4/6	-
Thickness (cm)		-	-	-	-	24-50+	-
Soil texture		-	-	-	-	Sandy loam	-
Sand/Silt/Clay						45/22/18	
Stones (%)		-	-	-	-	17.88	-
pH (H_2O)		-	-	-	-	4.55	-

Appendix Ib

Table 7. General stand variables for monospecific stands of *Pinus sylvestris*. N: stems per hectare; G: basal area per hectare; Ho: dominant height; dq: quadratic mean diameter. Age: normal age.

Stand type		*Pinus sylvestris* monospecific stands						
Triplet		1	2	3	4	5	6	Mean ± SE
N (trees ha^{-1})	Total	821.0	509.3	665.0	636.6	651.0	821.0	684.0 ± 48.9
	Scots	806.0	495.1	651.0	580.0	651.0	778.0	660.2 ± 48.0
	Maritime	14.0	14.1	14.0	56.6	0.0	42.0	23.5 ± 8.7
G (m^2 ha^{-1})	Total	54.2	49.2	47.7	48.9	54.9	33.3	48.0 ± 3.2
	Scots	50.7	47.0	45.5	40.7	54.9	30.8	44.9 ± 3.4
	Maritime	3.6	2.2	2.3	8.2	0.0	2.6	3.2 ± 1.1
dq (cm)	Total	28.0 ± 1.2	34.4 ± 1.1	27.5 ± 1.8	30.4 ± 1.2	32.4 ± 1.2	22.5 ± 0.5	29.2 ± 1.7
	Scots	27.8 ± 1.1	32.3 ± 1.0	27.2 ± 1.8	29.3 ± 1.0	32.4 ± 1.2	22.2 ± 0.4	28.5 ± 1.6
	Maritime	56.7 ± 0.0	44.7 ± 0.0	45.3 ± 0.0	45.4 ± 5.8	0.0 ± 0.0	27.7 ± 0.3	36.6 ± 8.2
Ho (m)	Total	17.0 ± 0.3	19.3 ± 0.3	18.5 ± 0.8	22.1 ± 0.2	21.8 ± 0.3	16.8 ± 0.2	19.3 ± 0.9
	Scots	17.1 ± 0.3	19.3 ± 0.3	18.4 ± 0.8	22.1 ± 0.2	21.8 ± 0.3	16.6 ± 0.1	19.2 ± 0.9
	Maritime	16.2 ± 0.0	19.9 ± 0.0	24.5 ± 0.0	22.2 ± 1.3	0.0 ± 0.0	19.5 ± 1.0	17.1 ± 3.6
Age (years)	Scots	100	151	105	78	121	44	99.8 ± 14.9
	Maritime	0	0	0	0	0	0	0.0 ± 0.0

Table 8. General stand variables for monospecific stands of *Pinus pinaster*. N: stems per hectare; G: basal area per hectare; Ho: dominant height; dq: quadratic mean diameter. Age: normal age.

Stand type		*Pinus pinaster* monospecific stands						
Triplet		1	2	3	4	5	6	Mean ± SE
N (trees ha^{-1})	Total	566.0	806.4	538.0	1429.0	722.0	594.2	775.9 ± 137.1
	Scots	57.0	14.1	0.0	283.0	0.0	0.0	59.0 ± 45.7
	Maritime	509.0	792.2	538.0	1146.0	722.0	594.2	716.9 ± 96.6
G (m^2 ha^{-1})	Total	59.4	67.9	68.6	69.4	70.3	37.5	62.2 ± 5.2
	Scots	1.2	0.1	0.0	3.3	0.0	0.0	0.8 ± 0.5
	Maritime	58.2	67.8	68.6	66.0	70.3	37.5	61.4 ± 5.1
dq (cm)	Total	36.2 ± 1.7	32.0 ± 1.2	39.6 ± 1.3	22.6 ± 1.1	34.9 ± 0.9	28.2 ± 0.7	32.3 ± 2.5
	Scots	15.8 ± 2.2	9.7 ± 0.0	0.0 ± 0.0	9.5 ± 1.8	0.0 ± 0.0	0.0 ± 0.0	5.8 ± 2.8
	Maritime	38.6 ± 1.3	32.4 ± 1.1	39.6 ± 1.3	26.0 ± 0.9	34.9 ± 0.9	28.2 ± 0.7	33.3 ± 2.2
Ho (m)	Total	17.3 ± 0.5	16.3 ± 0.3	20.5 ± 0.2	12.4 ± 0.4	19.5 ± 0.3	15.6 ± 0.2	16.9 ± 1.2
	Scots	10.8 ± 1.8	7.0 ± 0.0	0.0 ± 0.0	7.3 ± 0.9	0.0 ± 0.0	0.0 ± 0.0	4.2 ± 1.9
	Maritime	18.0 ± 0.3	16.5 ± 0.2	20.5 ± 0.2	13.6 ± 0.3	19.5 ± 0.3	15.6 ± 0.2	17.3 ± 1.0
Age (years)	Scots	0	0	0	0	0	0	0.0 ± 0.0
	Maritime	118	78	105	80	115	49	90.8 ± 10.9

Table 9. General stand variables for mixed stands of Scots pine and Maritime pine. N: stems per hectare; G: basal area per hectare; Ho: dominant height; dq: quadratic mean diameter. Age: normal age.

Stand type		Mixed stands					
Triplet		1	2	3	4	5	6	Mean ± SE
N (trees ha^{-1})	Total	523.0	693.2	693.0	1330.0	552.0	679.0	745.0 ± 120.9
	Scots	241.0	325.4	495.0	764.0	354.0	396.0	429.2 ± 75.1
	Maritime	283.0	367.8	198.0	566.0	198.0	283.0	316.0 ± 56.3
G (m^2 ha^{-1})	Total	53.0	58.2	63.5	55.3	68.2	33.3	55.3 ± 4.9
	Scots	19.9	19.2	33.0	23.2	45.9	13.0	25.7 ± 4.8
	Maritime	33.1	38.9	30.5	32.1	22.3	20.2	29.5 ± 2.9
dq (cm)	Total	32.3 ± 1.6	31.6 ± 1.2	32.0 ± 1.8	20.2 ± 1.2	39.4 ± 0.8	24.2 ± 0.9	30.0 ± 2.8
	Scots	32.3 ± 2.0	26.4 ± 1.6	27.3 ± 1.8	16.6 ± 1.5	40.3 ± 1.1	20.2 ± 0.6	27.2 ± 3.5
	Maritime	40.3 ± 2.2	36.4 ± 1.3	43.5 ± 2.4	25.0 ± 1.6	37.6 ± 1.1	29.8 ± 1.1	35.4 ± 2.8
Ho (m)	Total	18.0 ± 0.4	16.4 ± 0.4	20.9 ± 0.7	13.1 ± 0.5	24.6 ± 0.3	14.8 ± 0.2	18.0 ± 1.7
	Scots	17.5 ± 0.6	14.5 ± 0.6	19.8 ± 0.8	12.3 ± 0.7	24.3 ± 0.2	14.0 ± 0.3	17.1 ± 1.8
	Maritime	18.5 ± 0.3	18.1 ± 0.3	23.7 ± 0.5	14.2 ± 0.6	25.0 ± 0.6	15.9 ± 0.2	19.2 ± 1.7
Age (years)	Scots	118	117	100	78	109	44	94.3 ± 11.7
	Maritime	113	93	95	79	118	49	91.2 ± 10.2

Appendix Ic

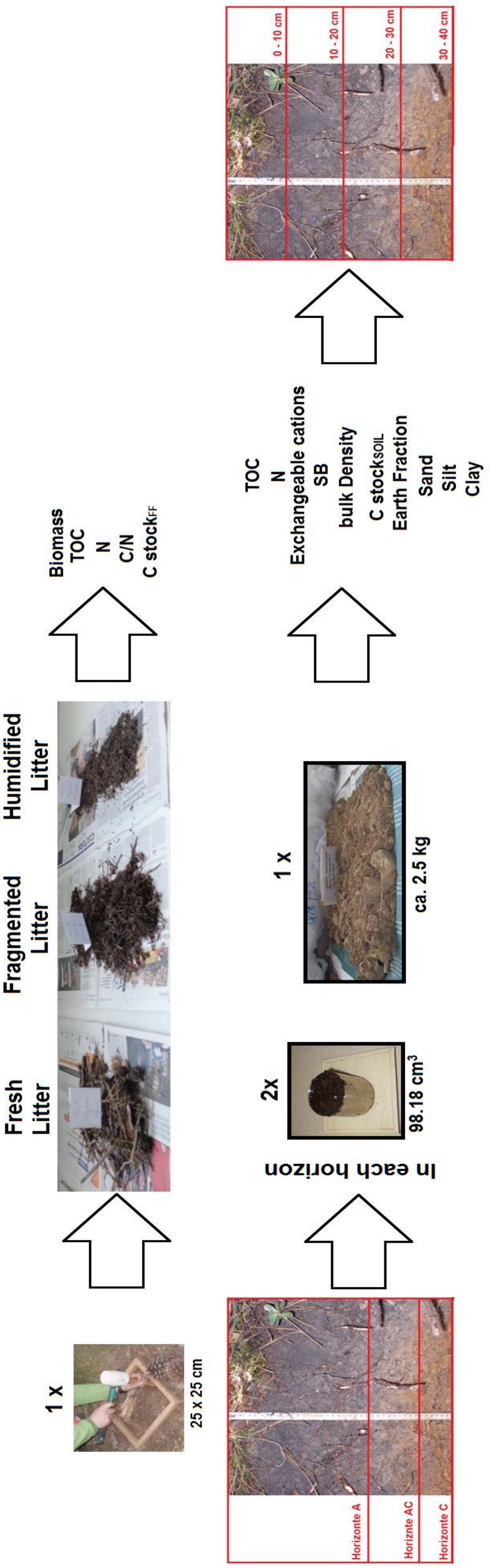

Figure 24. Soil sampling design.

Appendix Id

Table 10. Likelihood ratio test results. The p-values of the likelihood ratio tests are provided as well as the Akaike Information Criterion (Akaike 1973) of the null model (triplet as a random effect) and of the alternative model (triplet as a random effect + stand type as a fixed effect + %Sand as a fixed effect for the mineral soil). Other abbreviations as in Figure 21, 22 and 23.

	AIC		
	Null	Alternative	p-value
C $stock_{FF}$	89.39	88.38	0.08
C $stock_{FsL}$	32.26	31.59	0.10
C $stock_{FgL}$	28.49	25.52	0.03
C $stock_{HmL}$	28.67	31.77	0.64
C $stock_{0\text{-}40\ cm}$	166.69	167.84	0.18
C $stock_{0\text{-}10\ cm}$	-18.17	-18.42	0.10
C $stock_{10\text{-}20\ cm}$	139.24	141.40	0.28
C $stock_{20\text{-}30\ cm}$	13.64	12.94	0.08
C $stock_{30\text{-}40\ cm}$	-34.18	-35.44	0.06
B_{FF}	120.31	119.21	0.08
B_{FsL}	32.59	30.94	0.06
B_{FgL}	78.76	75.18	0.02
B_{HmL}	86.36	89.37	0.61
CN_{FF}	141.63	147.70	0.14
CN_{FsL}	160.46	154.86	0.01
CN_{FgL}	2.78	4.24	0.28
CN_{HmL}	-105.94	-102.33	0.82
$TOC_{0\text{-}10\ cm}$	74.39	69.36	0.01
$TOC_{10\text{-}20\ cm}$	70.47	73.42	0.38
$TOC_{20\text{-}30\ cm}$	41.13	40.27	0.08
$TOC_{30\text{-}40\ cm}$	34.09	36.43	0.30

Table 11. Likelihood ratio test results. The p-values of the likelihood ratio tests are provided as well as the Akaike Information Criterion (Akaike 1973) of the null model (triplet as a random effect) and of the alternative model (triplet as a random effect + stand type as a fixed effect + %Sand as a fixed effect). Other abbreviations as in Figure 21 and Table 3.

	AIC		
	Null	Alternative	p-value
$Na^{+}_{0\text{-}10\ cm}$	-35.80	-38.67	0.03
$Na^{+}_{10\text{-}20\ cm}$	-43.74	-52.42	0.00
$Na^{+}_{20\text{-}30\ cm}$	-40.36	-40.01	0.13
$Na^{+}_{30\text{-}40\ cm}$	-33.44	-39.13	0.01
$K^{+}_{0\text{-}10\ cm}$	-32.98	-52.19	0.00
$K^{+}_{10\text{-}20\ cm}$	26.61	23.96	0.03
$K^{+}_{20\text{-}30\ cm}$	34.36	32.79	0.06
$K^{+}_{30\text{-}40\ cm}$	30.01	22.70	0.00
$Ca^{+2}_{0\text{-}10\ cm}$	58.54	41.12	0.00
$Ca^{+2}_{10\text{-}20\ cm}$	54.49	56.08	0.23
$Ca^{+2}_{20\text{-}30\ cm}$	56.11	55.57	0.09
$Ca^{+2}_{30\text{-}40\ cm}$	6.12	-7.99	0.00
$Mg^{+2}_{0\text{-}10\ cm}$	5.83	-14.65	0.00
$Mg^{+2}_{10\text{-}20\ cm}$	6.60	4.11	0.04
$Mg^{+2}_{20\text{-}30\ cm}$	5.22	3.04	0.04
$Mg^{+2}_{30\text{-}40\ cm}$	45.80	24.22	0.00
$SB_{0\text{-}10\ cm}$	66.92	48.79	0.00
$SB_{10\text{-}20\ cm}$	63.16	63.90	0.15
$SB_{20\text{-}30\ cm}$	64.21	63.10	0.07
$SB_{30\text{-}40\ cm}$	11.98	-5.69	0.00

Chapter II

Respuesta del sotobosque al estrato arbóreo y a los gradientes edáficos en pinares mediterráneos mixtos y monoespecíficos

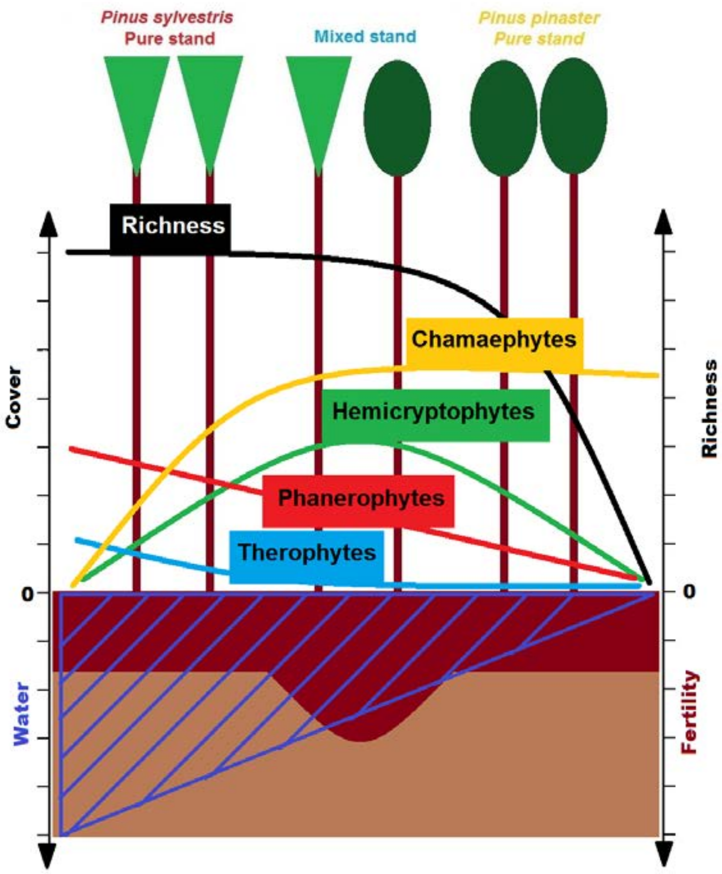

Figure 25. Graphical abstract of the article that gives rise to chapter II of the thesis (López-Marcos et al. 2019).

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López-Marcos D[1,2*], Turrión MB[1,2], Bravo F[1,3], Martínez-Ruiz C[1,2] (2019). **Understory response to overstory and soil gradients in mixed vs. monospecific Mediterranean pine forests.** European Journal of Forest Research 138(6):939-955 doi: 10.1007 / s10342-019-01215-0

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Understory response to overstory and soil gradients in mixed vs. monospecific Mediterranean pine forests

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Abstract

Many studies highlight the role of mixed versus monospecific forests to provide numerous ecosystem services. Most reports of the positive effects of tree mixture on biodiversity focus on coniferous-deciduous combinations, but little is known about the effects of mixtures combining two coniferous tree species. We assessed the effects of mixed versus monospecific stands of *Pinus sylvestris* and *P. pinaster* on the understory richness and composition and its relationship with the soil status, based on research with six triplets in northern Spain. In ten square meter quadrats randomly located per plot, the cover of every understory vascular plant species was estimated visually and data were codified according to Raunkiær´s life-forms. One soil pit of 50 cm depth was dug in each plot to determine the soil water (water holding capacity) and fertility (carbon and exchangeable-cations stocks) status. A water-stress gradient associated with the overstory composition indicated that *P. pinaster* tolerates lower soil water content than *P. sylvestris*. Mixed stands are under greater water stress than monospecific *P. sylvestris* stands but maintain the same level of understory richness. Also, a soil fertility gradient defined by organic carbon and exchangeable-magnesium stocks was identified. Hemicryptophytes, whose abundance is greater in mixed stands, were the only understory life-form positively correlated to soil fertility. We conclude that the mixture of both *Pinus* species should continue to be favored in the study area because it helps to maintain understory richness under greater waterstress conditions and improves soil fertility.

Keywords: Mixed pine forests, *Pinus sylvestris*, *P. pinaster*, understory composition, water stress gradient, fertility status.

Introduction

Mixed forests' potential to provide multiple goods and services to a wide variety of end users more efficiently than monospecific forests (Gamfeldt et al. 2013) has led to an increasing interest in mixed forests management (Bravo-Oviedo et al. 2014). Some potential benefits of the admixture of tree species include biodiversity conservation (Felton et al. 2010), soil conditions amelioration (Brandtberg et al. 2000) or carbon sequestration increase (European Commission 2010); additionally, under certain conditions mixed forests can produce higher yield than monocultures (Saetre et al. 1997). The mixture of tree species also performs as a measurement of adaptive management to climate change, increasing the resilience of forest ecosystems and improving their adaptability (Temperli et al. 2012). Taking into consideration that mixed forests account for around 40% of forests in Europe (MCPFE 2003) and 19% in Spain (MAGRAMA 2012), the development of appropriate management techniques to maintain and improve mixed forests is considered to be paramount to achieve forest management sustainability in the framework of global change and biodiversity conservation.

To assess the potential advantages of mixed vs monospecific stands, field plots should have similar characteristics, i.e. *ceteris paribus* conditions, as in studies based on triplets (Del Río et al. 2015). One triplet consists of three plots (one mixed plot and their corresponding monospecific plots) located less than 1 km from each other in order to share climatic and soil conditions. Plots within triplets have similar site conditions, age, and density and they belong to the same management compartments where the same silviculture regime has been applied, thus, facilitating a pair-wise plausible comparison of mixed vs monospecific stands(Riofrío et al. 2017b). In the last decade in Europe, several studies based on triplets have been carried out and most of them analyze the tree component of ecosystems focusing on productivity (Thurm and Pretzsch 2016; Riofrío et al. 2017b; Condés et al. 2018), structural heterogeneity (Pretzsch et al. 2016; Riofrío et al. 2017b), growth efficiency (Pretzsch et al. 2015; Riofrío et al. 2017a) or modified tree morphology (Thurm and Pretzsch 2016; Dirnberger et al. 2017; Zeller et al. 2017; Cattaneo et al. 2018; Forrester et al. 2018). Others associate the tree and soil ecosystem components analyzing carbon stocks (Cremer et al. 2016; López-Marcos et al. 2018) and nutrients in the soil profile (Cremer and Prietzel 2017; López-Marcos et al. 2018) and in the forest floor (Cremer et al. 2016; López-Marcos et al. 2018; Sramek and Fadrhonsova 2018). Nevertheless, the relationship between three ecosystem components such as overstory, understory, and soil in *ceteris paribus* conditions has not yet been addressed.

Since the overstory tree species differ in their effects on microclimatic and edaphic conditions, it has been suggested that environmental gradients (i.e. changes in soil fertility and water availability) may be broader in mixed than in monospecific stands (Barkman 1992a; Saetre et al. 1997). Thus, mixed stands have the potential to host a more heterogeneous and species-rich flora than monospecific stands (Hill 1992; Saetre et al. 1997). However, the effects of the overstory composition of mixed vs monospecific forests on the understory composition (Brown 1982; Enoksson et al. 1995; Saetre et al. 1997) and dynamics (Cavard et al. 2011) need to be studied more in depth: especially the effects of the overstory on the understory functional groups and their relationship with soil status.

The understory is known to be strongly influenced by the composition and structure of the overstory through its influence on temperature, light, water, soil nutrients, and litter accumulation (Saetre et al. 1999; Felton et al. 2010; Rodríguez-Calcerrada et al. 2011). However, managers and ecologists have traditionally paid less attention to the understory component of forests (Nilsson and Wardle 2005; Antos 2009), despite the fact that the understory participates in a great variety of aboveground processes (e.g. tree seedling regeneration, forest succession, species diversity and stand productivity) and also in belowground processes, such as litter decomposition, soil nutrient cycling and soil water conservation (Liu et al. 2017).

Understory plants represent the largest component of plant biodiversity in most forest ecosystems (Mestre et al. 2017). Although understory vegetation accounts for only a small portion of forest biomass (Pan et al. 2018), it is an important component of forest ecosystems driving ecosystem processes such as carbon cycling (Chen et al. 2017), nutrient recycling (Yarie 1978) and, thus, influencing the soil nutrient status (Cavard et al. 2011). The lower contribution of the understory to the forest biomass carbon pool is offset by its higher turnover rate, which allows a high annual carbon input into the understory relative to its total biomass (Cavard et al. 2011). In addition, it has been found that the understory removal has an important impact on biological and/or environmental parameters such as soil water content, soil temperature, and thus, on evapotranspiration, tree growth and soil properties (Wang et al. 2011). Therefore, the understory deserves more direct attention, especially in mixtures that combine coniferous tree species.

Most reports of the overstory-understory relationship in mixed forests focus on mixtures that combine deciduous and coniferous tree species (Saetre et al. 1997, 1999; Barbier et al. 2008; Cavard et al. 2011; Inoue et al. 2017), not only in natural forests but also in plantations (Ou et al. 2015). They test the overstory effect on the understory biomass (Cavard et al. 2011), cover and structural heterogeneity (Saetre et al. 1997), biodiversity and the mechanisms involved (Barbier et al. 2008), the spatial relationship between the overstory and understory species distribution and soil nitrogen availability (Inoue et al. 2017), or soil microbial biomass and activity (Saetre et al. 1999). However, the effect of the overstory on the understory in mixtures that combine coniferous tree species or even tree species of the same genus remains virtually unknown, at least in Europe (but see Mestre et al. 2017). This is so despite these mixtures are frequent in many environments, such as the admixtures of Scots pine (*Pinus sylvestris* L.) and Maritime pine (*Pinus pinaster* Aiton) in Spain. Both *Pinus* species show similar crown architecture and slight differences in shade tolerance (Riofrío et al. 2017b). Maritime pine is an important species of Mediterranean forests and Scots pine is the most widely distributed species of pine in the world (Bogino and Bravo 2014). They are two of the main forest species in Spain (Scots pine: 1.20 million ha; Maritime pine: 0.68 million ha) and they grow in monospecific and mixed stands, either naturally or as a result of species selection for afforestation (Serrada et al. 2008).

Plant species characteristics, such as life-form, provide information on how plants have adapted to the environment, particularly to climate (Smith and Smith 2003). The classification of species within a community into life-forms provides a way of describing the structure of a community for comparison purposes. Raunkiær´s classification of life-forms (1934), which establishes a relationship between the embryonic or meristematic tissues that remain inactive over the winter or prolonged dry periods and their height above ground, allows us to compare communities according to their adaptability to the critical season (Smith 1913), that is to say, the summer drought under Mediterranean conditions but also frost in winter.

On the other hand, soil properties can also play an important role in changes in the understory richness and composition (Cavard et al. 2011). Likewise, the understory can directly influence soil properties, such as temperature and moisture (Rodríguez et al. 2007a). Understanding the ecology of the understory vegetation has important implications for both biodiversity conservation and production-oriented forest management (Nilsson and Wardle 2005).

Here, we investigated the influence of the mixture of two widely distributed pine species (*Pinus sylvestris* and *P. pinaster*) on the understory plant community compared to monospecific stands, as well as the role played by relevant soil properties. Raunkiær´s life-forms classification of the understory vegetation was used. The aims of this study were: (i) to assess the effect of the overstory on the understory life-forms composition; (ii) to link differences in the life-forms composition of the understory to soil properties; and (iii) to model the response of the understory richness and cover of different life-forms along the main gradients identified. We hypothesize that: (1) the admixture of both pine species has a positive interactive effect on the understory richness compared to monospecific stands; and (2) the understory composition and richness are positively correlated with (and can be derived from) the availability of nutrients and water.

Material and methods

Study sites

The research was carried out in eighteen forest plots (6 triplets) located in the 'Sierra de la Demanda' between the Burgos and Soria regions, in North-Central Spain (41°47'35''N and 41°53'41''N latitude and 2°56'12''W and 3°20'46''W longitude; Figure 26). The climate is Temperate with dry or temperate summer (Cfb, Csb), according to the Köppen (1936) classification for the Iberian Peninsula. The mean annual temperature ranges from 8.7 to 9.8 °C and the annual precipitation ranges from 684 to 833 mm (Nafría-García et al. 2013). Altitude varies from 1093 to 1277 m a.s.l., and the slope from 0.9 to 20%. The geological parent materials are sandstones and marl from the Mesozoic era (IGME 2015). The soils are Inceptisols with a xeric soil moisture regime and mesic soil temperature regime and they are classified as Typic Dystroxerept or Typic Humixerept (sensu Soil-Survey-Staff 2014). The sandy soil texture was dominant and the pH varies from extremely acid to strongly acid (see López-Marcos et al. 2018). The natural dominant vegetation in the study area, highly degraded by anthropogenic action, is characterised by Pyrenean oak (*Quercus pyrenaica* Willd.) forests or communities dominated by junipers (López-Marcos et al. 2018).

Each triplet consisted of two plots dominated either by *Pinus sylvestris* (PS) or *Pinus pinaster* (PP) and one plot with a mixture of both species (MM) located less than 1 km from each other so that the environmental conditions were homogeneous within the triplet (Figure 26). Plots were circular of radius 15 m and the tree species composition was the main varying factor (López-Marcos et al. 2018). The percentage of the basal area of the dominant species in the monospecific plots was greater than 83% or 95% for *P. sylvestris* or *P. pinaster* respectively, whereas the basal area percentage of both species in the mixed plots ranged from 33 to 67%. Historically, this area has been occupied by forests and, for decades, it has been traditionally managed through selective thinning, benefiting *P. sylvestris*. The stands have had no silvicultural intervention or damage in the last ten years in an attempt to minimize the effect of the thinning or another type of intervention in what is intended to study, either growth, floristic richness or soil nutrients. The age of trees in the plots ranged from 44 to 151 years, the stand density from 509 to 1429 trees ha^{-1}, the basal area from 33.3 to 70.3 m^2 ha^{-1} and the dominant height between from 15.6 to 25.0 m (see López-Marcos et al. 2018). These plots belong to the network of permanent plots of iuFOR-UVa and they have been previously used in a series of studies recently (Riofrío et al. 2017a; Cattaneo 2018; López-Marcos et al. 2018).

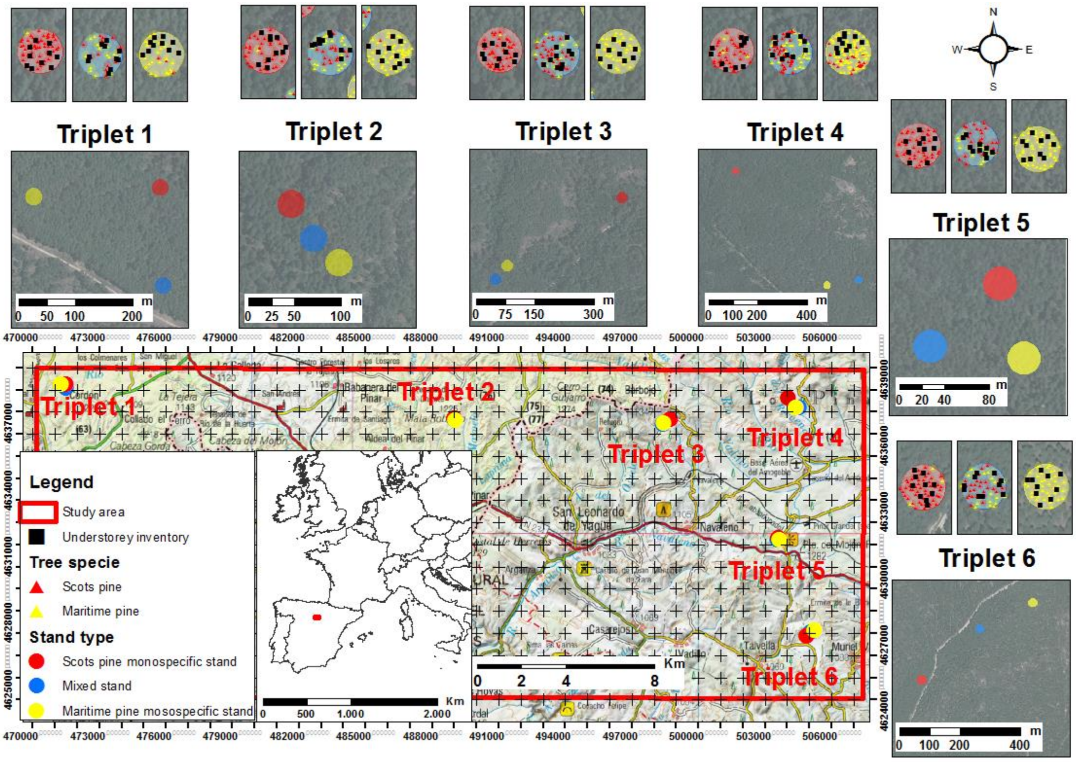

Figure 26. Location of the triplets in the 'Sierra de la Demanda' in North-Central Spain and location of the plots in each triplet. *Pinus sylvestris* monospecific plots (PS): red circles; *Pinus pinaster* monospecific plots (PP): yellow circles; Mixed plots of both *Pinus* species (MM): blue circles.

<u>Understory and soil sampling</u>

Within each plot, 10 quadrats (1m×1m) were randomly located and the cover (%) of every understory vascular plant species present in each quadrat, including tree regeneration, was estimated visually by the same observer in June 2016 to encompass and better identify the maximum number of vascular plant species (Martínez-Ruiz and Fernández-Santos 2005). Vascular plant species were classified according to the Raunkiær´s classification of life-forms (1934) following (Aizpiru et al. 2007); see Appendix IIb. Therophytes are annuals plants whose shoot and root systems die after seed production and which complete their whole life cycle within one year; hemicryptophytes are perennial herbaceous plants with periodic shoot reduction to a remnant shoot system that lies relatively flat on the ground surface; geophytes have subterranean resting buds (i.e. bulbs, rhizomes…); chamaephytes (dwarf shrubs) are woody plants whose natural branch or shoot system remains perennially between 25 and 50 cm above ground surface; and phanerophytes (tree regeneration and shrubs) are woody plants that grow taller than 25-50 cm.

Tree regeneration included the main tree species found as seedlings/saplings (i.e. *Pinus sylvestris*, *P. pinaster*, *Quercus pyrenaica*, and *Q. faginea* Lam.). In these stands, there are not subordinate tree species. Only two layers of vegetation can be distinguished (overstory and understory): the overstory measuring c.a. 20 m in height, and the understory with only 20 cm in height c.a., and never higher than 1 m.

At the same time as the vegetation sampling, one soil pit of at least 50 cm depth was dug in each plot for soil profile characterization (López-Marcos et al. 2018). Two undisturbed soil samples were collected from each pit's soil horizon with steel cylinders (98.2 cm^3) to keep their original structure. Likewise, one disturbed sample was also taken from each pit's soil horizon (ca. 2.5 kg).

Laboratory analyses

Both undisturbed and disturbed soil samples were dried at 105°C for 24 h before analyses. Undisturbed soil samples were weighed (±0.001 g) and used to calculate the soil bulk density. Disturbed soil samples were sieved (2 mm) before physical and chemical analyses. Physical analyses included percentage by weight of coarse fraction (>2 mm; %stones) and earth fraction (<2 mm; %EF). Available water was determined by the MAPA (1994) method as the difference between water content at field capacity (water remaining in a soil after it has been thoroughly saturated for two days and allowed to drain freely) and the permanent wilting point (soil water content retained at 1500 kPa using Eijkelkamp pF Equipment).

Chemical parameters analyzed for each soil horizon included: easily oxidizable carbon using the K-dichromate oxidation method (Walkley 1947); total organic carbon and total nitrogen by dry combustion using a LECO CHN-2000 elemental analyzer; available phosphorus using the Olsen method (Olsen and Sommers 1982) and exchangeable cations (Ca^{+2}, Mg^{+2}, K^{+}, Na^{+}) were extracted with 1M ammonium acetate at pH=7 (Schollenberger and Simon 1945) and determined using an atomic absorption/emission spectrometer.

Data analyses

In each horizon, the water holding capacity (WHC) and the stock of different soil properties were calculated as indicated in Appendix IIb). The water holding capacity and the stocks of different soil properties in the soil profile (0-50 cm) were then calculated as the sum of the values of each horizon (see Appendix IIb).

Richness was calculated as the total number of vascular plant species present in each plot (Colwell 2009), including understory vegetation and tree regeneration. Although several indices of diversity were tested, only the number of species showed to differ among stand types and thus is shown in results. The cover (%) of each Raunkiær's life-form in each plot was calculated as the average of the 10 vegetation sampling quadrats per plot. χ^2 tests of independence were carried out to compare the relative contribution of Raunkiær's life-forms to the total cover and richness within each stand type.

A redundancy analysis (RDA), as a linear-constrained ordination method with data scale standardization for units homogenization, was performed to describe the plant community using as vegetation variables the absolute cover data of Raunkiær's life-forms, and the basal area (G) of all stems > 7.5 cm in diameter for every *Pinus* species in each plot. The vegan 'envfit' function fitted onto the RDA ordination plot with 9999 permutations (Oksanen 2016) was used to show that the type of stand but not the triplet determined differences in floristic composition between plots. Additionally, sample ordination scores were tested for a significant correlation with the vegetation variables by means of the Pearson's coefficient.

To assist in the interpretation of the ordination axes according to the soil properties (Appendix IIc), these were fitted as vectors onto the RDA ordination plot using the vegan 'envfit' function. The advantage of the method is that it allows to test the significance of each vector adjusted by 9999 permutations, being able to calculate the R^2 of each variable. The explanatory variables considered in the analysis were the water holding capacity and the stocks of different soil properties in the whole soil profile (0-50 cm). Moreover, sample ordination scores along RDA1 and RDA2 were tested for a significant correlation with the significant soil properties by means of Pearson's coefficient.

The responses of each functional group (Raunkiær's life-forms) and understory richness along RDA1 and the values of the significant soil properties (WHC, total organic carbon stock (Cstock), and exchangeable magnesium stock (Mg^{+2}stock) were modeled by Huisman-Olff-Fresco (HOF) models (Huisman et al. 1993). These are a hierarchical set of five response models, ranked according to their increasing complexity (Model I, no species trend; Model II, increasing or decreasing trend where the maximum is equal to the upper bound; Model III, increasing or decreasing trend where the maximum is below the upper bound; Model IV, symmetrical response curve; Model V, skewed response curve. The AIC statistic (Akaike Information Criterion; Akaike 1973) was used to select the most appropriate response model for each life form (Johnson and Omland 2004); smaller values of AIC indicate better models.

All statistical analyses were implemented in the R software environment (version 3.3.3; R Development Core Team 2016), using the vegan package for multivariate analyses (version 2.3-5; Oksanen 2016), and the eHOF package for HOF modeling (version 3.2.2; Jansen and Oksanen 2013). One monospecific plot of *P. sylvestris* was considered an outlier and excluded from all analyses because it was the only one that presented aquic conditions (see López-Marcos et al. 2018). Soils which have an aquic moisture regime are saturated long enough to cause anaerobic conditions (Soil-Survey-Staff 2014).

Results

Raunkiær's life-forms in the understory

The relative contribution of Raunkiær's life-forms to the total cover and richness of the understory within each stand type differed significantly (cover: χ^2=43.7, df = 8, p<0.001, Figure 27a; richness: χ^2=16.4, df=8, p<0.04, Figure 27b). In both monospecific stands, phanerophytes (mostly in PS) and chamaephytes (mostly in PP) reached the highest relative cover and also contributed to high relative percentages of species richness; hemicryptophytes presented lower relative cover but higher or similar relative species richness than phanerophytes and chamaephytes; and geophytes and therophytes showed the lowest relative cover and scarce relative contribution to the total species richness, especially in PP.

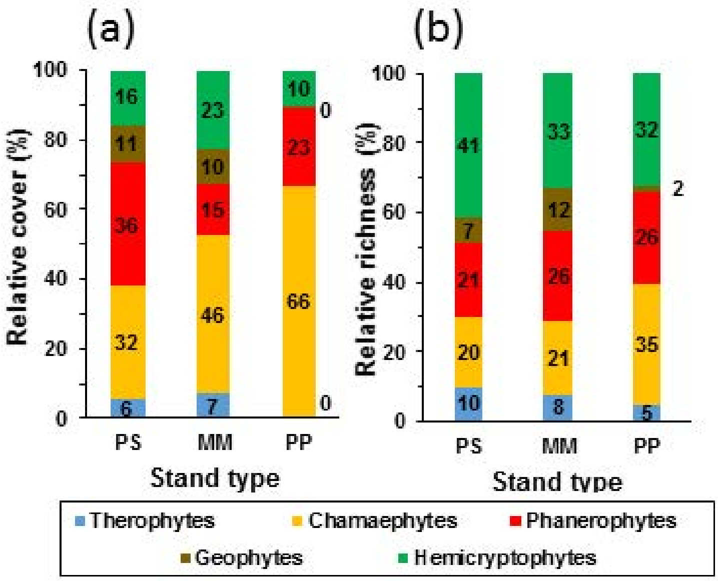

Figure 27. Relative cover (a) and species richness (b) of different Raunkiær's life-forms in the understory of the three stand types. Abbreviations as in Figure 26.

Nevertheless, in mixed stands (MM), chamaephytes and hemicryptophytes were the life-forms with the highest relative cover (45.6±14.7 and 22.8±6.8%, respectively) and contributed also to high relative percentages of species richness (21.1±6.7 and 33.0±6.2%, respectively); phanerophytes reached lower relative cover (14.5±5.8%) but higher or lower relative species richness (25.7±8.2%) than chamaephytes and hemicryptophytes, respectively; and geophytes and therophytes continue to be the life-forms that less contribute to the total cover and richness.

Relationship between the overstory and the understory vegetation

The RDA ordination of the plots produced eigenvalues (λ) of 2.52 and 1.14 for the first two axes, and accounted for 36 and 23 % of the overall species variance, respectively (Figure 28). The plots dominated by *P. sylvestris* cluster together on the right of the diagram, those dominated by *P. pinaster* cluster on the left, whereas the mixed plots occupy an intermediate position (Figure 28). Thus, RDA1 showed an overstory composition gradient to which the understory responds. In fact, highly significant correlation between plot scores along RDA1 and basal area (G) of *P. sylvestris* (r = 0.89, p<0.005) and of *P. pinaster* (r = -0.93, p<0.005) were found, showing both an opposite tendency; the basal area of *P. pinaster* increases towards the negative end of the RDA1 while the basal area of *P. sylvestris* increases towards the positive end. Also the cover of therophytes (r = 0.59, p<0.01) and chamaephytes (r = -0.46, p<0.05) were correlated to RDA1 with an opposite trend, suggesting greater cover of therophytes in PS and greater cover of chamaephytes in PP, in accordance with what is shown in Figure 27a. On the other hand, hemicryptophytes (r = 0.68, p<0.005), phanerophytes (r = -0.64, p<0.005) and geophytes (r = 0.71, p<0.005) were significantly correlated to RDA2, suggesting greater cover of hemicryptophytes and geophytes in some *P. sylvestris* monospecific plots and mixed plots, and greater cover of phanerophytes in some *P. sylvestris* monospecific plots.

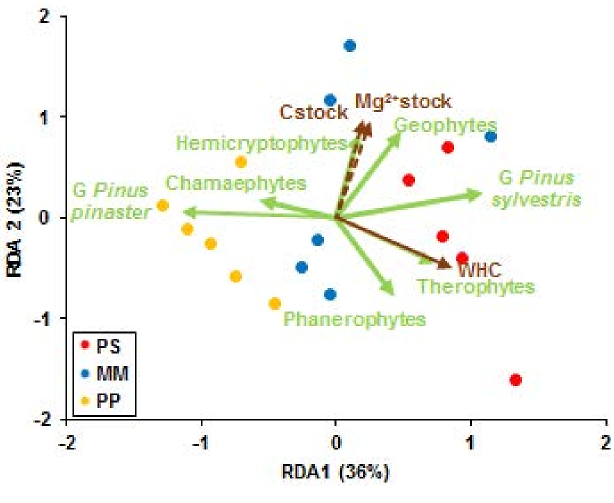

Figure 28. RDA biplot of plots (dots) and vegetation variables (green lines), i.e. the Raunkiær's life-forms cover, and the basal area (G) of *Pinus sylvestris* and *P. pinaster*; and the significant explanatory soil properties fitted onto the RDA as vectors using the envfit function (brown solid line: p<0.05; brown dashed lines: p<0.10; explained variation > 50%). WHC (water holding capacity), Cstock (total organic carbon stock), Mg^{+2}stock (exchangeable magnesium stock). Other abbreviations as in Figure 26.

Understory compositional change along the main gradients identified

Understory richness showed an increasing trend bounded below the maximum attainable response along RDA1 (HOF model III; Figure 29a), i.e. as the basal area (G) of *P. sylvestris* increases. Understory richness also showed an increasing trend but where the maximum is equal to the upper bound (HOF model II) as WHC (Figure 29c) and Mg^{+2}stock (Figure 29d) increase, whereas richness showed no response (HOF model I) to Cstock and, thus, it was not shown in Figure 29.

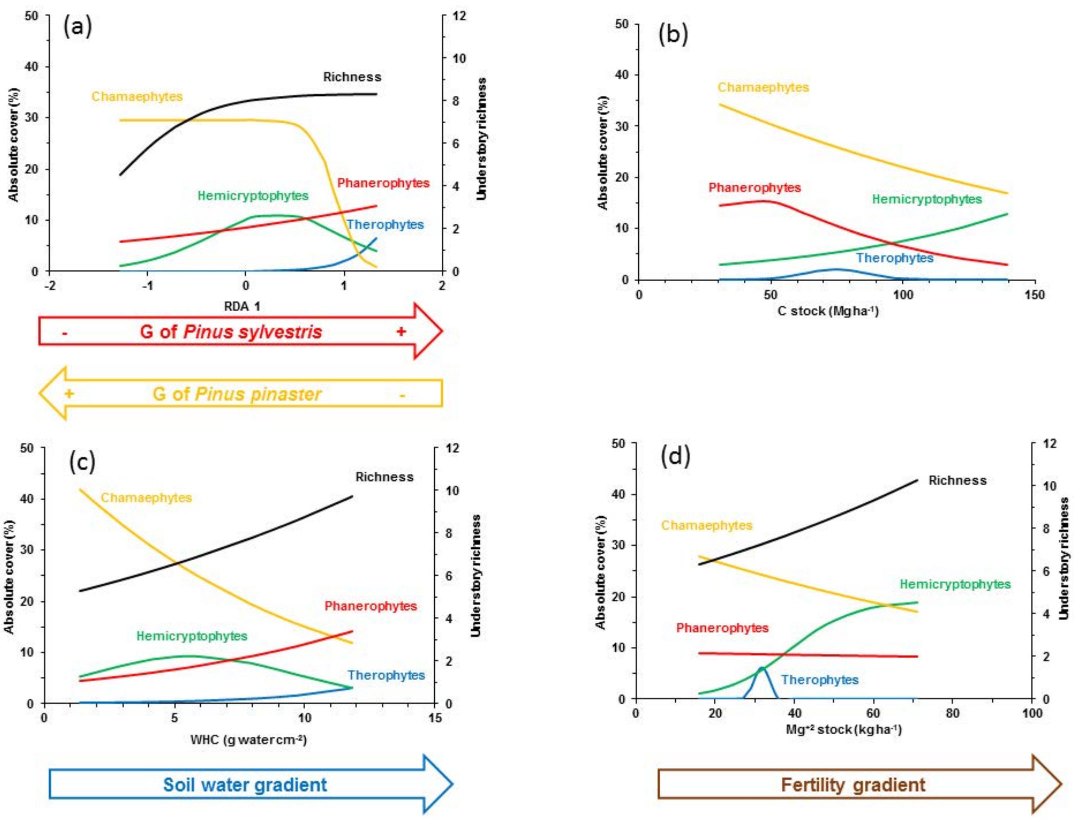

Figure 29. HOF-derived response curves for the Raunkiær's life-forms cover and total species richness of the understory, relative to RDA1 (a), and to significant soil properties, i.e. Cstock (b), WHC (c) and Mg^{+2}stock (d). Abbreviations as in Figure 28.

Relationship between vegetation composition and soil properties

Among the Raunkiær's life-forms, only geophytes showed indeterminate response curve (i.e. HOF model I), with low and constant cover (<0.5%) along RDA1, and for all significant soil properties (WHC, Cstock, and Mg^{+2}stock), and, thus, it was not shown in Figure 29. Therophytes showed HOF model II with increasing trend along RDA1 (Figure 29a) as WHC increases (Figure 29c), whereas therophytes showed skewed response curve (HOF model V) for Cstock with a maximum around 75 Mg ha^{-1} (Figure 29b) and for Mg^{+2}stock with a maximum around 30 $kgha^{-1}$ (Figure 29d). Hemicryptophytes showed unimodal response curves along RDA1 (HOF model V;

Figure 29a) and along the WHC gradient (HOF model IV; Figure 29c) with optima in the middle part of the gradients, where mixed plots are located. However, hemicryptophytes showed HOF model II with increasing trend as Cstock increases (Figure 29b), and HOF model III with increasing trend bounded below the maximum attainable response as Mg^{+2}stock increases (Figure 29d). Chamaephytes showed a decreasing trend bounded below the maximum attainable cover on the left end of RDA1 (HOF model III), and a decreasing trend (HOF model II) as WHC (Figure 29c), Cstock (Figure 29b) and Mg^{+2}stock (Figure 29d) increase. Finally, phanerophytes showed a cover increasing trend (HOF model II) as G of *P. sylvestris* increases (RDA1 right-end; Figure 29a), and as WHC increases (Figure 29c), whereas they showed skewed response curve (HOF model V) for Cstock with a maximum around 50 Mg ha^{-1} (Figure 29b) and a decreasing trend (HOF model II) as Mg^{+2}stock increases (Figure 29d).

Discussion

Our results show how the composition of the overstory influences the understory. Primarily, the understory responds to differences in the basal area of both *Pinus* species associated with differences in the water holding capacity (RDA1). Secondarily, the understory responds to differences in the stocks of the total organic carbon and exchangeable Mg^{+2} (RDA2). Both carbon content (i.e. soil organic matter) and nutrient content are known to be highly correlated (Beldin et al. 2007). As a matter of fact, this has been shown e.g. for Mg^{+2}, which serves as a good indicator of soil fertility and is a critical nutrient for plant and microbial metabolism (Wang et al. 2017).

Overstory composition responds to soil water content

In the study area, monospecific stands of *P. sylvestris* are located where WHC is higher, while *P. pinaster* monospecific stands occupy areas with lower soil water content (i.e. the lowest WHC). However, in the mixed stand, with intermediate values of WHC, both *Pinus* species cohabit, probably because they occupy different microsites according to WHC. Therefore, the overstory composition is related to WHC of the soil profile (0-50 cm), and the behavior of both tree species is consistent with the xeric-mesophilic character of *P. sylvestris* and the xerophytic character of *P. pinaster* described by Bravo-Oviedo and Montero (2008).

Understory richness responds to overstory composition and soil fertility

Understory richness attained the maximum level for intermediate values of basal area of *P. sylvestris* (Figure 29a) so that mixed stands will preserve similar understory richness to that of monospecific stands of *P. sylvestris*. Therefore, the lower soil water content (WHC) in mixed stands compared to *P. sylvestris* monospecific stands (Figure 29c) does not seem to have a negative impact, in terms of understory richness or productivity. This is probably due to the greater availability of microsites with different WHC in mixed stands.

In addition, the understory richness was positively correlated with Mg^{+2}stock, according to the relationship between nutrient retention increase and biodiversity described by Tilman et al. (1997). This is really interesting since magnesium is known to be a critical component in the carbon fixation and transformation processes in the vegetation, and its deficiency can affect forest decline (Huettl 1992; Zas and Serrada 2003). In the study area, both the greater productivity and overyielding found in mixed stands, compared to monocultures (Riofrío et al. 2017b), could be partially explained by greater soil fertility (Mg^{+2}stock). Even though the impact of soil on overyielding still remains ambiguous and debated (Lu et al. 2018), further scientific evidence suggests that a positive relationship between biodiversity and productivity can be found (Ahmed et al. 2016; Liang et al. 2016; Schmid and Niklaus 2017; Lu et al. 2018).

Furthermore, it is known that variations in the relative proportion of certain tree species within mixed forests affect the composition and richness of species in the understory through distinct species responses to soil leaf litter accumulation (Rodríguez-Calcerrada et al. 2011). Litter generally reduces species richness in Mediterranean forests (Casado et al. 2004). We found the higher leaf litter biomass in *P. sylvestris* monospecific stands (see López-Marcos et al. 2018), but these stands also presented similar understory richness to that of mixed forests. In all probability, the higher leaf litter accumulation below *P. sylvestris* in the study area has no negative effect on understory richness due to its specific characteristics. Scots pine needles appear to be less recalcitrant than that of Maritime pine, since they have a significantly lower C/N ratio in the fresh fraction (see Herrero et al. 2016; López-Marcos et al. 2018), suggesting a faster decomposability of *P. sylvestris* leaf litter relative to *P. pinaster* (Santa-Regina 2001).

<u>Understory life-forms respond to the overstory composition and soil fertility</u>

The cover of therophytes increases as the basal area of *P. sylvestris* increases, i.e. as WHC increases, contrary to what is expected for grasslands (Madon and Médail 1997), but reaches its maximum at very low levels of fertility, i.e. 75 Mg ha^{-1} of Cstock and 30 kg ha^{-1} of Mg^{+2}stock. Since the seed is the organ of therophytes that survives the unfavorable season, its germination might be limited by water stress, but not by soil fertility as the seed provides the necessary nutrients to germinate (Rivas-Martínez et al. 2002). However, in the study area, the soil moisture gradient is not large enough to significantly affect the germination of therophytes, and many other factors may be playing a role. In fact, annuals are known to be ruderal and not stress-tolerant in productive habitats (Madon and Médail 1997).

Phanerophytes are also positively correlated with WHC but negatively linked to Cstock and Mg^{+2}stock in the soil profile. Phanerophytes are woody perennial plants with resting buds more than 25 cm above the soil level, they retain reserve compounds and, thus, they are not so dependent on soil fertility, although their buds' growth is limited by soil water (Rivas-Martínez et al. 2002). Moreover, in this study, the phanerophytes include the tree regeneration (saplings) that might be adversely affected at the seedling stage by scarcity of water resources (Mcintyre 1995).

Contrary to phanerophytes, chamaephytes decrease in cover as WHC increases, from maximum attainable cover for a higher basal area of *P. pinaster*. The negative correlation between chamaephytes cover and WHC suggests the stress-tolerant character of chamaephytes in the study area, probably because of higher water-use efficiency (Scartazza et al. 2014). On the other hand, as phanerophytes, chamaephytes decrease in cover as Cstock and Mg^{+2}stock increase. The soils under shrubs (phanerophytes or chamaephytes) indicate a higher rate of recalcitrant organic-matter (Chabrerie et al. 2003) due to the higher lignin content of woody species (mainly pine saplings and *Ericaceae* species in the study area), which reduces the decomposition rate of the soil organic matter by microorganisms (Clark and Paul 1970) and the speed of nutrient release into the soil (Condron and Newman 1998). Consequently, lower values of Cstock and Mg^{+2}stock were found with the increase of shrub cover in the stands.

The cover of hemicryptophytes is maximum in MM (intermediate WHC). It seems that the mixture of both *Pinus* species in the study area, under moderate water-stress conditions, favors this Raunkiær's life-form. Nevertheless, the higher cover of hemicryptophytes in MM might also be partly the result of abiotic facilitation of chamaephytes under moderate soil water shortage, according to the refinement of the stress-gradient hypothesis (SGH) proposed by Maestre et al. (2009). The SGH predicts that the frequency of facilitative and competitive interactions will vary inversely across abiotic stress gradients, with facilitation being more common in conditions of high abiotic stress relative to more benign abiotic conditions (Bertness and Callaway 1994). However, Maestre et al. (2009) predict that other combinations are likely to yield different results. For example, that the effect of neighbors can be negative at both ends of the stress gradient when both interacting species have similar 'competitive' or 'stress-tolerant' life histories and the abiotic stress gradient is driven by a resource (e.g. water). In the study area, under moderate water stress conditions, as found in MM with intermediate values of WHC, the facilitation can be expected to be the dominant net outcome whereas competition would prevail at both ends of the water-stress gradient (i.e. under monospecific stands of *P. sylvestris* or *P. pinaster*). In mixed stands, chamaephytes might assume the benefactor/facilitator role whereas hemicryptophytes act as the beneficiary/facilitated, and both life-forms can be considered to be water-stress tolerant (sensu Grime 1977) since both are more abundant at lower WHC (Figure 29c). In fact, the cover of chamaephytes is similar in PS and MM (Figure 29a), yet the cover of hemicryptophytes reaches its maximum in MM in moderate water-stress conditions. It is worth noting that further research would be needed to support this possibility.

Furthermore, hemicryptophytes are the only life-form whose cover was significantly related to the fertility gradient, showing an increase in cover as Cstock and Mg^{+2}stock increase (Figure 29d). Previous studies also showed that many hemicryptophytes were indicative of sites with relatively good soil fertility (Mark et al. 2000; Sigcha et al. 2018).

<u>Implications for forest management</u>

These results have important implications for forest management in the context of the supply of ecosystem services, such as biodiversity conservation. Firstly, the mixture of Scots pine and Maritime pine, widely distributed in Spain (Serrada et al. 2008), should be maintained and favored over pure stands since this mixture maintains higher understory richness under water-stress conditions. This could, therefore, be regarded as a biodiversity conservation strategy in the current climate change scenario. It should also be noted that some understory species, such as *Quercus pyrenaica*, which has been granted critically-endangered protection status all across Spain (see Appendix IIa), enjoys higher regeneration when both *Pinus* species cohabit (López-Marcos et al. 2020a). Secondly, the positive relationships of hemicryptophytes with Cstock and Mg^{+2}stock, and of the understory richness with WHC and Mg^{+2}stock emphasize the importance of considering the understory in forest management plans. This will enhance, among other things, biodiversity conservation, carbon sequestration, and productivity by improving soil fertility.

Conclusions

The mixture of both *Pinus* species maintains similar understory richness to that of monospecific stands of *Pinus sylvestris* but for lower soil water content. The understory responds to the gradient of the basal area of both *Pinus* species associated with a water-stress gradient. Hemicryptophytes are linked to better soil fertility status (defined by the total organic carbon and exchangeable Mg^{+2} stocks). We conclude that the mixture of both *Pinus* species should continue to be favored in the study area because it helps to maintain the understory richness under greater water-stress conditions (i.e. under expected climate change) and improves soil fertility.

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Author contributions

DLM carried out the field and laboratory work, ran the data analysis and discussed the results. DLM and CMR discussed data analysis and commented on the results and discussion. CMR supported DLM with the statistical analysis. MBT supported DLM with the laboratory analysis. DLM, CMR, MBT and FB edited the manuscript. FB coordinated the research project.

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Appendix IIa

Table 12. Species classification according to the Raunkiær's life-forms (Raunkiær 1934), following Aizpiru et al. (2007), their protection status in Spain according to Anthos (2017) project [(http://www.anthos.es/): CR: critically endangered; EN: endangered; VU: vulnerable (UICN 2012) and SpI: speciel interest], and Raunkiær's life-forms cover (%) of each stand type.

Life-forms	Species	Protection status				Raunkiær's life-forms cover (%)		
		Status	Law	Red book	Region	PS	MM (mean±SE)	PP
Therophytes	*Aira caryophyllea* L.					1.37±1.02	1.37±0.81	0.17±0.11
	Geranium robertianum L.							
	Melampyrum pratense L.							
Geophytes	*Pteridium aquilinum* (L.) Kuhn	VU	7	b	Murcia	5.75±2.37	2.08±1.04	0.08±0.08
	Asphodelus albus Mill.							
	Simethis mattiazzii (Vand.) Sacc.	EN	14	e	Cataluña			
Hemicryptophytes	*Viola montcaunica* Pau	SI	5		Castilla la Mancha	8.87±2.66	7.32±2.69	4.92±3.24
	Polygala vulgaris L.	VU		a	Baleares			
	Potentilla montana Brot.							
	Agrostis castellana Boiss. & Reut.							
	Galium saxatile L.							
	Juncus conglomeratus L.							
	Hypochaeris radicata L.							
	Lotus corniculatus L.	SpI	6		Extremadura			
	Sanguisorba minor Scop.							
	Deschampsia flexuosa (L.) Trin.							
Chamaephytes	*Erica australis* L.					21.13±8.21	26.08±9.21	29.00±7.32
	Erica arborea L.	EN		b	Murcia			
	Arenaria montana L.							
	Calluna vulgaris (L.) Hull							
	Arctostaphylos uva-ursi (L.) Spreng.	SI	7	b	Murcia			
	Vaccinium myrtillus L.							
Phanerophytes	*Quercus pyrenaica* Willd.	CR	5,8,10,11	d	Spain	11.53±3.10	5.83±2.5	7.50±2.22
	Ilex aquifolium L.	VU	1,2,3,5,6,9,11,13	d	Spain			
	Pinus sylvestris L.							
	Pinus pinaster Aiton	SpI	5,10	a,b	Baleares, Castilla la Mancha, Murcia			
	Quercus faginea Lam.	EN	4,7,13	b,c,d	Spain			
	Cistus laurifolius L.							
	Juniperus oxycedrus L.	EN	7	a	Murcia			

i

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Appendix IIb

Table 13. Data analyses of soil properties: Water holding capacity.

Water holding capacity of each horizon (WHC_{Hi})

$WHC_{Hi} = UW_{Hi} \cdot bD_{Hi} \cdot \%EF_{Hi}\ T_{Hi}$	UW_{Hi}: Useful water of each horizon bD_{Hi}: bulk density of each horizon $\%EF_{Hi}$: % of earth fraction of each horizon T_{Hi}: thickness of each horizon

Water holding capacity in the whole mineral soil profile (0-50cm; WHC):

$$WHC = \sum WHC_{Hi}$$

Table 14. Data analyses of soil properties: Easily oxidizable carbon stock.

Easily oxidizable carbon stock of each horizon ($oxCstock_{Hi}$)

$oxCstock_{Hi} = oxC_{Hi} \cdot bD_{Hi} \cdot \%EF_{Hi}\ T_{Hi}$	oxC_{Hi}: Easily oxidizable carbon of each horizon bD_{Hi}: bulk density of each horizon $\%EF_{Hi}$: % of earth fraction of each horizon T_{Hi}: thickness of each horizon

Easily oxidizable carbon stock in the whole mineral soil profile (0-50cm; oxCstock)

$$oxCstock = \sum oxCstock_{Hi}$$

Table 15. Data analyses of soil properties: Total organic carbon stock.

Total organic carbon stock of each horizon ($Cstock_{Hi}$)

$Cstock_{Hi} = TOC_{Hi} \cdot bD_{Hi} \cdot \%EF_{Hi}\ T_{Hi}$	TOC_{Hi}: Total organic carbon of each horizon bD_{Hi}: bulk density of each horizon $\%EF_{Hi}$: % of earth fraction of each horizon T_{Hi}: thickness of each horizon

Total organic carbon stock in the whole mineral soil profile (0-50cm; Cstock)

$$Cstock = \sum Cstock_{Hi}$$

Table 16. Data analyses of soil properties: Total nitrogen stock.

Total nitrogen stock of each horizon ($Nstock_{Hi}$)

$Nstock_{Hi} = TN_{Hi} \cdot bD_{Hi} \cdot \%EF_{Hi}\ T_{H}$ i	TN_{Hi}: total nitrogen of each horizon bD_{Hi}: bulk density of each horizon $\%EF_{Hi}$: % of earth fraction of each horizon T_{Hi}: thickness of each horizon

Total nitrogen stock in the whole mineral soil profile (0-50cm; Nstock)

$$Nstock = \sum Nstock_{Hi}$$

Table 17. Data analyses of soil properties: Available phosphorus stock.

Available phosphorus stock of each horizon ($Pavstock_{Hi}$)

$Pavstock_{Hi} = TN_{Hi} \cdot bD_{Hi} \cdot \%EF_{Hi}\ T_{Hi}$	Pav_{Hi}: total nitrogen of each horizon bD_{Hi}: bulk density of each horizon $\%EF_{Hi}$: % of earth fraction of each horizon T_{Hi}: thickness of each horizon

Available phosphorus stock in the whole mineral soil profile (0-50cm; Pavstock)

$$Pavstock = \sum Pavstock_{Hi}$$

Table 18. Data analyses of soil properties: Exchangeable sodium stock.

Exchangeable sodium stock of each horizon (Na^+stock_{Hi})

$Na^+stock_{Hi} = TN_{Hi} \cdot bD_{Hi} \cdot \%EF_{Hi}\ T_{Hi}$	Na^+_{Hi}: Exchangeable sodium of each horizon bD_{Hi}: bulk density of each horizon $\%EF_{Hi}$: % of earth fraction of each horizon T_{Hi}: thickness of each horizon

Exchangeable sodium stock in the whole mineral soil profile (0-50cm; Na^+stock)

$$Na^+stock = \sum Na^+stock_{Hi}$$

Table 19. Data analyses of soil properties: Exchangeable potassium stock.

Exchangeable potassium stock of each horizon (K^+stock_{Hi})

$K^+stock_{Hi} = TN_{Hi} \cdot bD_{Hi} \cdot \%EF_{Hi}\ T_{Hi}$	K^+_{Hi}: Exchangeable potassium of each horizon bD_{Hi}: bulk density of each horizon $\%EF_{Hi}$: % of earth fraction of each horizon T_{Hi}: thickness of each horizon

Exchangeable potassium stock in the whole mineral soil profile (0-50cm; K^+stock)

$$K^+stock = \sum K^+stock_{Hi}$$

Table 20. Data analyses of soil properties: Exchangeable calcium stock.

Exchangeable calcium stock of each horizon ($Ca^{+2}stock_{Hi}$)

$Ca^{+2}stock_{Hi} = TN_{Hi} \cdot bD_{Hi} \cdot \%EF_{Hi}\ T_{Hi}$	Ca^{+2}_{Hi}: Exchangeable calcium of each horizon bD_{Hi}: bulk density of each horizon $\%EF_{Hi}$: % of earth fraction of each horizon T_{Hi}: thickness of each horizon

Exchangeable calcium stock in the whole mineral soil profile (0-50cm; $Ca^{+2}stock$)

$$Ca^{+2}stock = \sum Ca^{+2}stock_{Hi}$$

Table 21. Data analyses of soil properties: Exchangeable magnesium stock.

Exchangeable magnesium stock of each horizon ($Mg^{+2}stock_{Hi}$)

$Mg^{+2}stock_{Hi} = TN_{Hi} \cdot bD_{Hi} \cdot \%EF_{Hi}\ T_{Hi}$	Mg^{+2}_{Hi}: Exchangeable magnesium of each horizon bD_{Hi}: bulk density of each horizon $\%EF_{Hi}$: % of earth fraction of each horizon T_{Hi}: thickness of each horizon

Exchangeable magnesium stock in the whole mineral soil profile (0-50cm; $Mg^{+2}stock$)

$$Mg^{+2}stock = \sum Mg^{+2}stock_{Hi}$$

Appendix IIc

Table 22. Soil properties (mean±SE), in each stand type, fitted as vectors onto the RDA ordination (Figure 28). PS*: Pinus sylvestris* monospecific plots; PP: *Pinus pinaster* nmonospecific plots; MM: Mixed plots of both *Pinus* species.

	PS			MM			PP			R^2	p-value	r
	mean±SE			mean±SE			mean±SE					
WHC (g water cm^{-2})	8.65	±	0.93	6.61	±	1.54	5.36	±	1.57	0.39	0.03	0.62
oxCstock (Mg ha^{-1})	85.42	±	12.48	94.40	±	21.18	71.83	±	13.40	0.08	0.53	0.29
Cstock (Mg ha^{-1})	88.07	±	11.42	97.84	±	13.53	75.35	±	10.33	0.32	0.07	0.56
Nstock (Mg ha-1)	3.83	±	0.56	3.59	±	0.48	3.97	±	1.60	0.03	0.81	0.18
Pavstock (Mg ha^{-1})	18.98	±	1.66	17.07	±	2.52	15.03	±	2.14	0.24	0.14	0.49
Na^{+}stock (Mg ha^{-1})	0.91	±	0.07	0.93	±	0.08	0.82	±	0.11	0.16	0.29	0.40
K^{+}stock (Mg ha^{-1})	0.33	±	0.08	0.28	±	0.05	0.21	±	0.03	0.30	0.10	0.55
Ca^{+2}stock (Mg ha^{-1})	1.98	±	0.13	2.00	±	0.38	1.67	±	0.33	0.27	0.12	0.52
Mg^{+2}stock (Mg ha^{-1})	0.33	±	0.04	0.35	±	0.08	0.30	±	0.06	0.31	0.08	0.55

Chapter III

¿Pueden los pinares mixtos conservar la riqueza del sotobosque al mejorar el establecimiento de especies de sotobosque típicas de los robledales nativos?

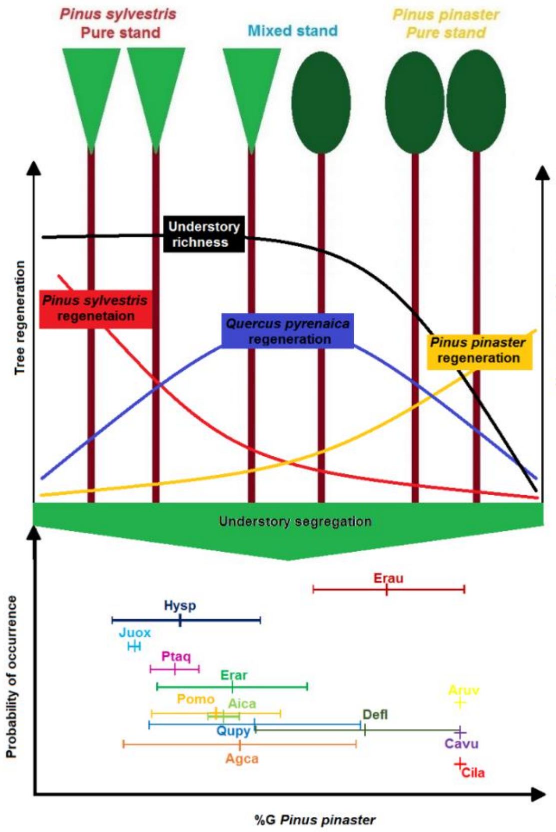

Figure 30. Graphical abstract of the article that gives rise to chapter III of the thesis (López-Marcos et al. 2020a).

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Can mixed pine forests conserve understory richness by improving the establishment of understory species typical of native oak forests?

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Key message: A positive effect of mixed pine forests (*Pinus sylvestris* L. and *Pinus pinaster* Ait.) on the understory richness and tree regeneration was observed with respect to monospecific stands. Understory species typical of the native Pyrenean oak forests in the Iberian Peninsula contribute to maintaining high understory richness in such mixed pine forests.

Abstract

Context: The influence of stand characteristics on the understory in mixtures that combine coniferous tree species of the same genus deserves more study since they are frequent in Spain.
Aims: To assess the effect of mixed versus monospecific stands of *Pinus sylvestris* L. and *Pinus pinaster* Ait. on the main tree species regeneration and understory species composition.
Methods: Tree regeneration and understory species composition were inventoried in eighteen forest plots (6 triplets) in North-Central Spain. Each triplet consisted of two plots dominated either by Scots pine or Maritime pine and one mixed plot that contained both species.
Results: The basal area (%) of both *Pinus* species was the only characteristic of the stand that significantly influenced the understory composition and tree regeneration. Characteristic species of humid and temperate zones, including *P. sylvestris* regeneration, dominated in Scots pine stands, and typical species of well-drained Mediterranean areas, including *P. pinaster* regeneration, dominated in Maritime pine stands. In mixed stands, the highest regeneration of the native Pyrenean oak with respect to monospecific stands was accompanied by understory species typical of native oak forests that share the same regeneration niche.
Conclusion: Mixed pine forests allow the development of understory species better than monospecific forests.

Keywords: Mixed pine forests, *Pinus sylvestris*, *Pinus pinaster*, Pyrenean oak regeneration, Niche amplitude, Understory richness

Introduction

The management of mixed forests is becoming a new paradigm (Bravo-Oviedo et al. 2014) in order to improve natural tree regeneration (Carnevale and Montagnini 2002; Löf et al. 2018), soil conditions (Brandtberg et al. 2000), and the provision of many high-value ecosystem services, including carbon sequestration (Gamfeldt et al. 2013; López-Marcos et al. 2018) or biodiversity conservation (Barbier et al. 2008; Gomez-Aparicio et al. 2009; Felton et al. 2010; Cavard et al. 2011; Korboulewsky et al. 2016); additionally, under certain conditions mixed forests can produce higher yields than monocultures (Saetre et al. 1997; Pretzsch et al. 2010; Gamfeldt et al. 2013; Toïgo et al. 2015; Jactel et al. 2018).

Since the overstory tree species differ in their effects on microclimatic and edaphic conditions, it has been suggested that the environment in mixed stands is more heterogeneous compared with monocultures (Barkman 1992; Saetre et al. 1997). Thus, mixed stands have the potential to host a more heterogeneous and species-rich flora (Hill 1992; Saetre et al. 1997). Additionally, the greater variability of habitat conditions in mixed stands than in monospecific stands may be a favorable condition for seed dispersers, and germination and growth of native tree species (Carnevale and Montagnini 2002). The structure of the stands can also influence the establishment of native species through biotic interactions such as competition (Grace and Tilman 2003) and facilitation (Bruno et al. 2003; Callaway 2007; Brooker et al. 2008). Therefore, regeneration of mixed forests has become an important topic of practical concern throughout the world (Löf et al. 2018).

The mass ratio hypothesis predicts that the ecosystem function is driven by the (traits of the) most abundant species in plant communities (Grime 1998; Ali and Yan 2017), such as specific leaf area or leaf nitrogen and phosphorus concentrations (Ali and Yan 2017). This hypothesis uses the relative abundance of each plant species to predict the effect of the most abundant species of plant communities on the ecosystem functions and services, like biodiversity (Grime 1998; Ali and Yan 2017). The application of this hypothesis is restricted to the role of autotrophs in ecosystem processes, and it postulates that the relationships between plant diversity and ecosystem properties can be explored by classifying species into categories, as dominants and subordinates (Grime 1998). Dominants are relatively large and make a substantial contribution to the plant community biomass, whereas subordinates show high fidelity of association with particular vegetation types but they are smaller and tend to occupy microhabitats delimited by the architecture and phenology of their associated dominants (Grime 1998).

Most reports of the overstory-understory relationship in mixed forests focus on mixtures that combine deciduous-coniferous tree species (Saetre et al. 1997, 1999; Barbier et al. 2008; Cavard et al. 2011; Inoue et al. 2017). They test the overstory effect on the understory biomass, songbirds, soil fauna, and ectomycorrhizae (Cavard et al. 2011), cover and structural heterogeneity (Saetre et al. 1997), plant biodiversity and the associated mechanisms (Barbier et al. 2008; Rodríguez-Calcerrada et al. 2011), the spatial relationship between the overstory and understory species distribution and soil nitrogen availability (Inoue et al. 2017), soil fauna diversity (Korboulewsky et al. 2016), or soil microbial biomass and activity (Saetre et al. 1999). However, the effect of the stand characteristics on the understory in mixtures that combine coniferous tree species or even tree species of the same genus remains virtually unknown (but see Mestre et al. 2017; López-Marcos et al. 2019). This is so despite these mixtures being frequent in many environments, such as the admixtures of Scots pine (*Pinus sylvestris* L.) and Maritime pine (*Pinus pinaster* Ait.) in Spain. Both *Pinus* species show similar crown architecture and slight differences in shade tolerance (Riofrío et al. 2017a), but differ in water-stress tolerance (López-Marcos et al. 2019). They are two of the main forest species in Spain and grow in pure and mixed stands either naturally or as a result of species selection for afforestation (Serrada et al. 2008).

On the other hand, the facilitating effect of *Pinus* species in succession processes has already been well explored among restoration strategies such as the reintroduction of endangered tree species through the use of assisted regeneration; thus, the ecological and functional role of certain pioneer species may be of vital importance for the reestablishment of native ecosystems (Aguirre et al. 2006; Arrieta and Suárez 2006; Avendaño-Yáñez et al. 2016). Nevertheless, the use of evergreen conifers as nurse plants to establish *Quercus* spp. could reduced the cover of the understory and its species content (Pigott 1990). Additionally, the identification of realized niches of understory plant species and knowledge of their composition and dynamics can be important information to consider in the prediction models of potential responses to climate change (Olthoff et al. 2016).

Based on the same experiment, we found that the composition of the overstory (i.e., the proportion of *Pinus* species) influenced the Raunkiær's life-forms composition of the understory, with the abundance of hemicryptophytes being greater in mixed stands (López-Marcos et al. 2019). The effects of mixed versus monospecific stands on the understory were also related to soil water and fertility status (see also López-Marcos et al. 2019). In particular, mixed stands occupied areas with intermediate soil moisture whereas *P. pinaster* tolerated lower soil water content than *P. sylvestris*. The organic carbon and exchangeable magnesium stocks were also higher in mixed stands (see also López-Marcos et al. 2018). In the present paper, we addressed the influence of a mixture of these two widely distributed pine species (*P. sylvestris* and *P. pinaster*) on the understory plant community composition (at the species level) and the regeneration of main tree species, including native *Quercus* species, compared with monospecific stands. For that, we used the same sampling design in triplets (monospecific *P. sylvestris*, monospecific *P. pinaster* and mixed *P. sylvestris*-*P. pinaster* plots), well balanced for stand composition but not necessarily for other stand characteristics. The aims of this study were: (i) to test the effect of stand characteristics on species composition in the understory and tree regeneration; (ii) to model the response of distinct understory species and tree species regeneration to stand characteristics; and (iii) to estimate the niche amplitude of the main understory species, including tree regeneration, with respect to the stand characteristics. We hypothesized that (1) the proportion of Pinus species in the overstory is the most influential stand characteristic on the understory composition and tree regeneration according to previous studies; (2) the mixture of pine species favors the regeneration of native tree species like Pyrenean oak; and (3) the regeneration of native Pyrenean oak is accompanied by a group of associated understory species that contribute to maintain a high understory species richness in mixed stands as in monospecific *P. sylvestris* stands.

Material and methods

Study sites

The research was carried out in eighteen forest plots (6 triplets) located in the Northern Iberian Range, in North-Central Spain (41º47'35''N and 41º53'41''N latitude, and 2º56'12''W and 3º20'46''W longitude; Figure 31). The climate is temperate with dry or temperate summer (Cfb, Csb) according to the Köppen (1936) classification for the Iberian Peninsula. The mean annual temperature is 9.0ºC and the annual precipitation around 800mm. Plots are located at an elevation ranging from 1093m to 1277m a.s.l. Soils are acidic with mostly sandy texture and medium to low water-retention capacity (see López-Marcos et al. 2018, 2019). Nearby climax vegetation (Rivas-Martínez 1987), highly degraded by anthropogenic action, is characterized by Pyrenean oak forests (*Luzulo forsteri-Quercetum pyrenaicae* S. and *Festuco heterophyllae-Quercetum pyrenaicae* S.) or juniper forests (*Juniperetum hemisphaerico-thuriferae* S.).

Each triplet consisted of three circular plots of 15m radius, including two plots dominated either by Scots pine or Maritime pine and one mixed plot that contained both species, located less than 1km from each other so that the environmental conditions were homogeneous within triplets although they could differ among distinct triplets (see López-Marcos et al. 2018 for differences in soil properties). The sampling design in triplets was well balanced for stand composition (six repetitions per stand type) but not necessarily balanced for other stand characteristics (i.e., density, total basal area, dominant height, mean quadratic diameter, age) that were intended to be similar within the triplet (avoiding biases in the sampling design) but differed between triplets to be able to be contrasted (see Table 25 in Appendix IIIb). The percentage of the basal area (%G) of the dominant species in the monospecific plots was greater than 83% or 95% for *P. sylvestris* or *P. pinaster* respectively, whereas the basal area percentage of both species in the mixed plots ranged from 33 to 67%. The age of the selected plots ranged between 44 and 151years, the stand density between 509 and 1429 trees ha^{-1}, the basal area between 33.3 and 70.30m^2ha^{-1}, and the dominant height between 15.60 and 25.04m. Traditionally, forest management consists of strip clear-cutting with soil movement and planting or sowing when necessary, and moderate thinning from below (Riofrío et al. 2019). The stands have had no silvicultural intervention or damage in the last 10 years (López-Marcos et al. 2018). There were no statistical differences in the distance between the plots of the three stand types and forests of other tree species (*Quercus pyrenaica* Willd., *Q. faginea* Lam., or *Juniperus* spp.; see Figure 36 in Appendix IIIa). Triplets belong to the network of permanent plots of the Sustainable Forest Management Research Institute UVa-INIA (iuFOR) and they have been previously used in a series of recent studies (Riofrío et al. 2017a, b, 2019; Cattaneo 2018; López-Marcos et al. 2018, 2019).

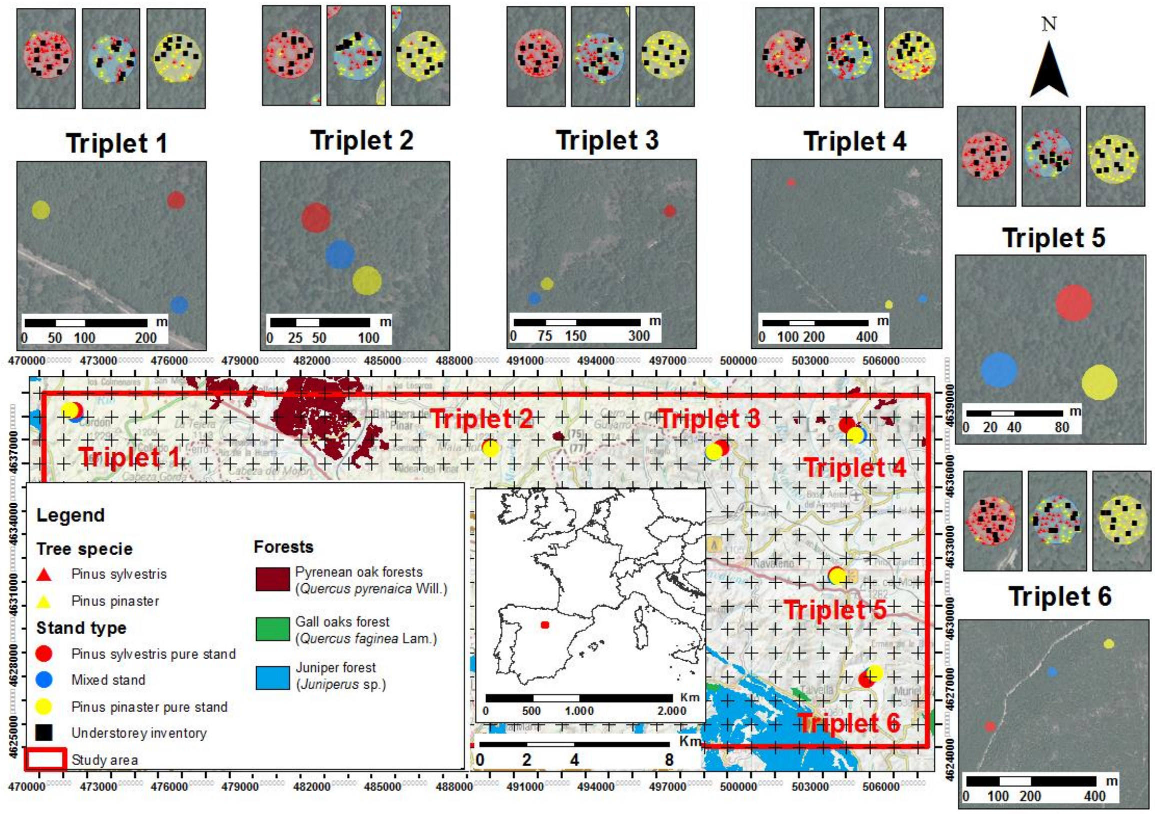

Figure 31. Location of the triplets in the 'Sierra de la Demanda' in North-Central Spain, the plots within each triplet, and the native forests (Pyrenean oak forest, Gall oak forest and Juniper forest). *Pinus sylvestris* monospecific plots (PS): red circles; *Pinus pinaster* monospecific plots (PP): yellow circles; Mixed plots of both Pinus species (MM): blue circles. Location of understory inventories: black squares.

Sampling of understory vegetation and tree regeneration

Within each plot, 10 quadrats (1m×1m) were randomly selected and the vertical projection cover (%) of every understory vascular plant species, including tree regeneration, and bryophytes was estimated visually by the same observer in June 2016 (López-Marcos et al. 2019) to encompass and identify the maximum number of vascular plant species (Alday et al. 2010). Vascular plant species nomenclature follows Tutin et al. (1964-1980) and bryophytes nomenclature follows Crosby et al. (1992-1989). The number of individuals (stems) of the tree regeneration was also counted within each quadrat. Tree regeneration included the main tree species found at seedlings/saplings stages (i.e., *P. sylvestris*, *P. pinaster*, *Q. pyrenaica* and *Q. faginea*) because no old regeneration was found (it had probably been cleared by management for fire prevention); only seven old individuals of Juniperus oxycedrus L. were found that were considered to be part of the understory (height <1m) but not as regeneration, thus, estimating their cover but not counting them as individuals. In these stands, there were no subordinate tree species. Only two layers of vegetation could be distinguished (overstory and understory): the overstory measuring c.a. 20 m, and the understory never higher than 1 m.

Data analyses

The cover (%) of each species and density of main tree species regeneration (i.e. *P. sylvestris*, *P. pinaster*, *Q. pyrenaica*, and *Q. faginea*) in each plot were calculated as the average of the 10 quadrats. Richness was calculated as the total cumulative number of plant species in the 10 quadrats per plot (Colwell 2009), including understory vegetation and tree regeneration. Although several indices of diversity were tested, only the number of species showed any difference among stand types and thus is shown in results.

To identify the characteristics of the stands that determine the understory plant species composition, a Detrended Correspondence Analysis (DCA) was applied on the matrix of cover of the understory plant species (30 species x 17 plots). To assist in the interpretation of the ordination axes, the stand characteristics and tree regeneration were fitted as vectors onto the DCA ordination plot using the vegan 'envfit' function (Oksanen 2016). The advantage of this method is that it allows for testing the significance of each vector adjusted by 9999 permutations, with the R^2 of each variable able to be calculated. The explanatory variables considered in the analysis were (1) the stand characteristics: normal age (Age: years), density (N: trees ha^{-1}), total basal area (G: m^2ha^{-1}), dominant height (Ho: m), quadratic mean diameter (dq: cm), and the percentage of basal area (%G) of *P. sylvestris* and *P. pinaster*; and (2) the tree regeneration (individuals m^{-2}) of *P. sylvestris*, *P. pinaster*, *Q. pyrenaica* and *Q. faginea*. Additionally, in order to relate overstory composition to tree regeneration, and tree regeneration to main understory species, Pearson's correlation coefficients ($p<0.05$) between the regeneration density of the main tree species (*P. sylvestris*, *P. pinaster* and *Q. pyrenaica*) and the percentages of basal area of *P. sylvestris* and *P. pinaster*, as well as between the regeneration cover (%) of main tree species and the cover (%) of main species of the understory, were calculated.

The response of understory plant species (total species richness and individual species cover) and tree regeneration (density: individuals m^{-2}) with respect to the significant stand characteristics (i.e., the overstory composition by means of the percentage of basal area of *P. pinaster*) were modeled by Huisman-Olff-Fresco (HOF) models (Huisman et al. 1993). These are a hierarchical set of five response models, ranked by their increasing complexity (Model I, monotone trend, i.e. with constant abundance; Model II, increasing or decreasing trend where the maximum is equal to the upper bound; Model III, increasing or decreasing trend where the maximum is below the upper bound; Model IV, symmetrical response curve; Model V, skewed response curve). The Akaike Information Criterion (AIC; Akaike 1973) was used to select the most appropriate response model (Johnson and Omland 2004); smaller values of AIC indicate better models. HOF models were validated using "bootstrapping" because the frequency of appearance of 33% of species in the plots was low (< 10%; mostly for species following HOF model I). Finally, the location of species optima (µ) and niche widths (2t) for those species with unimodal responses were derived from the HOF models (Lawesson and Oksanen 2002). The 2t values were found by solving for the gradient points of the fitted HOF model relative to a strict Gaussian model at 2t (Lawesson and Oksanen 2002) . In the case of a symmetric unimodal response, the lower and upper t values are identical, while with a skewed model, the 2t intervals are not necessarily equal.

All statistical analyses were implemented in the R software environment (version 3.3.3; R Development Core Team 2016) using the vegan package for multivariate analyses (version 2.3-5; Oksanen 2016), and the eHOF package for HOF models (version 3.2.2; Jansen and Oksanen 2013). One monospecific plot of *P. sylvestris* was considered an outlier and excluded from all analyses because it was the only one that presented aquic conditions (see López-Marcos et al. 2019). Soils that have an aquic moisture regime are saturated long enough to cause anaerobic conditions (Soil-Survey-Staff 2014).

Results

Effects of stand characteristics on the understory vegetation

The DCA ordination produced eigenvalues (λ) of 0.50 and 0.35 for the first two axes, with gradient lengths of 2.62 and 2.52 SD units, respectively (Figure 32). The adjustment of explanatory variables on the biplot ordination showed how the percentages of the basal area (%G) of *P. sylvestris* and *P. pinaster* were the stand characteristics that explained most variability (0.7 in both cases), with both showing an opposite tendency (Figure 32). This suggests a gradual change in the composition of the understory related to the overstory composition. The other characteristics of the stands were not significantly correlated with the DCA ordination, and thus they are not displayed in results (but see Table 23).

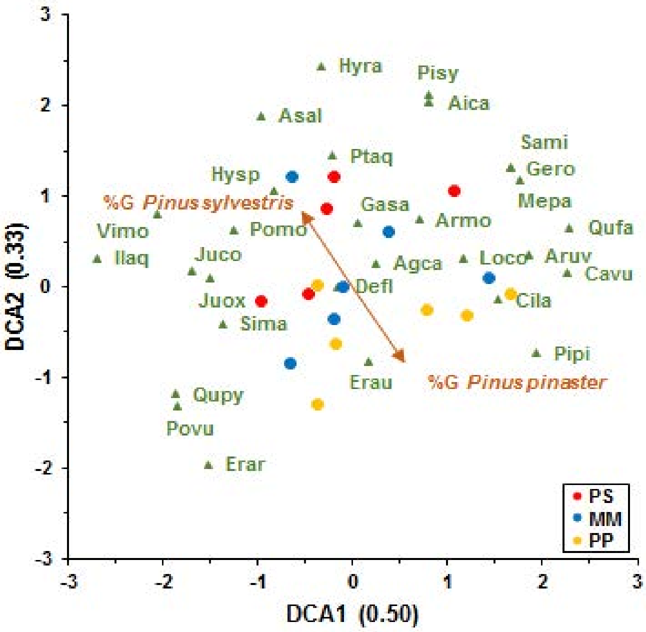

Figure 32. DCA biplot of plots and species and projection of the significant two significant explanatory variables ($p<0.05$ and explained variation >50%). Stand characteristics other than %G of *Pinus sylvestris* and % G of *Pinus pinaster* were not significantly correlated with the DCA axes. PS *Pinus sylvestris* monospecific plots, PP *Pinus pinaster* mpnospecific plots, and MM mixed plots pf two *Pinus species.* Species codes: Agca (Agrostis castellana Boiss. & Reut), Aica (*Aira caryophyllea* L.), Armo (*Arenaria montana* L.,; Aruv (*Arctostaphylos uva-ursi* (L.) Spreng), Asal (*Asphodelus albus* Mill.), Cavu (*Calluna vulgaris* (L.) Hull), Cila (*Cistus laurifolius* L.), Defl (*Deschampsia flexuosa* (L.) Trin.), Erar (*Erica arborea* L.), Erau (*Erica australis* L.), Gasa (*Galium saxatile* L.), Gero (*Geranium robertianum* L.), Hysp (*Hypnum* spp.), Hyra (*Hypochaeris radicata* L.), Ilaq (*Ilex aquifolium* L.), Juco (*Juncus conglomeratus* L.), Juox (*Juniperus oxycedrus* L.), Loco (*Lotus corniculatus* L.), Mepa (*Melampyrum pratense* L.), Pipi (*Pinus pinaster* Aiton), Pisy (*Pinus sylvestris* L.), Povu (*Polygala vulgaris* L.), Pomo (*Potentilla montana* Brot.), Ptaq (*Pteridium aquilinum* (L.) Kuhn), Qufa (*Quercus faginea* Lam.), Qupy (*Quercus pyrenaica* Willd.), Sami (*Sanguisorba minor* Scop.), Sima (*Simethis mattiazzii* (Vand.) Sacc.) and Vimo (*Viola montcaunica* Pau).

Thirty understory species from twenty-one families were recorded, with *Ericaceae* being the most frequent (88%) and abundant (24%) taxonomical group, with greater cover in monospecific stands of *P. pinaster* (29%) and mixed stands (26%), followed by bryophytes (*Hypnaceae*; 94% frequency and 5% cover), most abundant in monospecific stands of *P. sylvestris* (15%). *Rosaceae* was more abundant in monospecific stands of *P. sylvestris* (2.4%) and mixed stands (1.8%), and *Poaceae* in mixed stands (6.3%). A wide group of families displayed residual cover (<1%; *Aquifoliaceae*, *Asteraceae*, *Caryophyllaceae*, *Fabaceae*, *Geraniaceae*, *Juncaceae*, *Liliaceae*, *Poligalaceae*, *Rubiaceae*, *Scrophulariaceae*, *Violaceae*, and *Xanthorrhoeaceae*).

Table 23. Explanatory variables fitted as vectors onto the DCA ordination plot using the vegan 'envfit' function. Significance of each vector adjusted by 9999 permutations, and R^2 of each variable. N: density (trees ha^{-1}), G: total basal area (m^2 ha^{-1}), Ho: dominant height (m), dq: quadratic mean diameter (cm), Age: normal age (years); % G PS: the percentage of basal area of *Pinus sylvestris*, % G PP: the percentage of basal area of *P. pinaster*; and the tree regeneration density (individuals m^{-2}) of *P. sylvestris*, *P. pinaster*, *Q. pyrenaica* and *Q. faginea*.

	DCA1	DCA2	R^2	*p*	
	Stand characteristics				
% G PS	-0.544	0.839	0.484	0.019	*
% G PP	0.544	-0.839	0.484	0.019	*
N (trees ha^{-1})	-0.114	-0.993	0.309	0.087	
G (m^2 ha^{-1})	-0.751	-0.665	0.237	0.160	
Ho (m)	-0.829	0.559	0.305	0.081	
dq (cm)	-0.524	0.851	0.162	0.298	
Age (years)	-0.744	0.668	0.360	0.090	
	Tree regeneration density (ind/m^2)				
P. sylvestris	0.284	0.959	0.365	0.015	*
P. pinaster	0.977	-0.212	0.583	0.001	***
Q. pyrenaica	-0.556	-0.831	0.413	0.011	*
Q. faginea	0.985	0.171	0.602	0.004	**

<u>Tree regeneration patterns along the overstory composition gradient</u>

The adjustment of tree regeneration, i.e. density (individuals m^{-2}) of *P. sylvestris*, *P. pinaster*, *Q. pyrenaica,* and *Q. faginea* on the DCA ordination (Figure 33a) showed how tree regeneration was significantly correlated with the understory composition (r = 0.61, p = 0.015; r = 0.76, p = 0.001; r = 0.64, p = 0.011; and r = 0.78, p = 0.004, respectively), and is also related to the tree overstory composition. Indeed, *P. sylvestris* regeneration was positively correlated with the percentage of basal area of *P. sylvestris* (r = 0.48, p<0.05) and negatively correlated with the percentage of basal area of *P. pinaster* (r = -0.48, p=0.03). The *P. pinaster* regeneration was positively correlated with the percentage of basal area of *P. pinaster* (r = 0.46, p<0.05) and negatively correlated with the percentage of basal area of *P. sylvestris* (r = -0.46, p<0.05).

On the other hand, the regeneration of distinct tree species with respect to overstory composition (Figure 33b) showed four different types of responses. *Q. faginea* (HOF model I) showed monotone response and is not shown in Figure 33b; its presence was sporadic; only 12 individuals were found covering less than 1%. *P. sylvestris* showed a decreasing trend (HOF model II) as the percentage of basal area of *P. pinaster* increased. *P. pinaster* showed an increasing trend (HOF model II) as the percentage of basal area of *P. pinaster* increased. Lastly, the regeneration of *Q. pyrenaica* exhibited a symmetrical unimodal response curve (HOF Model IV), with higher density for intermediate percentages of *P. pinaster* basal area, i.e., in mixed stands. As a whole, 291 individuals of *P. sylvestris*, 215 individuals of *P. pinaster* and 129 individuals of *Q. pyrenaica* were recorded.

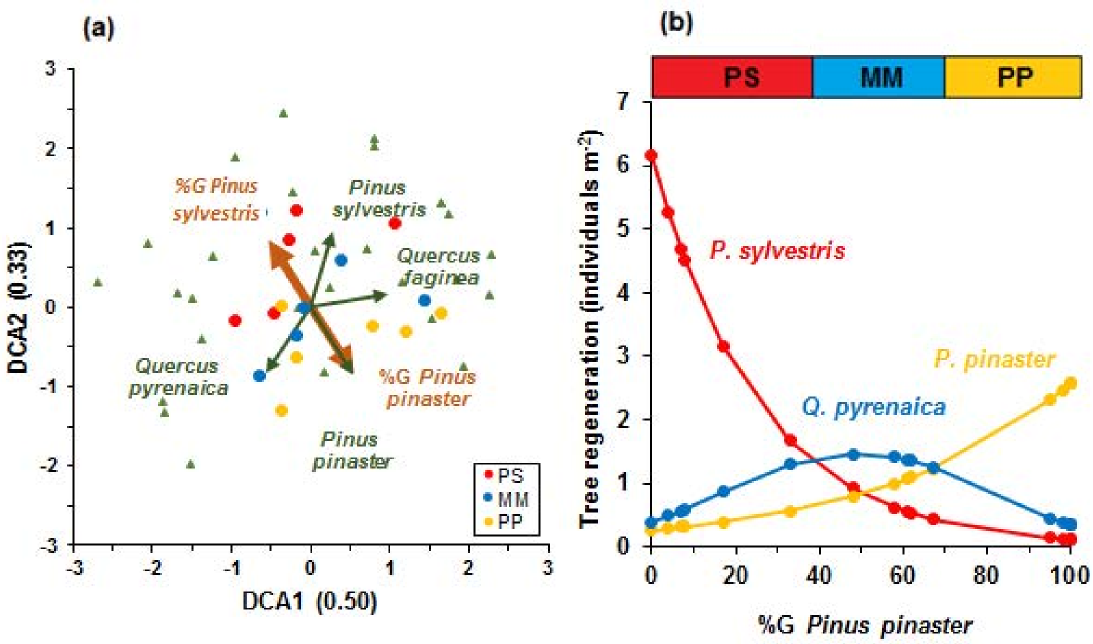

Figure 33. (a) DCA of plots and projection of the significant explanatory variables (p<0.05 and explained variation >50%),. i.e. % G of *Pinus sylvestris* and % G of *Pinus pinaster* in brow, and the tree regeneration i.e. individuals m^{-2} of *Pinus sylvestris*, *Pinus pinaster, Quercus pyrenaica* and *Quercus faginea* in green. (b) HOF-derived response curves of the regeneration of tree species relative to the main gradient (% of G of *Pinus pinaster*). Abreviations as in figure 31.

Relating the regeneration of main tree species to the species of the understory

The regeneration cover of *P. sylvestris* was positively correlated with the cover of some hemicryptophytes (*Hypochaeris radicata*, *Sanguisorba minor*) and some therophytes (*Geranium robertianum, Melampyrum pratense*), and negatively correlated with the cover of the chamaephyte *Erica australis* (see Table 24). The regeneration cover of *P. pinaster* was positively correlated with the cover of *Calluna vulgaris* (chamaephyte) and negatively correlated with the cover of bryophytes (*Hypnum* spp.). The regeneration cover of *Q. pyrenaica* was positively correlated with the cover of some hemicryptophytes (*Viola montcaunica*, *Polygala vulgaris*, *Agrostis castellana*), and some shrub species: *Erica arborea* (chamaephyte) and *Ilex aquifolium* (phanerophyte).

Table 24. Pearson's correlation coefficients between the regeneration cover (%) of main tree species, i.e. *Pinus sylvestris* (Pisy), *Pinus pinaster* (Pipi) and *Quercus pyrenaica* (Qupy), and the cover (%) of main understory species. Only significant correlations are shown (p<0.05). Species codes in Figure 32.

	Pisy	Qupy	Pipi
Agca		+0.54	
Cavu			+0.80
Erar		+0.84	
Erau	-0.46		
Gero	+0.69		
Hyra	+0.46		
Hysp			-0.48
Ilaq		+0.57	
Mepa	+0.68		
Povu		+0.55	
Sami	+0.69		
Vimo		+0.42	

Understory species patterns along the overstory composition gradient

The understory richness showed a decreasing trend bounded below the maximum attainable response where the percentage of basal area of *P. pinaster* was lower (HOF model III; Figure 34a). Responses of individual species with respect to the overstory composition separated the understory species into four groups. Group 1 (HOF model I) included 14 species that showed a monotone response and which are not shown in Figure 34; they mostly had cover ≤ 1%: *Arenaria montana* (0.09%), *Asphodelus albus* (0.24%), *Galium saxatile* (0.32%), *Geranium robertianum* (0.01%), *Hypochaeris radicata* (0.10%), *Ilex aquifolium* (0.06), *Juncus conglomeratus* (0.09%), *Lotus corniculatus* (0.03%), *Melampyrum pratense* (0.28%), *Polygala vulgaris* (0.18%), *Quercus faginea* (0.16%), *Sanguisorba minor* (0.01%), *Simethis mattiazzii* (0.12%) and *Viola montca*nica (0.28%). Group 2 (Figure 34a) contained two species, *P. sylvestris* (Pisy; HOF model II) with a decreasing trend as the *P. pinaster* basal area increased and *Hypnum* spp. (Hysp; HOF model V) with asymmetrical response curve and with the maximum skewed at the minimum *P. pinaster* basal area. Group 3 (Figure 34b) included four woody species showing HOF model II with an increasing trend as the *Pinus pinaster* basal area increased, which were *Arctostaphylos uva-ursi* (Aruv), *Pinus pinaster* (Pipi), *Calluna vulgaris* (Cavu), and *Cistus laurifolius* (Cila), and two species with skewed response curve (HOF model V) with the maximum at the maximum values of *Pinus pinaster* basal area, which were *Erica australis* (Erau) and *Deschampsia flexuosa* (Defl). Lastly, seven species in Group 4 (Figure 34c) exhibited symmetrical unimodal response curves (HOF Model IV): *Pteridium aquilinum* (Ptaq), *Erica arborea* (Erar), *Q. pyrenaica* (Qupy), *Juniperus oxycedrus* (Juox), *Aira caryophyllea* (Aica), *Agrostis castellana* (Agca) and *Potentilla montana*

(Pomo), with optima at different values of *P. pinaster* basal area, suggesting a gradual turnover of these species in response to the overstory composition.

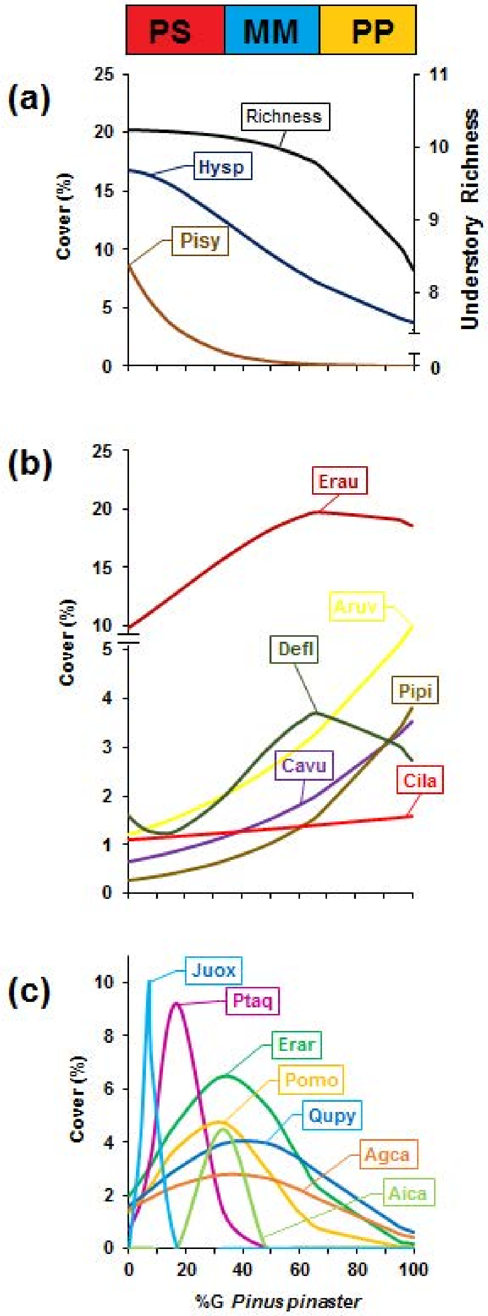

Figure 34. HOF-derived response curves of understory species (including tree regeneration) and understory richness relative to the main gradient (% of G of *Pinus pinaster*); the best HOF model according to the AIC criterion is showed. Graphs separated for clarity accordingly to different species-response groups. *Pinus sylvestris* monospecific plots (PS); *Pinus pinaster* monospecific plots (PP); Mixed plots of both *Pinus* species (MM), and species codes: Agca (*Agrostis castellana* Boiss. & Reut), Aica (*Aira caryophyllea* L.), Aruv (*Arctostaphylos uva-ursi* (L.) Spreng), Cavu (*Calluna vulgaris* (L.) Hull), Cila (*Cistus laurifolius* L.), Defl (*Deschampsia flexuosa* (L.) Trin.), Erar (*Erica arborea* L.), Erau (*Erica australis* L.), Hysp (*Hypnum* spp.), Juox (*Juniperus oxycedrus* L.), Pipi (*Pinus pinaster* Aiton), Pisy (*Pinus sylvestris* L.), Pomo (*Potentilla montana* Brot.), Ptaq (*Pteridium aquilinum* (L.) Kuhn), Qupy (*Quercus pyrenaica* Willd.)

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<u>Species optima and niche widths along the overstory composition gradient</u>

The location of the optimum of the understory species with unimodal response with respect to the overstory composition (percentage of *P. pinaster* basal area; Figure 35, and Table 26 in Appendix IIIc) showed how the two species with the greatest probability of occurrence (h>15) had their optima in monospecific stands: the bryophyte *Hypnum* spp. with optimum in monospecific stands of *P. sylvestris* (μ < 33% of *P. pinaster* basal area), and the chamaephyte *Erica australis* with optimum in monospecific stands of *P. pinaster* (μ > 67% of *P. pinaster* basal area). Both species had large niche widths (2t of 42.55 and 43.50, respectively) and also appear in mixed stands. *Juniperus oxycedrus* and *Pteridium aquilinum* with intermediate probability of occurrence (7<h<15) had narrow niche widths (2t of 3.21 and 13.95, respectively) and optima (μ < 33% of *P. pinaster* basal area) in monospecific stands of *P. sylvestris*. Lastly, six species (*Erica arborea*, *Quercus pyrenaica*, *Aira caryophyllea*, *Agrostis castellana*, *Potentilla montana* and *Deschampsia flexuosa*) with low probability of occurrence (h<7) have their optimum mostly in mixed stands (μ= 30-70% of *P. pinaster* basal area) and showed, in general, large niche widths and appear in two or three types of stands.

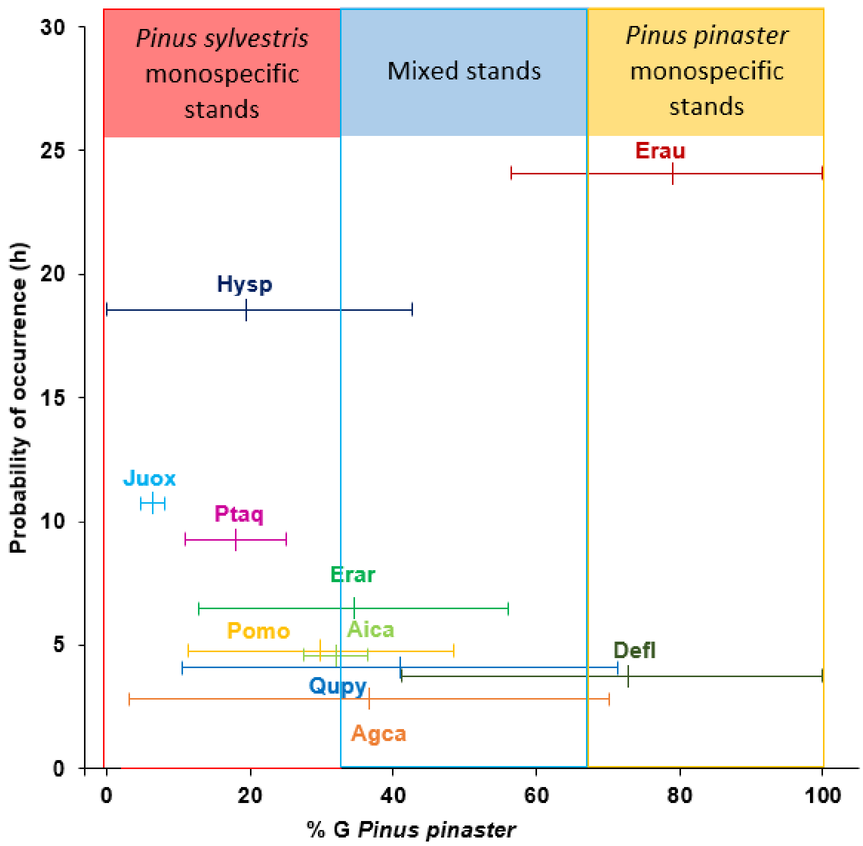

Figure 35. Location of species optima and 2t (tolerance) intervals relative to the percentage of basal area of *Pinus pinaster*, according to fitting of HOF models. Abreviations as in figure 31. Species codes: as in figure 32.

Discussion

Stand characteristics that influence the understory

Our results showed how the percentage of basal area (%G) of the two *Pinus species* (*P. sylvestris* and *P. pinaster*) is the only characteristic of the stand, among the variables tested in this study, which significantly influenced the understory composition and tree regeneration, in agreement with hypothesis 1. The other stand characteristics tested (i.e., density, total basal area, dominant height, mean quadratic diameter, age) had no detectable influence on the understory because the tree species composition was the main varying factor (see López-Marcos et al. 2018). Mestre et al. (2017) also reported that the overstory composition greatly influences the understory in southern temperate forests. The question that arises would therefore be how the tree species of the canopy exert their effect on the understory.

According to the mass ratio hypothesis (Grime 1998; Ali and Yan 2017), the dominant overstory species, *P. pinaster* and *P. sylvestris*, could exert their effect on the properties of the ecosystem, such as biodiversity, and on subordinate species, i.e., species of the understory, through traits of the dominant species, such as leaf nitrogen concentration or microhabitats provided by such traits. Indeed, in the same experimental device, we found a significant positive correlation between the percentage of basal area of *P. pinaster* and the C/N ratio of the fresh leaf litter (see López-Marcos et al. 2018). This finding suggests that the C/N ratio of the fresh leaf litter of dominant tree species, as a proxy of the leaf litter decomposition rate (Wang et al. 2016), could be one of the drivers of understory composition; the higher the C/N ratio is, the more recalcitrant the leaf litter, i.e. in monospecific stands of *P. pinaster* (Herrero et al. 2016), and in turn the lower C input into the soil as humic substances. Additionally, the tree species of the canopy can exert their effect on the understory by their influence on other soil properties such as water content. In the same experimental device, the overstory composition was related to soil water content (López-Marcos et al. 2019), indicating that *P. pinaster* tolerated lower soil water content than *P. sylvestris*, whereas mixed stands occupied areas with intermediate soil moisture. On the other hand, light availability, described as a control agent on forest regeneration (Rodríguez et al. 2007b; Ruano et al. 2015) and indirectly measured by the total basal area, seemed to have no effect on the understory species composition and tree regeneration in the studied experimental device (see Figure 32 and Table 23). In fact, the mixed stands, with higher total basal area than monospecific stands of *P. sylvestris* (see Table 25 in Appendix IIIb), maintain a similar understory richness and greater oak regeneration. Nor did leaf litter accumulation seem to have an effect on the understory composition and tree regeneration in our study (see López-Marcos et al. 2019) but leaf litter composition, as mentioned before.

Tree regeneration

According to the recruitment network approach described by Alcántara et al. (2019), a positive relationship is expected between the abundance (basal area) of canopy species and the frequency of recruit saplings, bearing in mind that the light availability (indirectly measured by the total basal area) does not seem to differ significantly between stand types in our experimental device so as to limit this assertion. Thus, higher *P. sylvestris* regeneration occurs in *P. sylvestris* monospecific stands, and higher *P. pinaster* regeneration occurs in *P. pinaster* monospecific stands, although both *Pinus* species also regenerated in mixed stands. Nevertheless, the highest *Q. pyrenaica* regeneration is found in mixed stands despite the distance to the acorn source is the same in the three stand types (Figure 36 in Apendix IIIa). Taking into account that the distance to the seed source is one of the most important processes limiting the recruitment of tree species (Caughlin et al. 2014), the larger distance from the tree source could explain the scarce and irregular regeneration of *Q. faginea* and Juniperus spp. in the study area (Figure 36 in Apendix IIIa).

The next question could be why the regeneration of *Q. pyrenaica* is greater in mixed stands than in the pure stands, in agreement with Carnevale and Montagnini (2002) who reported that mixed stands facilitate native tree regeneration. In Mediterranean ecosystems, recruitment relies to a greater extent on the capacity of seedlings to endure a combination of multiple stresses and disturbances, such as nutrient or water shortages, wildfires, or herbivore damage (Rodríguez-Calcerrada et al. 2008). Acorns depend entirely on animals for long-distance dispersion (Yu et al. 2014). Many rodent species, as well as jays, play important roles in the secondary dispersal of oak species via their hoarding behaviors (Gómez 2003; Yu et al. 2014), and it is generally believed that Quercus species can colonize the understory of pine forests via the jay- or rodent-mediated dispersion of acorns (Gómez 2003; Yu et al. 2014). Moreover, long-distance dispersal events can determine the spatial pattern of seed distribution at the landscape scale (Gómez 2003). Therefore, one of the issues that deserves more study is why dispersing animals seem to prefer mixed stands instead of pure stands to hoar acorns, if that was the case in the study area. In fact, the greater variability of habitat conditions in mixed stands than in monospecific stands has been described as a favorable condition for seed dispersers and germination and growth of native tree species (Carnevale and Montagnini 2002). It could also be that predation in monospecific stands is higher or emergence lower (Carnevale and Montagnini 2002), or simply that the higher soil fertility in mixed stands than in monospecific stands (López-Marcos et al. 2019) favors oak regeneration.

Tree regeneration and understory composition

The importance of the understory vegetation on tree regeneration has already been described, since the understory directly influences soil properties such as temperature and moisture (Rodríguez et al. 2007). Our results showed a relationship between tree regeneration and understory species composition (Figure 33a). In particular, the regeneration cover of *P. sylvestris* was positively correlated with the cover of some ruderal species, mainly hemicryptophytes (*Hypochaeris radicata*, *Sanguisorba minor*) and therophytes (*Geranium robertianum*, *Melampyrum pratense*), and negatively linked to the cover of the chamaephyte *Erica australis*, typical of poor soils (Gil-López et al. 2017) where *P. sylvestris* regenerates worst.

The regeneration cover of *P. pinaster* was positively correlated with the cover of the chamaephyte, *Calluna vulgaris*, which has been described as an accompanying species in Maritime pine forests (Herranz-Sanz et al. 2008), but was negatively linked to *Hypnum* spp., mosses with higher moisture requirements than vascular plant species present in *P. pinaster* stands.

The *Q. pyrenaica* regeneration cover was positively correlated with the cover of *Erica arborea*, *Viola montcaunica*, *Polygala vulgaris*, *Agrostis castellana* and *Ilex aquifolium*. All these species have already been described as typical of the Pyrenean oak native forests of the Iberian Peninsula (Velasco-Aguirre 2014), thus, they share with *Q. pyrenaica* the same regeneration niche (see Figure 35). Mixed stands may favor the presence of this group of species by providing greater soil fertility for intermediate water-stress conditions. This group of accompanying species for native oak could be responsible for the maintenance of the understory richness in mixed stands at the same level as in *P. sylvestris* monospecific stands, but under higher water-stress conditions (see López-Marcos et al. 2019).

Understory composition change along the overstory composition gradient

Our results showed a change in the composition of the understory in relation to the overstory composition. The absence of exclusive species in mixed stands could mean that they represent the transition area where *P. sylvestris* and *P. pinaster* coexist (meet and integrate), as previously mentioned for mixed forest of evergreen and deciduous species (Mestre et al. 2017).

As commented above, the overstory composition in the study area was related to soil water content (López-Marcos et al. 2019) and the C/N ratio of the leaf litter (López-Marcos et al. 2018). Consequently, species such as *Pteridium aquilinum*, *Pinus sylvestris,* or *Juniperus* spp., characteristic of humid and temperate zones (Rivas-Martínez et al. 2002), showed most of their niche amplitude in *P. sylvestris* monospecific stands, where soil water retention capacity is higher and the C/N ratio of the leaf litter is lower (López-Marcos et al. 2018, 2019). On the opposite end of the gradient, species such as *Erica australis*, *Arctostaphylos uva-ursi*, *Pinus pinaster*, *Calluna vulgaris,* and *Cistus laurifolius*, characteristic of sandy well-drained Mediterranean areas (Herranz-Sanz et al. 2008), reached their maximum cover in *P. pinaster* monospecific stands, where soil water retention capacity is lower and the C/N ratio of the leaf litter is higher (López-Marcos et al. 2018, 2019). In the middle part of this gradient, that is in the mixed stands, where the tree-regeneration cover of native species such as *Q. pyrenaica* achieved their maximum values, the optima of other species such as *Erica arborea*, *Aira caryophyllea*, *Potentilla montana* or *Agrostis castellana* were found for intermediate values of soil water retention capacity and leaf-litter C/N ratio (López-Marcos et al. 2018, 2019). The niche amplitude of these species matches the niche amplitude of the *Quercus pyrenaica* regeneration, encouraging the idea that mixed pine stands allow the presence of a group of species typical of Pyrenean oak native forests in the Iberian Peninsula (Velasco-Aguirre 2014), which are responsible for maintaining understory richness in mixed stands at the same level as in *P. sylvestris* monospecific stands but under higher water-stress conditions (López-Marcos et al. 2019).

<u>Implications for forest management</u>

It is worth noting here that our results have important implications for forest management in the context of the supply of multiple ecosystem services (Gamfeldt et al. 2013), like biodiversity conservation. Firstly, the mixture of Scots pine and Maritime pine, widely distributed in Spain (Serrada et al. 2008), should continue to be favored over pure stands in the study area because it favors the regeneration of a larger variety of tree species, including the endemic of western Europe *Q. pyrenaica* (Velasco-Aguirre 2014). This could, therefore, be regarded as an adaptive management strategy for climate change (Temperli et al. 2012) and to promote forest conservation. In fact, *Pinus* species are suggested as being pioneer species during succession that are usually replaced by late-successional *Quercus* species (Yu et al. 2014). Nevertheless, the maintenance of monospecific pine stands at the landscape scale should also be recommended since species such as *Juniperus oxycedrus* and *Pteridium aquilinum* (restricted to Scots pine monospecific stands) or *Calluna vulgaris* and *Arctostaphylos uva-ursi* (far more abundant in Maritime pine monospecific stands) deserve to be preserved (see species protection status in (López-Marcos et al. 2019). Secondly, the maintenance of high understory richness in mixed stands under higher water-stress conditions could be possible by means of the regeneration of *Q. pyrenaica*. A greater variety of understory species associated with the *Quercus pyrenaica* regeneration and sharing niche amplitude was found. This could be considered as a biodiversity conservation strategy in the current climate change scenario (Felton et al. 2010). Finally, since productivity is often higher in mixtures than in monocultures and can increase by increasing tree-species richness (Brockerhoff et al. 2017), the encouraging of native tree regeneration in forest management plans is needed, not only in forest management plans whose objective is to include forest biodiversity as an ecosystem service but also when production is the main objective. Understanding the ecology of the understory vegetation has important implications for both biodiversity conservation and production-oriented forest management (Nilsson and Wardle 2005).

Conclusion

The composition of the understory and tree regeneration are influenced by the overstory composition but, according to previous studies, also by the soil conditions (soil water and fertility) that vary with the overstory composition. Species characteristic of humid and temperate zones, including *P. sylvestris* regeneration, dominate in *P. sylvestris* monospecific stands, and typical species of well-drained Mediterranean areas, including *P. pinaster* regeneration, dominates in *P. pinaster* monospecific stands. In mixed stands, where fertility is higher, the regeneration of the western European endemic species, *Q. pyrenaica*, is added to the regeneration of *Pinus* species. Also a positive effect of the studied mixture is observed on understory richness, similar to that of *P. sylvestris* monospecific stands but under lower soil water content. Understory species typical of the native Pyrenean oak forests in the Iberian Peninsula, which share with *Q. pyrenaica* the same regeneration niche, contribute to maintain high understory richness in such mixed pine forests. These results should make us reflect on the use of mixed stands (even when tree species are of the same genus) as a strategy for biodiversity conservation, through native tree regeneration and their accompanying understory species conservation.

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Contributions of the co-authors

Conceptualization: DLM, CMR, MBT, FB. Methodology, Software: DLM, CMR; Validation: DLM, CMR. Formal analysis: DLM, CMR. Investigation: DLM, CMR, MBT, FB. Resources: CMR, MBT, FB. Data curation: DLM, CMR, MBT, FB. Writing: original draft: DLM, CMR, MBT, FB. Writing: review and editing: DLM, CMR, MBT, FB. Visualization: DLM, CMR, MBT, FB. Supervision: CMR, MBT, FB. Project administration: FB, funding acquisition: CMR, MBT, FB.

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Data availability

The data that support the findings of this study are available from Daphne LópezMarcos but restrictions apply to the availability of these data, which were used under license for the current study, and so are not publicly available. Data are however available from the authors upon reasonable request and with permission of Felipe Bravo.

Compliance with ethical standards

The authors declare that they have no conflict of interest

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Appendix IIIa

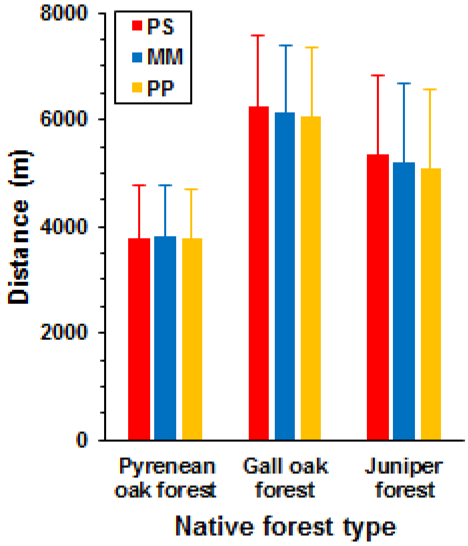

Figure 36. Distance from the center of the plots of different overstory composition (PS, MM, PP) to the nearest native forest of Pyrenean oak (*Quercus pyrenaica* Will.), Gall oak (*Quercus faginea* Lam.), or Juniper (*Juniperus* spp.), according to the cartographic server (WMS) of the Ministry for the Ecological Transition of the Government of Spain (http://wms.mapama.es/sig/Biodiversidad/).

Appendix IIIb

Table 25. Descriptive statistics (Minimum (Min) ,Maximum (Max), and mean ± standard error (Mean±SE)) of stand characteristics (N: density (trees ha^{-1}), G: basal area (m^2ha^{-1}), Ho: dominant height (m), dq: quadratic mean diameter (cm), and Age: normal age (years)) of three types of stands.

		Scots pine monospecific stands					Mixed stands					Maritime pine monospecific stands				
		Min	Max	Mean	±	SE	Min	Max	Mean	±	SE	Min	Max	Mean	±	SE
N (trees ha^{-1})	Total	509.3	821.0	684.0	±	48.9	523.0	1330.0	745.0	±	120.9	538.0	1429.0	775.9	±	137.1
	Scots	495.1	806.0	660.2	±	48.0	241.0	764.0	429.2	±	75.1	0.0	283.0	59.0	±	45.7
	Maritime	0.0	56.6	23.5	±	8.7	198.0	566.0	316.0	±	56.3	509.0	1146.0	716.9	±	96.6
G (m^2 ha^{-1})	Total	33.3	54.9	480.	±	3.2	33.3	68.2	55.3	±	4.9	37.5	70.3	62.2	±	5.2
	Scots	30.8	54.9	44.9	±	3.4	13.0	45.9	25.7	±	4.8	0.0	3.3	0.8	±	0.5
	Maritime	0.0	8.2	3.2	±	1.1	20.2	38.9	29.5	±	2.9	37.5	70.3	61.4	±	5.1
Dq (cm)	Total	22.5	34.4	29.2	±	1.7	20.2	39.4	30.0	±	2.8	22.6	39.6	32.3	±	2.5
	Scots	22.2	32.4	28.5	±	1.6	16.6	40.3	27.2	±	3.5	0.0	15.8	5.8	±	2.8
	Maritime	0.0	56.7	36.6	±	8.2	25.0	43.5	35.4	±	2.8	26.0	39.6	33.3	±	2.2
Ho (m)	Total	16.8	22.1	19.3	±	0.9	13.1	24.6	18.0	±	1.7	12.4	20.5	16.9	±	1.2
	Scots	16.6	22.1	19.2	±	0.9	12.3	24.3	17.1	±	1.8	0.0	10.8	4.2	±	1.9
	Maritime	0.0	24.5	17.1	±	3.6	14.2	25.0	19.2	±	1.7	13.6	20.5	17.3	±	1.0
Age (years)	Scots	44	151	99.8	±	14.9	44	118	94.3	±	11.7	0	0	0	±	0
	Maritime	0	0	0	±	0	49	118	91.2	±	10.2	49	118	90.8	±	10.9

Appendix IIIc

Table 26. Location of optimum (μ), predicted maximum probability of occurrence (h) and niche amplitude based on 2t tolerances, for species with unimodal response along the main coecocline (%G of *Pinus pinaster*), as well as the frequency of species appearance in the plots (%).

Specie	Model	h	μ	2t	%
Agrostis castellana Boiss. and Reut	IV	2.83	36.68	66.94	70.59
Aira caryophyllea L.	IV	4.61	31.97	9.03	41.18
Deschampsia flexuosa (L.) Trin.	V	3.76	72.89	58.75	41.18
Erica arborea L.	IV	6.48	34.46	43.25	23.53
Erica australis L.	V	24.10	78.97	43.50	82.35
Hypnum spp.	V	18.58	19.47	42.55	94.12
Juniperus oxycedrus L.	IV	10.74	6.37	3.21	11.76
Potentilla montana Brot.	IV	4.79	29.86	36.93	52.94
Pteridium aquilinum (L.) Kuhn	IV	9.28	18.02	13.95	29.41
Quercus pyrenaica Willd.	IV	4.08	40.93	60.88	29.41

Chapter IV

Sobrerendimiento a pequeña escala espacial en pinares mixtos como resultado de la complementariedad del nicho edáfico: implicaciones para la conservación de la riqueza del sotobosque

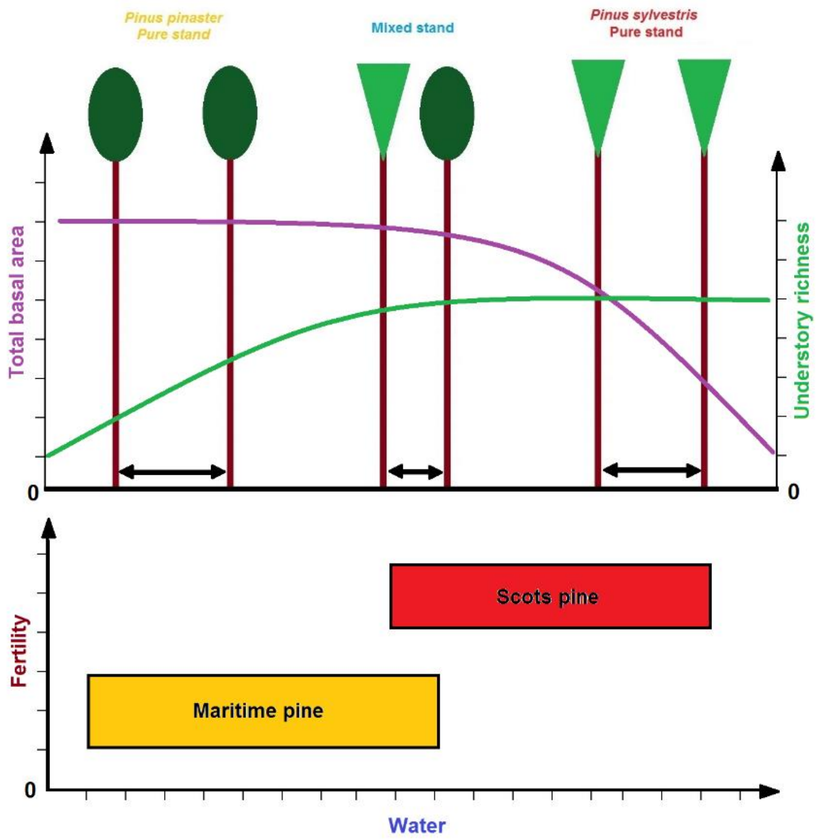

Figure 37. Graphical abstract of the article that gives rise to chapter IV of the thesis.

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Overyielding at a small scale in mixed pine forest as result of belowground resources complementarity: implications for understory richness conservation

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Abstract

Many studies highlight the biodiversity-productivity relationships in mixed forests in the context of ecosystem services supply. Most reports of the positive effects of tree mixture on productivity focus on mixtures combining species with contrasting traits, but little is known about the mixture effect on productivity at different spatial scales when two *Pinus* species are mixed, and less of its impact on the understory. Thus, based on research with six triplets in North-Central Spain, we assessed the effect of mixed vs monospecific stands of *Pinus sylvestris* and *P. pinaster* on productivity at two spatial scales and its relation with the understory richness and soil moisture and fertility. A small-scale overyielding was found in mixed stands, related to soil water and fertility niche complementarity, which has no negative effect on the understory richness. The fundamental role of scale in determining the relationship between species richness and ecosystem functioning in forests is emphasized.

Keywords: overstory overyielding, understory richness, soil niche complementarity, small spatial scale, mixed forest, Scots pine, Maritime pine.

Introduction

The impact of biodiversity loss on the functioning of ecosystems has become a central issue in ecology (Loreau and Hector 2001). Accordingly, mixed forests are receiving more and more attention since they can provide multiple ecosystem services more efficiently than monospecific forests (Knoke et al. 2008; Jactel et al. 2009; Del Río et al. 2015). Many studies that examined the significance of biodiversity for ecosystem functioning in mixed forests focus on biomass productivity (Balvanera et al. 2006; Cardinale et al. 2007; Pretzsch et al. 2012; Liang et al. 2016), analyzing the biodiversity–productivity relationship (BPR) in tree communities (Liang et al. 2016; Fichtner et al. 2018).

Biodiversity is thought to promote productivity via complex mechanisms that involve organism–organism and organism-environment interactions (Van de Peer et al. 2018). The niche complementarity theory (Tilman et al. 1997b; Luo et al. 2019) is thus the most cited to explain how species richness contributes to the increase in forest productivity (Madrigal-González et al. 2016; Luo et al. 2019). It is pointed to niche complementarity as the best potential explanation for species packing, and a chief mechanism by which the productivity of species mixtures is enhanced compared to the respective monocultures (Hooper and Dukes 2004), i.e. overyielding (Madrigal-González et al. 2016). By means of niche complementarity, the competing species change their pattern of resources use (Hector and Hooper 2002) what reduces competition and promotes co-existence between species (Chesson 2000). Species must be in the same trophic level and their resource requirements must overlap (Chesson 2000). Although this mechanism has been more widely described in short-lived communities (i.e. grasslands, arthropod communities and microbial microcosms; Madrigal-González et al. 2016), it has been also described recently in forests, both in the exploitation of above- (Forrester and Albrecht 2014) and below-ground resources (Brassard et al. 2013).

Forest management is commonly applied in small units called 'stands' (Bravo-Oviedo et al. 2014), defined by homogeneity in age, structure, composition and site conditions, and with sufficient area to permit independent treatments (Assmann 1970; Smith et al. 1997; Bravo-Oviedo et al. 2014). Nevertheless, this definition is not clear in the case of mixed forests since the spatial variability and pattern of tree mixture change with the spatial scale (Bravo-Oviedo et al. 2014). In fact, multiple studies in forests have analyzed the BPR at the scale of tree communities (Grossman et al. 2017; Van de Peer et al. 2018), although positive BPR was only demonstrated at smaller scale (Fichtner et al. 2018; Van de Peer et al. 2018). Since there is increasing recognition of the fundamental role of space in population, community and ecosystem processes (Ettema and Wardle 2002), the yield comparison between scales in mixed forests is welcome.

Mixed forests are the sum of co-occurring individuals of different species (Fichtner et al. 2018). As such, they can be considered as a network of locally interacting individuals (Michalet et al. 2015; Fichtner et al. 2018). Consequently, the mixture response should be the result of aggregated small-scale variations in neighborhood interactions (Fichtner et al. 2018; Van de Peer et al. 2018). Such small-scale interactions can be positive (e.g. niche complementarity) or negative (e.g. competition for resources) (Fichtner et al. 2018). Therefore, the niche complementarity-yield relationship at small-scale in mixed forests could help to better understand this process.

On the other hand, the understory is known to be strongly influenced by the composition and structure of the overstory through its influence on temperature, light, water, soil nutrients and litter accumulation (Saetre et al. 1999; Felton et al. 2010; Rodríguez-Calcerrada et al. 2011). Hence, the change in the overstory yield is expected to influence the understory. However, managers and ecologists have traditionally paid less attention to the understory component of forests (Nilsson and Wardle 2005; Antos 2009) less when the overstory yield is explored. Given that the understory participates in a great variety of aboveground processes (e.g., tree seedling regeneration, forest succession, species diversity and stand productivity) and also in belowground processes, such as litter decomposition, soil nutrient cycling and soil water conservation (Liu et al. 2017), the assessment of the repercussion of the mixed forest over-yielding on the understory is necessary.

In recent years, numerous experiments have explored the BPR in forests, from a global scale (Liang et al. 2016; Jactel et al. 2018) to a small-scale (Nguyen et al. 2012; Fichtner et al. 2018), and in mixed forest (Forrester et al. 2004, 2005, 2006) but also comparing monospecific vs mixed forests (Pretzsch et al. 2012; Thurm and Pretzsch 2016a; Riofrío et al. 2017b). Nevertheless, the BPR in monospecific vs mixed forests that combine coniferous tree species of the same genus remain virtually unknown (but see Riofrío et al. 2017a). This is so despite these mixtures being frequent in many environments, such as the admixtures of Scots pine (*Pinus sylvestris* L.) and Maritime pine (*Pinus pinaster* Aiton) in Spain, growing in pure and mixed stands either naturally or as a result of species selection for afforestation (Serrada et al. 2008). Both *Pinus* species show similar crown architecture and slight differences in shade tolerance (Riofrío et al. 2017b), but differ in water-stress tolerance (López-Marcos et al. 2019).

In this study, we assess differences in total basal area and density of the overstory at different spatial scales (at the stand level and at a smaller scale), and the distances between trees in mixed vs. monospecific stands of Scots pine and Maritime pine. We also analysed the role of some major mechanisms involved, such as soil water and fertility niche complementarity, and the overstory yield influence on the understory richness. The aims of this study were: (1) to test the spatial scale effect on the overstory yield; (2) to understand the mechanisms involved in determining the overstory yield differences by scale; and (3) to analyse the overstory yield effect on the understory richness in mixed vs. monospecific pine forests. We hypothesize that there is an overstory overyielding in mixed stand, only detected at small spatial scale, caused by soil niche complementarity.

Material and methods

Study sites

The research was carried out in eighteen forest plots (6 triplets) located in the Northern Iberian Range, in North-Central Spain (41°47'35''N and 41°53'41''N latitude, and 2°56'12''W and 3°20'46''W longitude; Figure 38). The climate is Temperate with dry or temperate summer (Cfb, Csb) according to the Köppen (1936) classification for the Iberian Peninsula. The mean annual temperature ranges from 8.7 to 9.8 °C and the annual precipitation ranges from 684 to 833 mm (Nafría-García et al. 2013). Altitude varies from 1093 m to 1277 m a.s.l., and the slope from 0.9 to 20% (López-Marcos et al. 2018, 2019). The geological parent materials are sandstones and marl from the Mesozoic era (IGME 2015). The soils are Inceptisols with a xeric soil moisture regime and mesic soil temperature regime and they are classified as Typic Dystroxerept or Typic Humixerept (sensu Soil-Survey-Staff 2014). The sandy soil texture was dominant and the pH varies from extremely acid to strongly acid (see López-Marcos et al. 2018). Nearby climax vegetation, highly degraded by anthropogenic action, is characterized by Pyrenean oak (*Quercus pyrenaica* Willd.) forests or communities dominated by junipers (López-Marcos et al. 2018).

Each triplet consisted of three circular plots of 15 m radius, including two plots dominated either by *P. sylvestris* (PS) or *P. pinaster* (PP) and one mixed plot that contained both species (MM), located less than 1 km from each other so that the environmental conditions were homogeneous within the triplet (Figure 38), although they could differ among distinct triplets (e.g. soil properties; see López-Marcos et al. 2018). In particular, a water-stress gradient associated with the overstory composition indicated that *P. pinaster* tolerated lower soil water content than *P. sylvestris* whereas mixed stands occupied areas with intermediate soil moisture. In addition, a soil fertility gradient defined by organic carbon and exchangeable magnesium stocks was identified, both being higher in mixed stands (López-Marcos et al. 2019).

The percentage of the basal area of the dominant species in the monospecific plots was greater than 83% or 95% for *P. sylvestris* or *P. pinaster* respectively, whereas the basal area percentage of both species in the mixed plots ranged from 33 to 67%. The sampling design in triplets was well balanced for stand composition (six repetitions per stand type) but not necessarily balanced for other stand characteristics (i.e. density, total basal area, dominant height, mean quadratic diameter, age) that were intended to be similar within the triplet (avoiding biases in the sampling design) but differed between triplets. However, a previous study showed how the percentage of the basal area of both *Pinus* species was the only characteristic of the stand that significantly influenced the understory composition and tree regeneration (López-Marcos et al. 2020a). Other characteristics of the stand structure such as density, total basal area, dominant height, mean quadratic diameter or age did not have a significant influence on the understory because the tree species composition was the main varying factor (López-Marcos et al. 2020a).

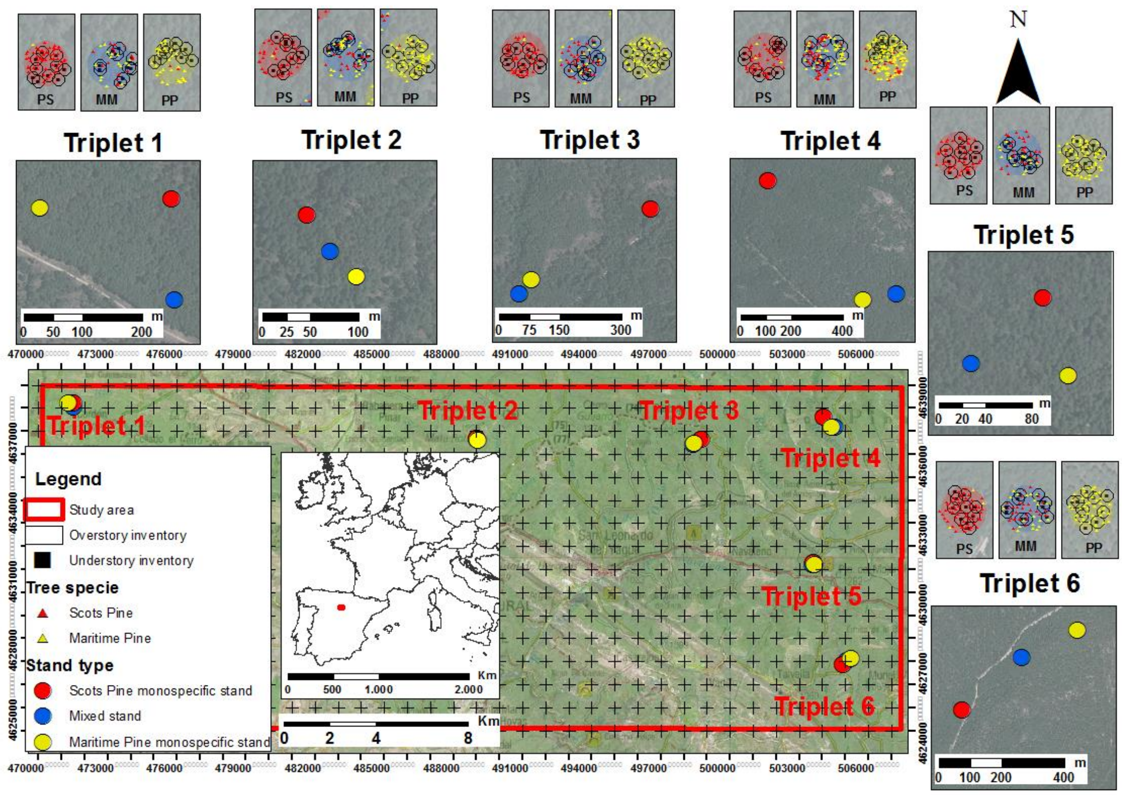

Figure 38. Location of the triplets in the 'Sierra de la Demanda' in North-Central Spain, the plots within each triplet (red circles: *Pinus sylvestris* monospecific plots, PS; yellow circles: *Pinus pinaster* monospecific plots, PP; blue circles: mixed plots of both *Pinus* species, MM), the understory inventories (small black squares), the overstory inventories at a smaller scale (black circumferences) and trees (*P. sylvestris*: small red triangles; *P. pinaster*: small yellow triangles) within each plot.

Traditionally, forest management consists of strip clear-cutting with soil movement and planting or sowing when necessary, and moderate thinning from below (Riofrío et al. 2019) benefiting *P. sylvestris* (López-Marcos et al. 2019c). The stands have had no silvicultural intervention or damage in the last ten years in an attempt to minimize the effect of the thinning or another type of intervention in what is intended to study, either growth, floristic richness or soil nutrients. Triplets belong to the network of permanent plots of the Sustainable Forest

Management Research Institute UVa-INIA (iuFOR) and they have been previously used in a series of recent studies (Riofrío et al. 2017a, b, 2019; Cattaneo 2018; López-Marcos et al. 2018, 2019, 2020a).

Understory sampling

Within each plot, 10 inventories (1m×1m) were randomly located and the cover (%) of every understory vascular plant species, including tree regeneration, was estimated visually by the same observer in June 2016 (López-Marcos et al. 2019) to encompass and better identify the maximum number of vascular plant species (Alday et al. 2010).

Vascular plant species were classified according to the Raunkiær's life-forms (1934) following Aizpiru et al. (2007); see López-Marcos et al. (2019). Therophytes are annuals plants whose shoot and root systems die after seed production and which complete their whole life cycle within one year; hemicryptophytes are perennial herbaceous plants with periodic shoot reduction to a remnant shoot system that lies relatively flat on the ground surface; geophytes have subterranean resting buds (i.e. bulbs, rhizomes…); chamaephytes (dwarf shrubs) are woody plants whose natural branch or shoot system remains perennially between 25-50 cm above ground surface; and phanerophytes (tree regeneration and shrubs) are woody plants that grow taller than 25-50 cm.

Tree regeneration included the main tree species found in seedling/sapling stages (i.e. *P. sylvestris*, *P. pinaster*, *Q. pyrenaica*, and *Q. faginea* Lam.). In these stands, there are no subordinate tree species. Only two layers of vegetation can be distinguished (overstory and understory): the overstory measuring c.a. 20 m in height, and the understory being only c.a. 20 cm in height, and never higher than 1 m (López-Marcos et al. 2019c).

Soil sampling and laboratory analyses

At the same time as the vegetation sampling, one soil pit of at least 50 cm depth was dug in each plot for soil profile characterization (López-Marcos et al. 2018). Two undisturbed soil samples were collected from each pit's soil horizon with steel cylinders (98.2 cm^3) to keep their original structure. Likewise, one disturbed sample was also taken from each pit's soil horizon (ca. 2.5 kg).

Both undisturbed and disturbed soil samples were dried at 105°C for 24 h before analyses. Undisturbed soil samples were weighed (±0.001 g) and used to calculate the soil bulk density. Disturbed soil samples were sieved (2 mm) before physical and chemical analyses. Physical analyses included percentage by weight of coarse fraction (>2 mm; %stones) and earth fraction (<2 mm; %EF). Available water was determined by the MAPA (1994) method as the difference between water content at field capacity (water remaining in a soil after it has been thoroughly saturated for two days and allowed to drain freely) and the permanent wilting point (soil water content retained at 1500 kPa using Eijkelkamp pF Equipment). Chemical analyses included exchangeable cations (Ca^{+2}, Mg^{+2}, K^{+}, Na^{+}) that were extracted with 1N ammonium acetate at pH=7 (Schollenberger and Simon 1945) and determined using an atomic absorption/emission spectrometer.

Overstory sampling

The number and diameter of all stems > 7.5 cm in diameter for every *Pinus* species in each plot were computed at two spatial scales: 1) at the stand level, i.e. within each circular plot of 15 m radius; and 2) at a smaller scale, i.e. within each circular 4 m radius subplot centered in each quadrat of understory sampling according to Rodríguez-Calcerrada et al. (2011).

In order to assess the 'randomness' of the spatial distribution pattern of trees (Byth and Ripley 1980), both without differentiating species (*P. sylvestris* + *P. pinaster*) and for each species separately (*P. sylvestris* or *P. pinaster*), two different distances were measured within each plot following Hopkins (1954): 1) the distance from a random point (the quadrat for understory sampling) to the nearest tree (piD), and 2) the distance from that tree to its nearest neighbor (iiD).

Data analyses

In each horizon, the water holding capacity (WHC) and the stock of the sum of bases (SBstock) were calculated as indicated in Appendix IV; the sum of bases (SB) was the sum of the Ca^{+2}, Mg^{+2}, K^{+} and Na^{+} concentrations ($cmol^{+}\ kg^{-1}$). WHC and SBstock in the soil profile (0-50 cm) were then calculated as the sum of the values of each horizon (see Appendix IV).

Richness was calculated as total cumulative number of plant species in the 10 quadrats per plot (Colwell 2009), including understory vegetation and tree regeneration (see López-Marcos et al. 2019). The cover (%) of each Raunkiær's life-form in each plot was calculated as the average of the 10 vegetation sampling quadrats per plot (see López-Marcos et al. 2019).

Tree density (N), total basal area (GT), and the basal area of each *Pinus* species (GPS: *P. sylvestris* basal area; GPP: *P. pinaster* basal area) were calculated at both spatial scales; GT, GPS and GPP as indicated in Appendix IV. At the smaller scale, the average of the ten circular 4 m radius subplots was made within each plot. The percentage of *P. pinaster* basal area was calculated as the ratio between the basal area of *P. pinaster* and the total basal area of each plot.

Differences among stands in GT and N, at two spatial scales, were analysed using linear mixed models (LMM; Pinheiro and Bates 2000) with the restricted maximum likelihood method (REML; Richards 2005). The Hopkins' coefficient of aggregation (1954) was calculated for determining the spatial distribution pattern of trees in each stand type. This test is based on the assumption that a population is randomly distributed whether the distance from a random point (the center of the quadrat for understory sampling) to the nearest tree (piD) is identical to the distance from that tree to its nearest neighbor (iiD). A t-Student test was used to check this assumption ($p<0.05$). Also differences among stands in piD and iiD were analysed using LMM with REML, both without differentiating species (*P. sylvestris* + *P. pinaster*) and for each species separately (*P. sylvestris* or *P. pinaster*).

Structural Equation Models (SEMs) were used to explore to what extent the water (WHC) and fertility (SBstock) in the soil were related to the overyilding in GT (through its components i.e., GPS and GPP) and the understory richness mediated by hemicryptophytes. The SEM approach is based on a general linear model and enables the simultaneous assessment of multiple relationships (direct and indirect) between variables (Grace 2006). These relationships between variables can be represented in a "path" diagram where the variables are connected by arrows representing the theoretical structural model for the system under consideration (Rosseel 2012). SEMs model simplification method was based on Akaike Information Criterion (AIC) deleting all the non-significant model's path coefficients (Alday et al. 2016). The goodness of fit of each model was evaluated with the chi-square statistic, the root mean square error of approximation (RMSEA), and the goodness-of-fit index (GFI). Chi-square values higher than 0.05, RMSEA below 0.08, and a GFI above 0.90 indicate an acceptable fit for the model (Grace 2006; Alday et al. 2016). For clarity, only the standardized path coefficients are reported in the figure.

Finally, the response pattern of both *Pinus* species along the significant soil properties (i.e. WHC and SBstock), as well as of the understory richness (S) along the percentage of *P. pinaster* basal area were modeled by Huisman-Olff-Fresco (HOF) models (Huisman et al. 1993). These are a hierarchical set of five response models, ranked by their increasing complexity (Model I, monotone trend, i.e. with constant abundance; Model II, increasing or decreasing trend where the maximum is equal to the upper bound; Model III, increasing or decreasing trend where the maximum is below the upper bound; Model IV, symmetrical response curve; Model V, skewed response curve. The Akaike Information Criterion (AIC; Akaike 1973) was used to select the most appropriate response model (Johnson and Omland 2004); smaller values of AIC indicate better models. Finally, the location of species optima (μ) and niche widths (2t) for those species with unimodal responses were derived from the HOF models (Lawesson and Oksanen 2002). The 2t values were found by solving for the gradient points of the fitted HOF model relative to a strict Gaussian model at 2t (Lawesson and Oksanen 2002). In the case of a symmetric unimodal response, the lower and upper t values are identical, while with a skewed model, the 2t intervals are not necessarily equal.

All statistical analyses were implemented in the R software environment (version 3.3.3; R Development Core Team 2016) using the nlme package for Linear Mixed Models (LMM, version 3.1-137; Pinheiro et al. 2018), the eHOF package for HOF modeling (version 3.2.2; Jansen and Oksanen 2013) and the lavaan package for Structural Equation Models (SEMs, Rosseel 2012).

Results

Overstory density and basal area at two spatial scales

No differences in total density among stands (PS, MM and PP) were found at neither of both spatial scales (Figure 39a,b). Nevertheless, at the stand level (Figure 39a) density seamed to increase from PS (683.99±48.91 ind. ha^{-1}) to PP (775.93±137.12 ind. ha^{-1}), whereas at the smaller scale (Figure 39b) density seamed to be higher in MM (868.72±128.49 ind. ha^{-1}) with respect to the monospecific stands (PS: 566.99±96.48 ind. ha^{-1}; PP: 727.46±107.41 ind. ha^{-1}).

In contrast, significant differences in the total basal area were found among stands at both spatial scales (Figure 39c,d). At the stand level (Figure 39c), the total basal area increased from PS (48.04±3.19 m^2 ha^{-1}) to PP (62.19±5.19 m^2 ha^{-1}), being intermediate in MM (55.24±4.94 m^2 ha^{-1}). At a smaller spatial scale (Figure 39d), the total basal area increased from PS (39.15±4.93 m^2 ha^{-1}) to MM (66.21±8.00 m^2 ha^{-1}) and no differences between MM and PP (63.31±6.79 m^2 ha^{-1}) were found.

Tree spatial distribution pattern

The spatial distribution of trees regardless of species was random in the three stand types (Table 27). However, the spatial distribution of *P. sylvestris* and *P. pinaster* considered separately changed from random in monospecific stands to regular in mixed stands (Table 27).

Without differentiating *Pinus* species, the distance from a random point to the nearest tree (piD) and the distance from that tree to the nearest neighbor (iiD) were lower in mixed stands than in monospecific stands, although, only the first was significantly different (Figure 40a,c). However, for each species separately (*P. sylvestris* or *P. pinaster*), piD was lower in mixed stands than in monospecific stands but iiD was higher in MM than in monospecific stands (Figure 40b,d).

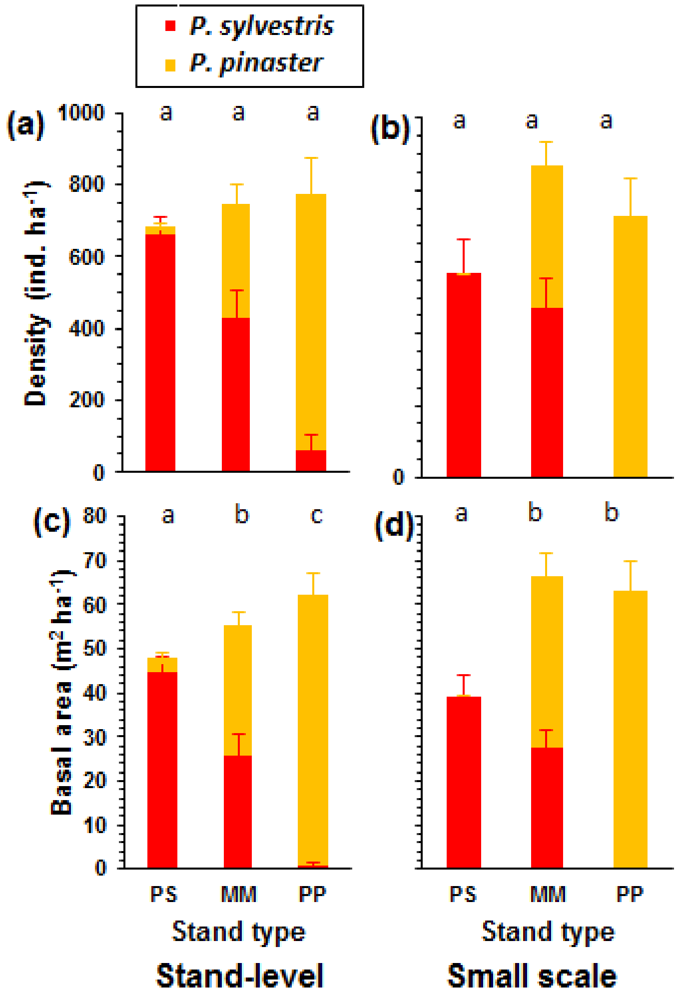

Figure 39. (a) Density (ind. ha^{-1}; mean+SE), and (c) basal area (m^2 ha^{-1}; mean+SE) at stand level (i.e. within the circular plots of 15 m radius); and (b) density, and (d) basal area at a smaller scale (i.e. within the circular subplots of 4 m radius). PS: *P. sylvestris* monospecific stands (n=6), MM: mixed stands (n=6), and PP: *P. pinaster* monospecific stands (n=6). Diferent letters indicate differences among stand types ($p<0.05$) in total density and basal area.

Table 27. Spatial distribution of trees regardeless of species (all tress: *P. sylvestris* + *P. pinaster*), and for each *Pinus* species separately, in each type of stand, calculed by Hopkins' coefficient of aggregation (1954) with $p< 0.05$; piD: distance from a random point (the center of the quadrat for understory sampling) to the nearest tree, and iiD: distance from that tree to its nearest neighbor.

	P. sylvestris monospecific stand	Mixed stand	P. pinaster monospecific stand
All trees	Random (piD = iiD)	Random (piD = iiD)	Random (piD= iiD)
Pinus sylvestris	Random (piD = iiD)	Regular (piD < iiD)	-
Pinus pinaster	-	Regular (piD < iiD)	Random (piD = iiD)

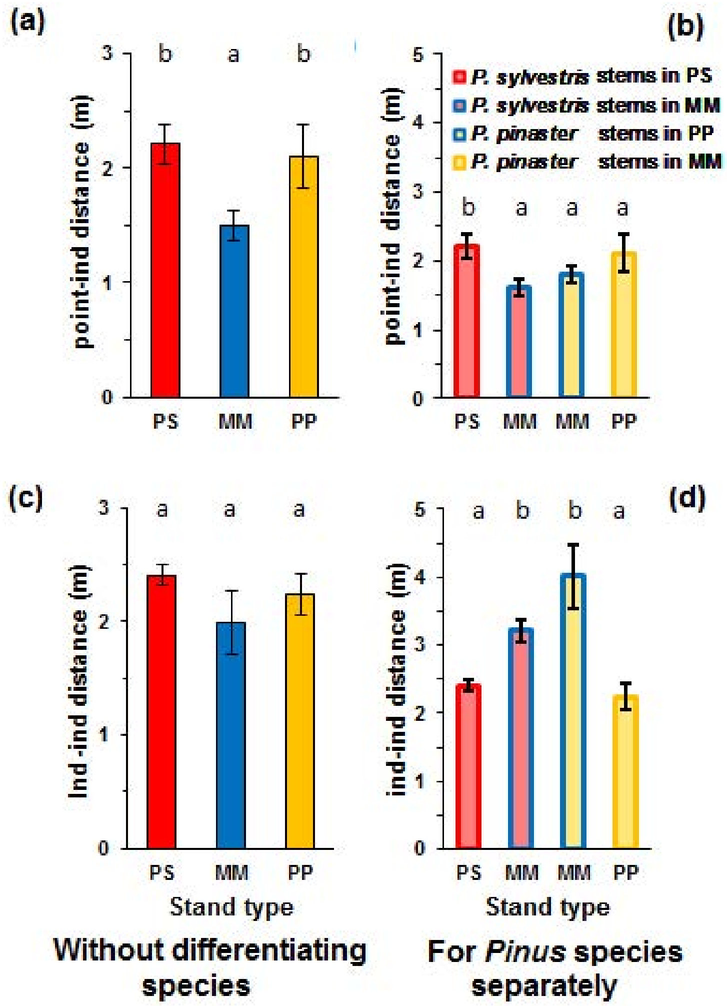

Figure 40. Comparing stands for each distance (piD: the distance from a random point to the nearest tree; iiD: the distance from that tree to its nearest neighbor), both without differentiating species (*P. sylvestris* + *P. pinaster*) and for each species separately (*P. sylvestris* or *P. pinaster*).

Understory richness

Thirty understory species from twenty-one families were recorded, with chamaephytes (mostly *Ericaceae)* being the most abundant (25% of absolute cover), following by phanerophytes (8%) and hemicryptophytes (7%). The understory richness showed an increasing trend bounded below the maximum attainable response as the percentage of basal area of *P. sylvestris* increased (HOF model III; Figure 41).

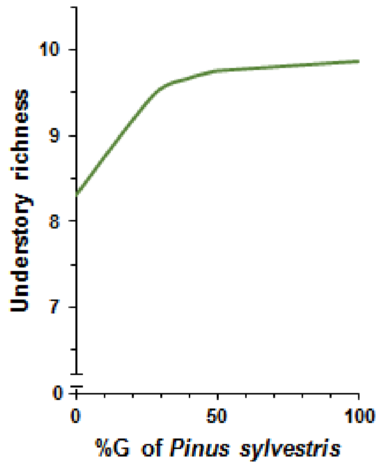

Figure 41. HOF-derived response curve of understory richness relative to the percentage (%) of basal area (G) of *P. sylvestris*.

Understory richness maintenance and overyielding at small scale as a result of overstory-soil-understory interactions

The structural equation model (SEM) showed a reasonably good fit as GFI value was greater than 0.90 and RMSEA was near to 0.08 (Figure 42). The SEM clearly showed that soil fertility (SBstock) affected positively the basal area of *P. sylvestris* (GPS) and the cover of hemicryptophytes, whereas soil moisture (WHC) affected negatively the basal area of *P. pinaster* (GPP) and the cover of hemicryptophytes. There is also a negative relation between the basal area of both *Pinus* species. Finally, the standardized path coefficients indicated that soil moisture (WHC) and hemicryptophytes affected positively the understory richness (S). The overall goodness of the model fit increased when including hemicryptophytes.

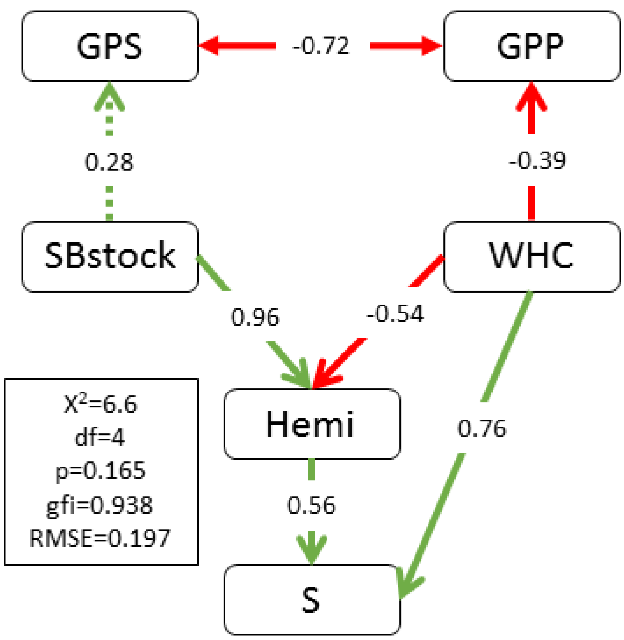

Figure 42. Conceptual model of the effects of soil moisture (WHC: water holding capacity) and fertility (SBstock: stock of sum of bases) on the basal area of the overstory species (GPS: basal area of *P. sylvestris*, GPP: basal area of *P. pinaster*) and the understory species richness (S) through the hemicryptophytes cover (Hemi). Continuous and dashed lines represent the signification level (p<0.1 or p>0.1, respectively). Red and green arrows represent negative and positive associations between variables, respectively.

Niche complementarity of *Pinus* species: soil water and fertility

Both Pinus species responded to soil moisture (WHC) and fertility (SBstock) with opposite trends (Figure 43a,b). *P. sylvestris* showed both asymmetrical response curves (HOF-model V) with the maximum skewed at the highest WHC and SBstock values. Conversely, *P. pinaster* showed both asymmetrical response curves (HOF-models V) with the maximum skewed at the lowest WHC and SBstock values.

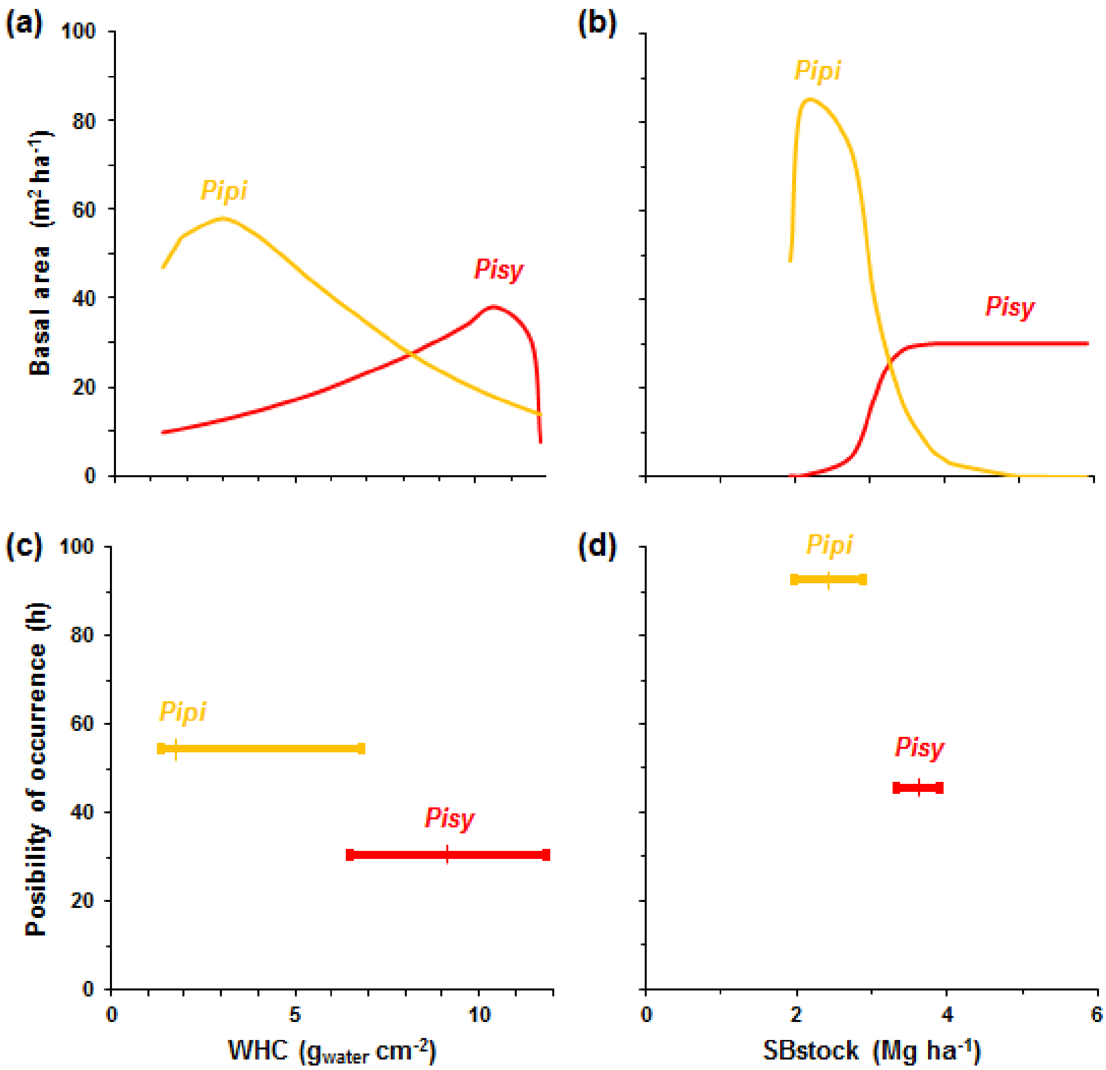

Figure 43. HOF-derived response curves of overstory species (Pisy: *Pinus sylvestris* and Pipi: *Pinus pinaster*) relative to (a) soil moisture (WHC: water holding capacity) and (b) fertility (SBstock: stock of sum of bases) gradients; and location of the optimum (µ) and niche withd (2t) for both *Pinus* species relative to (c) soil moisture (WHC) and (d) fertility (SBstock) gradients.

In fact, the location of the optimum of overstory species along WHC and SBstock gradients (Figure 43c,d and Table 28) showed how *P. pinaster* had the greatest probability of occurrence (h > 50 and h>90 for WHC and SBstock respectively) in soils with low WHC (µ< 2 gwater cm^{-2}) and

SBstock (μ < 3 Mg ha^{-1}), whereas *P. sylvestris* had the greatest probability of occurrence (h > 30 and h>40 for WHC and SBstock respectively) in soils with higher WHC (μ > 5 gwater cm^{-2}) and SBstock (μ > 3 Mg ha^{-1}). Both Pinus species showed broader niches widths for WHC than for SBstock (Figure 43c,d and Table 28), and low degree of overlap between them (Figure 44).

Table 28. Location of optimum (μ), predicted maximum probability of occurrence (h) and niche amplitude based on 2t tolerances for both *Pinus* species along two soil gradients: moisture (WHC: water holding capacity) and fertility (SBstock: stock of sum of bases).

Soil gradients	Species	Model	h	μ	2t
WHC	*P. sylvestris*	V	30.56	9.12	5.35
	P. pinaster	V	54.21	1.75	5.45
SBstock	*P. sylvestris*	V	45.06	3.61	0.57
	P. pinaster	V	92.63	2.42	0.90

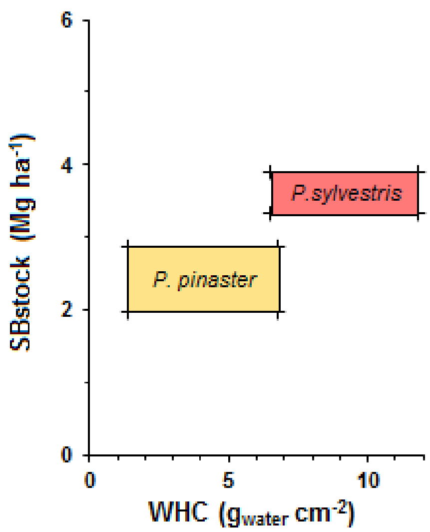

Figure 44. Bidimensional niche for both overstory species (*P. sylvestris* and *P. pinaster*) including simustaneosly the 2t tolerance intervals to soil moisture (WHC) and fertility (SBstock) shown in Figures 43c and d.

Discussion

<u>The spatial scale affects the overstory structure</u>

Overstory density and total basal area differ among stands in a different way depending on the spatial scale analysed. At the stand level, both density and total basal area increased from PS to PP, being intermediate at MM (differences were only significant for total basal area), whereas at a smaller scale a significant overyielding in the total basal area but non-significant in density were found. This change of pattern can be due to the change in the spatial pattern of tree mixture conditioned by the spatial scale (Bravo-Oviedo et al. 2014). In mixed stands, the 'patch mixture' is observed at the stand level, i.e. Scots pines surrounded by Maritime pines or vice versa, whereas at the smaller spatial scale an 'intensive tree-wise mixture' where both species are closely interlocked was observed. The intimate mixture at a small scale has a larger contact zone between species than the patch mixture at the stand level, so mixing effects are more likely to be significant (Bravo-Oviedo et al. 2014). Pretzsch et al. (2012) have already mentioned that productivity and resource-use efficiencies can change as a result of the different spatial mixing patterns (patch mixture vs. intimate mixture) since plant interactions at the neighbourhood scale play a fundamental role in regulating biodiversity–productivity relationships (Fichtner et al. 2018). Greater productivity in an intimate mixture than in a patch mixture has been already described in mixed forests (Ngo Bieng et al. 2013).

<u>Tree species mixture promotes the overstory overyielding at a small spatial scale</u>

Overyieldings in the total basal area and density in mixed stands were found when the overstory was studied at a small scale. That mixed forests can be more productive than single-species stands has been observed for many species combinations and ecosystems (Kelty 2006; Vilà et al. 2013; Forrester 2014; Riofrío et al. 2017a), suggesting that tree species richness fosters forest productivity (Fichtner et al. 2018). The biodiversity loss have also been linked to the productivity loss at global forests (Liang et al. 2016).

Here, we propose the greatest efficiency in the use of space where Scots pine and Maritime pine cohabit as the cause of this overyielding. Riofrío et al. (2017b) have already described the positive effects of this tree mixture on the efficiency in the use of the available space for growth. Thus, the distance from a random point (in our study, the center of the quadrat for understory sampling) to the nearest tree, and the distance from that tree to its nearest neighbor both decrease in mixtures at the stand level. Additionally, the spatial distribution pattern of both *Pinus* species considered separately changes from random in monospecific stands to regular in mixed stands; the productivity being greater for the regular spatial distribution pattern as Pukkala (1989) found. Competition leads to a more or less regular spacing of trees, and given that in the mixed forest the intra-specific competition is more intense than inter-specific competition, tree species should display a kind of mutual 'attraction', i.e. individuals of different species should grow close to each other (Szwagrzyk 1992) whereas individuals of the same species should grow more apart from each other (see Fig. 3d). Also Pretzsch and Schütze (2009) have pointed out that the increase in productivity in mixed stands can be caused by a more efficient exploitation of growth space compared to monospecific stands. As a result, in the same space, more trees fit in mixtures, and density could act as an index to quantify the space occupied by forest species (Reineke 1933; Cattaneo 2018a). A biodiversity-productivity relationship caused by a density increase has already been described in grasslands (Marquard et al. 2009).

More efficiency in the use of spaces thanks to the niche complementarity

Niche complementarity has been described as a driver of diversity-productivity relationships (Loreau and Hector 2001). In our study, the complementarity in the use of resources, such as fertility and water in the soil, could explain the greatest efficiency in the used of the space of both *Pinus* species when they coexist, resulting in the highest productivity in mixed stands. On the other hand, the spatial scale-dependence of our results is consistent with the niche complementarity theoretical models that predict greater niche complementarity at smaller spatial scales (Chisholm et al. 2013).

A previous study at the same experimental devise showed how *P. pinaster* tolerates lower soil water content than *P. sylvestris*, but mixtures occupied areas with intermediate soil moisture and higher fertility (López-Marcos et al. 2019). The mesophilic character of *P. sylvestris* and the xerophytic character of *P. pinaster* are well known (Bravo-Oviedo and Montero 2008), as well as the ability of *P. pinaster* to grow in very poor soils, and under prolonged summer droughts (Alía and Martín 2003a). Here, we found that the basal area of *P. sylvestris* (GPS) is positively related to soil moisture (WHC) and fertility (SBstock), whereas the basal area of *P. pinaster* (GPP) is negatively related to both soil variables, suggesting resource use complementarity when mixed. Additionally, a crown complementarity in mixed vs monospecific stand of Scots pine and Maritime pine, using Spanish forest inventory data, was described as a driver of the overyielding in the mixtures (Riofrío et al. 2017a). However, it was already suspected that belowground resources complementarity could be the cause of that major higher productivity in the mixtures.

The complementarity in the use of soil resources is one of the key mechanisms by which mixed stands may achieve greater productivity than monospecific stands (Seidel et al. 2013). In stands with a supply of resources spatially more heterogeneous (Pretzsch et al. 2016a) as in mixtures, the efficiency in the use of resources increase (Binkley et al. 2004) since no species are competitively superior (Tilman et al. 1997b). Each species has an optimal competitive ability where it consumes the resources, thus it would leave sufficient unconsumed resources in regions away from its optimum, and so other species could use them and persist there (Tilman et al. 1997b). This effect, however, was only observed at small-scale because the neighborhood interactions play a fundamental role in regulating biodiversity–productivity relationships (Fichtner et al. 2018).

Overstory overyielding and understory richness relationship

Light is commonly considered to be the major limiting factor of understory cover and richness (Barbier et al. 2008), thus it is expected the lower understory richness the higher the basal area due to the lower light availability (Reich et al. 2012). However, we found the highest understory richness for percentages of basal area of *P. sylvestris* above a certain value, i.e. in mixed stands and in monospecific *P. sylvestris* stands (Figure 41). The high understory richness found in monospecific *P. sylvestris* stands seams reasonable since they have the lowest total basal area at both spatial scales. However, in mixed stands where total basal area is the highest, at least at the smaller spatial scale, we found higher understory richness than expected according to Reich et al. (2012), and similar to that found in monospecific stands of *P. sylvestris*. In the study area, there is probably no direct effect of the basal area on the understory richness, but through the complementarity in the use of soil resources by both *Pinus* species. Thus, a larger basal area allows to host greater species richness in the understory. Since hemicryptophytes was the only Raunkiær's life-form whose cover increased in mixed stands with respect to monospecific stands (López-Marcos et al. 2019), we propose to the hemicryptophytes as responsible of the higher understory richness in mixed stands. In fact, the hemicryptophytes was the only Raunkiær's life-form whose inclusion in the structural equation model improved the goodness of model fit.

Implications for forest management

It is worth noting here that our results have important implications for forest management in the context of the supply of ecosystem services (Gamfeldt et al. 2013), such as biodiversity conservation and productivity. The mixture of Scots pine and Maritime pine allows achieving an overstory overyielding while maintaining high understory richness despite the increase in basal area in the mixtures with respect to the monospecific stands of *P. sylvestris*. Thus we think that the mixture of Scots pine and Maritime pine, widely distributed in Spain (Serrada et al. 2008), should continue to be favored over pure stands in the study area. Nevertheless, in order to promote productivity, we recommend encouraging a more intimate mixture of both *Pinus* species to get a larger contact zone between them. In this way, both pines could explore the soil resources more efficiently given the water and fertility soil niche complementarity previously described. Additionally, we recommended respecting the understory when performing silvicultural treatments to maintain high the understory richness, particularly in the admixtures, thanks to a great extent to the contribution of hemicryptophytes.

Conclusions

Our results highlight the fundamental role of scale in determining the observed relationship between species richness and ecosystem functioning in forests. In particular, a small-scale overyielding was found in mixed stands related to the more efficient use of the space by the species of the overstory, as distances between trees were reduced in admixtures in relation to monospecific stands. This greater efficiency in space use is related to soil water and fertility niche complementarity of both *Pinus* species, and it was only detected at small scale thanks to the more intimate *Pinus* species mixture at this level. The small scale overyielding found in mixed stands has no negative effect on the understory richness.

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Author contributions

DLM carried out the field and laboratory work, ran the data analysis and discussed the results. DLM and CMR discussed data analysis and commented on the results and discussion. CMR supported DLM with the statistical analysis. MBT supported DLM with the laboratory analyses. DLM, CMR, MBT and FB edited the manuscript. FB coordinated the research project.

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Appendix IV

Table 29. Data analyses of soil properties: Water holding capacity.

Water holding capacity of each horizon (WHC_{Hi})

$WHC_{Hi} = UW_{Hi} \cdot bD_{Hi} \cdot \%EF_{Hi}\ T_{Hi}$	UW_{Hi}: Useful water of each horizon bD_{Hi}: bulk density of each horizon $\%EF_{Hi}$: % of earth fraction of each horizon T_{Hi}: thickness of each horizon

Water holding capacity in the whole mineral soil profile (0-50cm; WHC)

$$WHC = \sum WHC_{Hi}$$

Table 30. Data analyses of soil properties: Sum of bases stock.

Sum of bases of each horizon ($SBstock_{Hi}$)

$SBstock_{Hi} = SB_{Hi} \cdot bD_{Hi} \cdot \%EF_{Hi}\ T_{Hi}$	SB_{Hi}: Sum of bases of each horizon bD_{Hi}: bulk density of each horizon $\%EF_{Hi}$: % of earth fraction of each horizon T_{Hi}: thickness of each horizon

Sum of bases stock in the whole mineral soil profile (0-50cm; SBstock)

$$SBstock = \sum SBstock_{Hi}$$

Table 31. Data analyses of overstory properties: Basal area of *Pinus sylvestris*.

Basal area of *Pinus sylvestris* (GPS)

$GPS = \sum g_{PSi} / Si$	g_{PSi}: Secction of *Pinus sylvestris* stem (m^2) Si: surface (ha)

Secction of *Pinus sylvestris* stem (g_{PSi})

$g_{PSi} = \pi/4\ dn_{PSi}^2$	dn_{PSi}: normal diameter of every *Pinus sylvestris* stem >7.5 cm at the breast height (m)

Table 32. Data analyses of overstory properties: Basal area of *Pinus pinaster*.

Basal area of *Pinus pinaster* (GPP)

$GPP = \sum g_{PPi} / Si$	g_{PPi}: Secction of *Pinus pinaster* stem (m^2) Si: surface (ha)

Secction of *Pinus pinaster* stem (g_{PPi})

$g_{PPi} = \pi/4\ dn_{PPi}^2$	dn_{PPi}: normal diameter of every *Pinus pinaster* stem >7.5 cm at the breast height (m)

Table 33. Data analyses of overstory properties: Total basal area.

Total basal area (GT)

GT = GPS+GPP	GPS: basal area of *Pinus sylvestris* GPP: basal area of *Pinus pinaster*

The results derived from this thesis are relevant in the context of the forest ecosystem services supply of the mixture of Scots pine and Maritime pine widely distributed in Spain (Serrada et al. 2008). A competitive advantage of the mixed forests of Scots pine and Maritime pine vs the monospecific stands in biodiversity conservation, carbon sequestration, fertility, and productivity is highlighted (Figure 45).

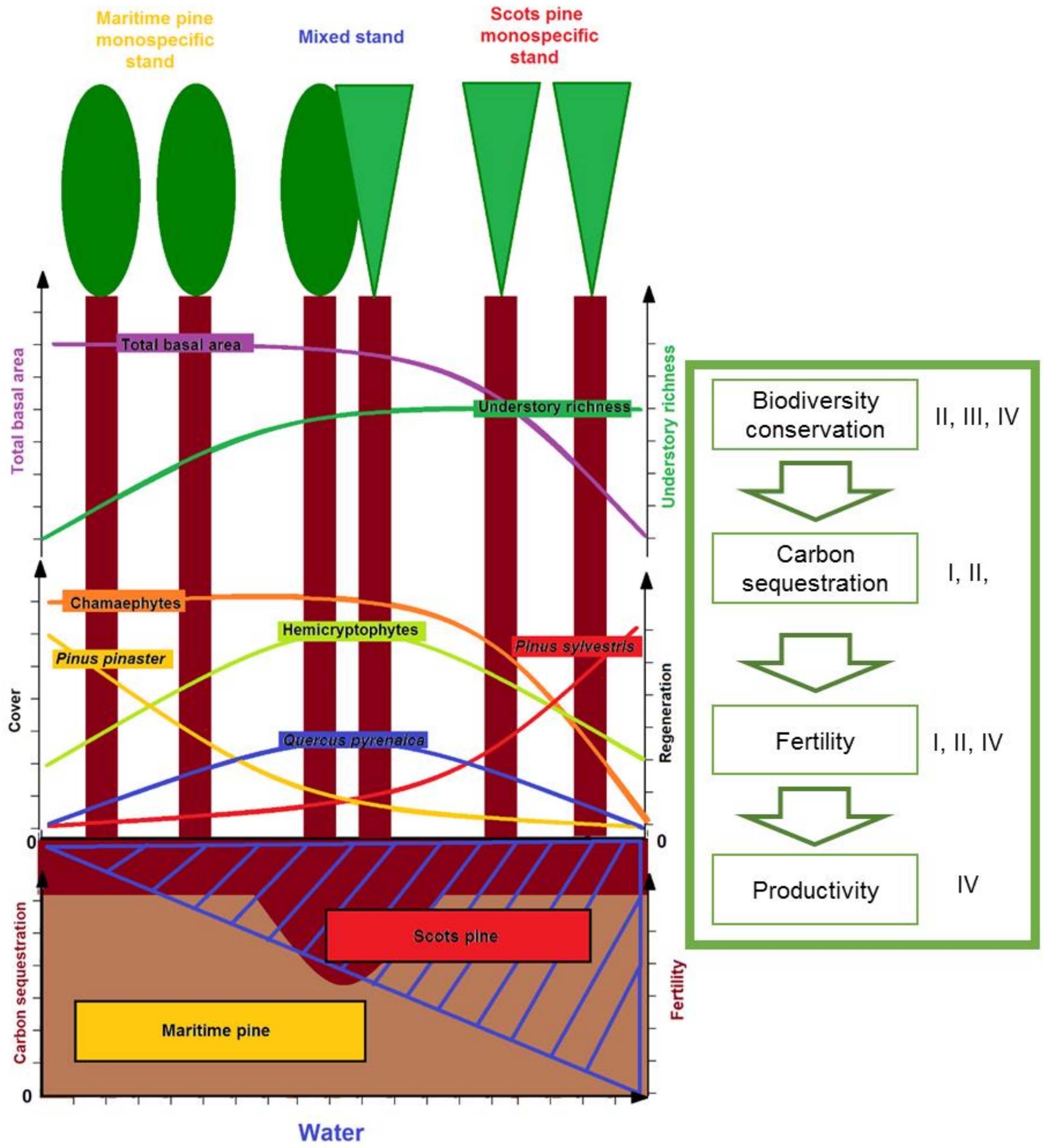

Figure 45. Graphical abstract of the whole thesis.

Initially, the objective of this thesis was to analyze the role of the mixed forests of Scots pine and Maritime pine in the provision of two ecosystem services: biodiversity conservation and carbon sequestration. However, derived from the relationship between them, other two ecosystem services emanate, such as fertility and productivity. Thus, the relationship between those other ecosystem services is also analyzed here: overstory biodiversity-soil carbon sequestration **(I)** (López-Marcos et al. 2018), soil carbon sequestration-soil fertility **(I)** (López-Marcos et al. 2018), understory biodiversity-soil fertility **(II)** (López-Marcos et al. 2019), soil fertility-overstory productivity **(IV)** (López-Marcos et al. 2020b), overstory biodiversity-understory biodiversity **(III)** (López-Marcos et al. 2020a), and overstory productivity-understory biodiversity **(IV)** (López-Marcos et al. 2020b).

Biodiversity conservation

First, it is worth noting here that *Pinus sylvestris* is present in the mixed stands under worse soil water content conditions than in monospecific stands. Probably, in these mixtures, *P. sylvestris* is able to occupy the most favorable microsites according to the water in soil **(II)** (López-Marcos et al. 2019). This is particularly interesting since in the study area the mixtures of both *Pinus* species are located at the rear-edges for Scots pine forests, where ecological conditions (high temperatures and frequent droughts) approach the species tolerance limit and the most drastic effects of climate change are predicted (Matías and Jump 2012). Thus the mixture of Scots pine and Maritime pine can be an opportunity to conserve *P. sylvestis* in the study area.

In addition, the mixed stands, allow the regeneration not only of both pine species but also of the Iberian Peninsula endemic oak, *Quercus pyrenaica* **(III)** (López-Marcos et al. 2020a). This encourages the nurse effect of the conifers on the *Quercus* spp. in the mixed pine stands (Pigott 1990b). This mixed pine forest also promotes the establishment of a greater variety of understory species associated with the *Quercus pyrenaica* forests and sharing niche amplitude **(III)** (López-Marcos et al. 2020b), contributing to the maintenance of high understory richness in mixed stands under higher water-stress conditions **(II)** (López-Marcos et al. 2019) and lower light availability **(IV)** (López-Marcos et al. 2020b). Thus, Scots pine and Maritime pine mixed forests could be considered as a biodiversity conservation strategy in the current climate change scenario (Felton et al. 2010).

On the other hand, hemicryptophytes are pointed out as the only Raunkiær's life-form linked to better soil fertility status **(II)** (López-Marcos et al. 2019) and responsible of the understory richness conservation in mixed stands by improving the goodness of the model fit **(IV)** (López-Marcos et al. 2020a).

Last, in the mixed pine forests, under moderate water-stress conditions, a facilitation effect of chamaetophytes on hemicryptophytes is described **(II)** (Grime 1977; Bertness and Callaway 1994; López-Marcos et al. 2019).

Carbon sequestration

When comparing monospecific and mixed pine forests, different trends in carbon inputs were found at different soil layers. The different soil carbon accumulation trends are a consequence of the different amount and nature of litter deposited in each soil layer since the decomposition of plant tissues in terrestrial ecosystems regulates the transfer of carbon and nutrients to the soil (Wang et al. 2014a,b). At the topsoil (0–10 cm), carbon stock reaches higher values in *P. sylvestris* monospecific stands, lower in *P. pinaster* monospecific stands and intermediate in mixed stands, whereas at the subsoil layers (10–30 cm), it reaches higher values in mixed stands than in monospecific stands **(I)** (López-Marcos et al. 2018). The lower carbon values at Maritime pine monospecific topsoil are related to the more sclerophyllous foliage of *Pinus pinaster* with higher lignin content (Augusto et al. 2015). The presence of more chemically recalcitrant compounds such as lignin could explain the lower decomposition rate of litter (Wang et al. 2016) and in turn the lower carbon input into the soil. Nevertheless, higher carbon accumulation at the subsoil layers reached in mixed stands is related to the higher amount of fine roots deeper soil layers **(I)** (Andivia et al. 2016; López-Marcos et al. 2018).

On the other hand, the higher carbon input from roots in deeper soil layers is related to a greater thickness of the first mineral horizon in mixed stands than monospecific stands **(I)** (López-Marcos et al. 2018). At the same time, this higher fine roots rate is related to the tree diversity **(I)** (López-Marcos et al. 2018); a positive correlation between the tree species diversity, fine root biomass and carbon stock in deeper soil layers have been previously described (Dawud et al. 2016).

The higher accumulation of soil carbon stocks caused by the greater root litter in deeper soil layers is related to the belowground niche complementarity (Dawud et al. 2016). This niche complementarity could be caused (1) by the rooting pattern change, because tree species may behave differently in a mixture compared with their behavior in monospecific stands **(I)** (Brandtberg et al. 2000; López-Marcos et al. 2018), it would mean that the fine roots reach deeper soil layers in the mixed stands; or (2) by the complementarity use of soil resources **(IV)** (Seidel et al. 2013; López-Marcos et al. 2020b).

These results encourage the forest management of the mixed stand in the context of adaptation and mitigation to climate change through carbon sequestration or at least soil carbon preservation (Schleuß et al. 2014), since the subsoil carbon is known to be more effectively stabilized as compared to topsoil or litter layer carbon (Rumpel and Kögel-Knabner 2011). Therefore, potential losses of soil carbon from subsoil induced by warming will lag in time and provide a temporal buffer **(I)** (Schleuß et al. 2014; López-Marcos et al. 2018).

Fertility

The exchangeable cations serve as good indicators of soil fertility because are critical nutrients for both plant and microbial metabolism and the lack of exchangeable cations availability constraints net primary productivity (Wang et al. 2017). Thus, the exchangeable cations are used here as a fertility indicator **(I) (II) (IV)** (López-Marcos et al. 2018; López-Marcos et al. 2019; 2020b).

First, an indirect effect of the admixture on the exchangeable cations and the sum of bases is reported **(I)** (López-Marcos et al. 2018) given that the soil organic matter improves the soil capacity to retain nutrients including exchangeable cations (Beldin et al. 2007). So the effect of tree species composition on the exchangeable cations and on the sum of bases is mediated by their effect on the carbon (Cremer and Prietzel 2017); a positive correlation between carbon and exchangeable cations from 0 to 30 cm depth was found. Thus, the exchangeable cations and the sum of bases describe the same two tendencies found for the carbon storage **(I)** (López-Marcos et al. 2018): at the topsoil higher values in Scots pine monospecific stands, lower in Maritime pine monospecific stands and intermediate in mixed forest are recorded, and fertility being higher in deeper soil layers when Scots pine and Maritime pine cohabit.

In addition, the greater thickness of the first horizon in the mixed pine forest allows achieving higher nutrient stock rates **(II)** (López-Marcos et al. 2019). The higher thickness of the A horizon in mixed stands in relation to monospecific stands has already reported by Schleuß et al. (2014).

On the other hand, Tilman et al. (1997) have been described as biodiversity increase with nutrient retention. This is related to the positive correlation between the understory richness and Mg^{+2}stock found **(II)** (López-Marcos et al. 2019). This is really interesting since magnesium is known to be a critical component in the carbon fixation and transformation processes in the vegetation (Guo et al. 2015), and its deficiency can affect forest decline (Huettl 1992; Zas and Serrada 2003).

In the study area, both greater productivity and overyielding are found in mixed stands, compared to monocultures **(IV)** (Riofrío et al. 2017b; López-Marcos et al. 2020b), and it is explained by greater soil fertility **(II)** (Mg^{+2}stock; Riofrío et al. 2017a; López-Marcos et al. 2019) and soil niche complementarity **(IV)** (López-Marcos et al. 2020b).

Furthermore, hemicryptophytes are the only life-form whose cover was positively related to the fertility in the study area, showing a cover increase as carbon and magnesium stocks increase **(II)** (López-Marcos et al. 2019). This finding is in agreement with the previously accepted idea that hemicryptophytes are indicative of sites with relatively good soil fertility (Mark et al. 2000; Sigcha et al. 2018).

Productivity

An overyielding in the basal area of mixed stands is found and related to the soil water and fertility niche complementarity **(IV)** (López-Marcos et al. 2020b) since the niche partitioning is a driver of the species mixing effect on productivity (Loreau and Hector 2001).

In stands with a supply of resources spatially more heterogeneous (Pretzsch et al. 2016a), as in mixtures, the efficiency in the use of resources increase (Binkley et al. 2004) since each species has an optimal competitive ability where it consumes the resources and a sufficient unconsumed resources leave in regions away from its optimum to be used by other species (Tilman et al. 1997b).

Accordingly, Scots pine prefers wetter and the most fertile positions (Scots pine basal area positively correlated to soil moisture and fertility) while Maritime pine occupies the drier and less fertile places (Maritime pine basal area negatively correlated to soil moisture and fertility) **(IV)** (López-Marcos et al. 2020b). These results are in agreement with the mesophilic character of Scots pine and xerophytic character of Maritime pine (Bravo-Oviedo and Montero 2008), the Scots pine and Maritime pine segregation along the soil water content gradient **(II)** (López-Marcos et al. 2019), and the ability of Maritime pine to grow in very poor soils, and under prolonged drought (Alía and Martín 2003a).

However, the overyielding in basal area was only detected at small-scale **(IV)** (López-Marcos et al. 2020b) since the spatial pattern of the mixture changes at different spatial scales (Bravo-Oviedo et al. 2014) and this changes the resource-use efficiency and in turn affect the productivity (Pretzsch et al. 2012); the mixture by patches is observed at the stand level, whereas an intensive mixture is observed at small scale **(IV)** (López-Marcos et al. 2020b).

On the one hand, a greater space use efficiency in mixed stands over the monospecific stand is described **(IV)** (López-Marcos et al. 2020b): the distances between trees are reduced when both pines cohabit **(IV)** (López-Marcos et al. 2020b). As a result, more trees fit in the same area when they are mixed (higher density) **(IV)** (López-Marcos et al. 2020b), thus showing a positive biodiversity-productivity relationship caused by a density increase (Marquard et al. 2009).

The spatial scale-dependence of these results is consistent with the niche complementarity theoretical models that predict greater niche complementarity at smaller spatial scales (Chisholm et al. 2013). Thus, the intimate mixture at a small scale has a larger contact zone between the species, so, mixing effects are more likely to be significant (Bravo-Oviedo et al. 2014). The plant interactions at the neighborhood scale play a fundamental role in regulating biodiversity–productivity relationships (Fichtner et al. 2018).

Conclusions / Conclusiones

Conclusions

I. The mixture of Scots pine and Maritime pine in the study area shows a competitive advantage in comparison with the respective monospecific stands to the ecosystem services supply. That is: (1) in terms of carbon sequestration through the carbon accumulation in the subsoil layers where is protected from external disturbance; in terms of biodiversity (2) through the understory richness conservation under worse soil water conditions, and (3) through the regeneration of the endemic Iberian Peninsula oak (*Quercus pyrenaica*) and associated understory species; (4) in terms of fertility thanks to the greater thickness of the first mineral horizon that allows to achieve higher nutrient stocks rates; and (5) in terms of the yield at small spatial scale because of the basal area increase as a result of more efficient space use.

II. The carbon input shows different patterns when comparing between layers of the soil profile due to the different amount and origin of the organic matter deposited at different depths. In the topsoil (0-10 cm), the carbon stock is higher in Scots pine monospecific stands thanks to the amount and nature of the forest floor leaf litter. Thus, a relatively strong tree species identity effect is observed in the forest floor and the topsoil layer. Nevertheless, in the subsoil (10-30 cm) the carbon stock is higher in the mixed pine stands as a result of the greater amount of the fine root litter. These influences of the stand type on carbon of the mineral soil profile are reflected in differences in the exchangeable cations.

III. The understory (plant species, Raunkiær's life-forms, and tree regeneration) responds to the gradient of the basal area of both *Pinus* species associated with a water-stress gradient (*P. pinaster* tolerates lower soil water content than *P. sylvestris*). The Scots pine monospecific stands, with species characteristic of humid and temperate zones, including *P. sylvestris* regeneration, are dominated by phanerophytes. At the opposite end of the gradient, the Maritime pine monospecific stands, with typical species of well-drained Mediterranean areas, including *Pinus pinaster* regeneration, are dominated by chamaephytes. In the mixed stands, where *Pinus sylvestris* and *Pinus pinaster* cohabit and hemicryptophytes show the maximum cover, regeneration of the western European endemic species, *Quercus pyrenaica*, is added to the regeneration of both *Pinus* species.

IV. The mixture of both *Pinus* species also improves soil fertility and maintains similar understory richness to that of monospecific stands of *Pinus sylvestris* but under lower soil water content. Understory species typical of the native Pyrenean oak forests in the Iberian Peninsula, which share with *Quercus pyrenaica* the same regeneration niche, contribute to maintaining high understory richness in such mixed pine forests. Hemicryptophytes are the only understory life-form positively linked to better soil fertility status (defined by the total organic carbon and exchangeable Mg^{+2} stocks).

V. A small-scale overyielding was found in mixed stands related to the more efficient use of the space by the species of the overstory (more intimate *Pinus* species mixture at this level), which in turn is related to soil water and fertility niche complementarity. The small scale overyielding found in mixed stands has no negative effect on the understory richness.

Conclusiones

I. La mezcla de pino resinero y pino albar en el área de estudio muestra una ventaja competitiva, en comparación con las masas monoespecíficas, en la provisión de servicios ecosistémicos. Esto es: (1) en el secuestro de carbono a través de la mayor acumulación de carbono en las capas del subsuelo donde está protegido de perturbaciones externas; en biodiversidad (2) a través de la conservación de la riqueza del sotobosque en peores condiciones de agua en el suelo, y (3) de la regeneración del robledal endémico de *Quercus pyrenaica* y el establecimiento de especies asociadas del sotobosque; (4) en fertilidad gracias al mayor espesor del primer horizonte que permite alcanzar mayores tasas de reservas de nutrientes; y (5) en la productividad a pequeña escala espacial debido al aumento del área basal como resultado del uso más eficiente del espacio.

II. El aporte de carbono muestra diferentes tendencias al comparar entre capas del perfil del suelo debido a la diferente cantidad y procedencia de la hojarasca depositada a diferentes profundidades. En la capa superior del suelo (0-10 cm) las reservas de carbono son más altas en los pinares monoespecíficos de pino albar gracias a la cantidad y la naturaleza de la hojarasca depositada en el suelo del bosque. Sin embargo, en el subsuelo (10-30 cm) las reservas de carbono son más altas en el pinar mixto como resultado de la mayor cantidad de raíces finas. La influencia de la composición del dosel en el carbono del perfil del suelo mineral se corresponde también en diferencias en los cationes intercambiables.

III. El sotobosque (especies vegetales, formas de vida de Raunkiær y regeneración de árboles) responde al gradiente de área basal de ambas especies de pinos asociado con un gradiente de disponibilidad de agua en el suelo (*P. pinaster* tolera un menor contenido de agua del suelo que *P. sylvestris*). Las masas monoespecíficas del pino albar, con especies características de zonas húmedas y templadas, incluyendo la regeneración de *P. sylvestris*, están dominados por fanerófitos. En el extremo opuesto del gradiente, las masas monoespecíficas del pino resinero, con especies típicas de áreas mediterráneas bien drenadas, incluida la regeneración *Pinus pinaster*, están dominadas por caméfitos. En las mass mixtas, donde *Pinus sylvestris* y *Pinus pinaster* conviven y los hemicriptófitos muestran la máxima cobertura, la regeneración de la especie endémica de Europa occidental, *Quercus pyrenaica*, se añade a la regeneración de ambas especies de pinos.

IV. La mezcla de ambas especies de pinos también mejora la fertilidad del suelo y mantiene una riqueza similar a la de las masas monoespecíficas de *Pinus sylvestris* pero bajo menor contenido de agua del suelo. Las especies de sotobosque típicas de los bosques nativos de robles pirenaicos de la Península Ibérica, que comparten con *Quercus pyrenaica* el mismo nicho de regeneración, contribuyen a mantener una alta riqueza de sotobosque en estos bosques mixtos de pinos. Los hemicriptofitos son la única forma de vida de sotobosque positivamente vinculada a un mejor estado de fertilidad del suelo (definido por el carbono orgánico total y los cationes intercambiables de Mg^{+2}).

V. Se encontró un sobrerendimiento a pequeña escala espacial en masas mixtas relacionado con el uso más eficiente del espacio por las especies arbóreas (mezcla más íntima de especies de pinos a este nivel), que a su vez se relaciona con la complementariedad de nicho edáfico (agua del suelo y fertilidad). La sobrerendimiento encontrado a pequeña escala espacial en los bosques mixtos no tiene ningún efecto negativo en la riqueza del sotobosque.

Management recomendations

Following the conclusions drawn from this thesis, it is necessary to issue a management recommendation of the Scots pine and Maritime pine mixed stands in the ecosystem services supply context.

I. Taking into account the relationships between the analyzed ecosystem services it seems obvious that the management of these ecosystem services cannot be done in isolation. The management of all ecosystem services should be considered in an integrated manner to achieve optimal results.

II. Since the presence of *Pinus sylvestris* in the mixed stand, under higher water-stress conditions, corresponds with its distribution limit, these mixtures are an opportunity to conserve *Pinus sylvestis* in the study area in the new climate change scenery.

III. The Scots pine and Maritime pine mixtures are postulated as a better biodiversity conservation strategy than monospecific stand because of the conservation of the understory richness under worse soil water and light availability conditions. The establishment of typical understory species of the native Pyrenean oak forests, including *Quercus pyrenaica* regeneration, contributes to the high understory richness in mixed stands.

IV. The management treatments should respect the understory since some Raunkiær's life-forms, such as hemicryptophytes, are in part responsible for the understory richness in mixed forests.

VI. The mixed stands can accumulate greater carbon amounts in the subsoil layers encouraging the forest management of the mixed stands in the context of adaptation and mitigation to climate change since potential losses of soil carbon from subsoil induced by warming will lag in time and provide a temporal buffer.

VII. The more intimate mixture of *Pinus* species in mixed forests is recommended to promote productivity since the soil niche complementarity is detected at the neighborhood scale.

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Supplementary material

Study area description

Location

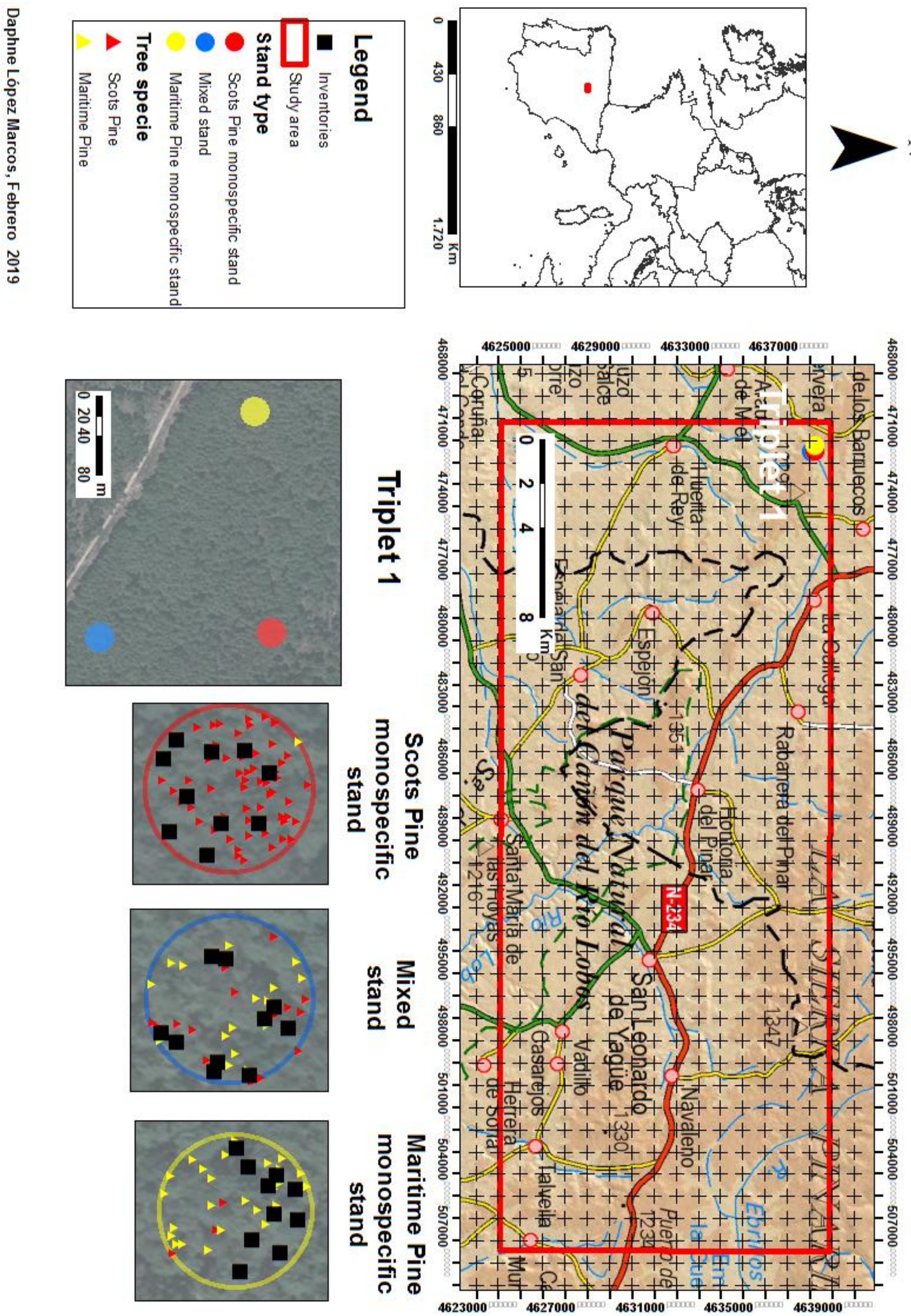


Figure 46. Location of the triplet 1, the three plots within the triplet, and the 10 quadrats for regeneration and vegetation sampling within each plot.

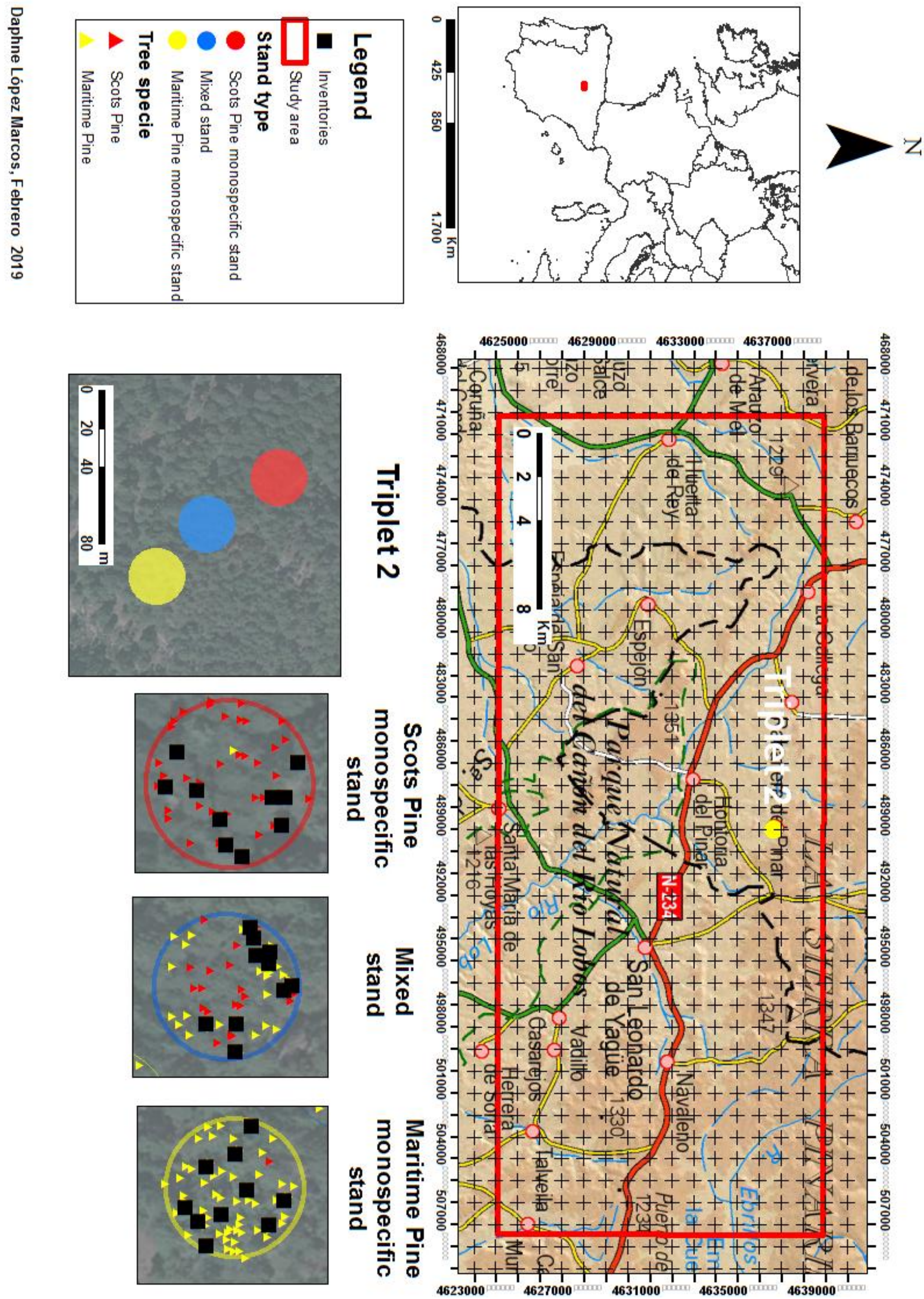


Figure 47. Location of the triplet 2, the three plots within the triplet, and the 10 quadrats for regeneration and vegetation sampling within each plot.

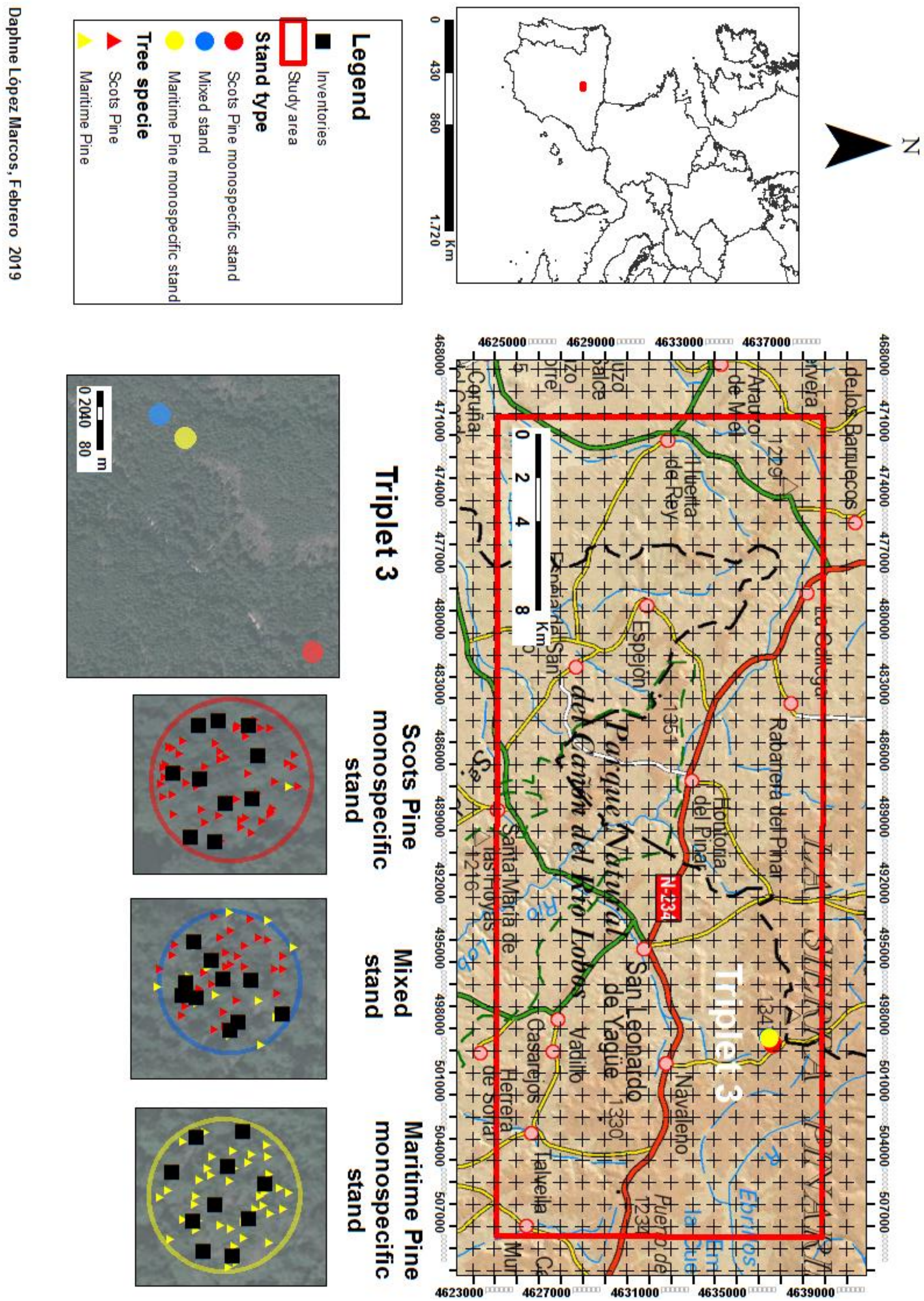


Figure 48. Location of the triplet 3, the three plots within the triplet, and the 10 quadrats for regeneration and vegetation sampling within each plot.

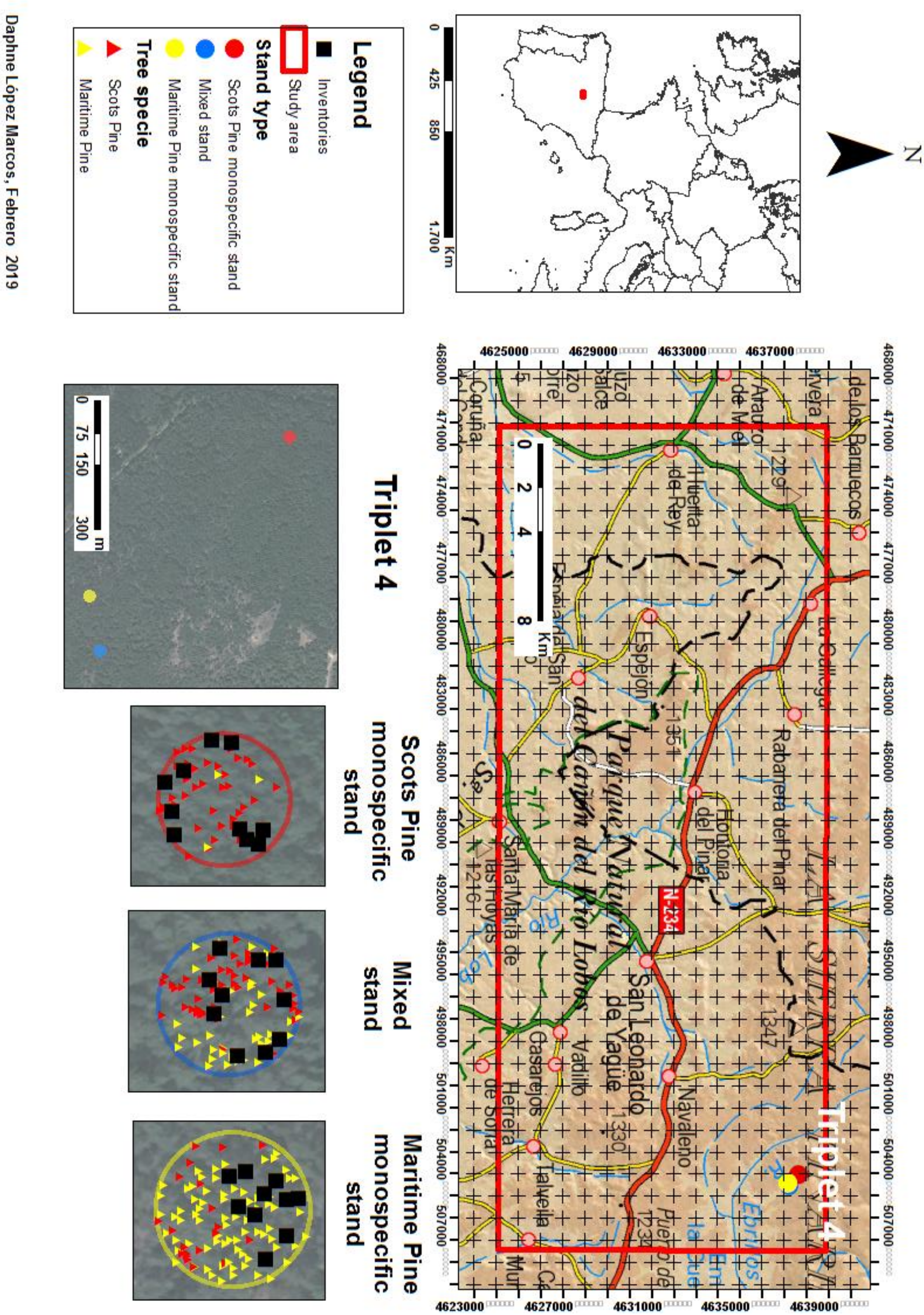


Figure 49. Location of the triplet 4, the three plots within the triplet, and the 10 quadrats for regeneration and vegetation sampling within each plot.

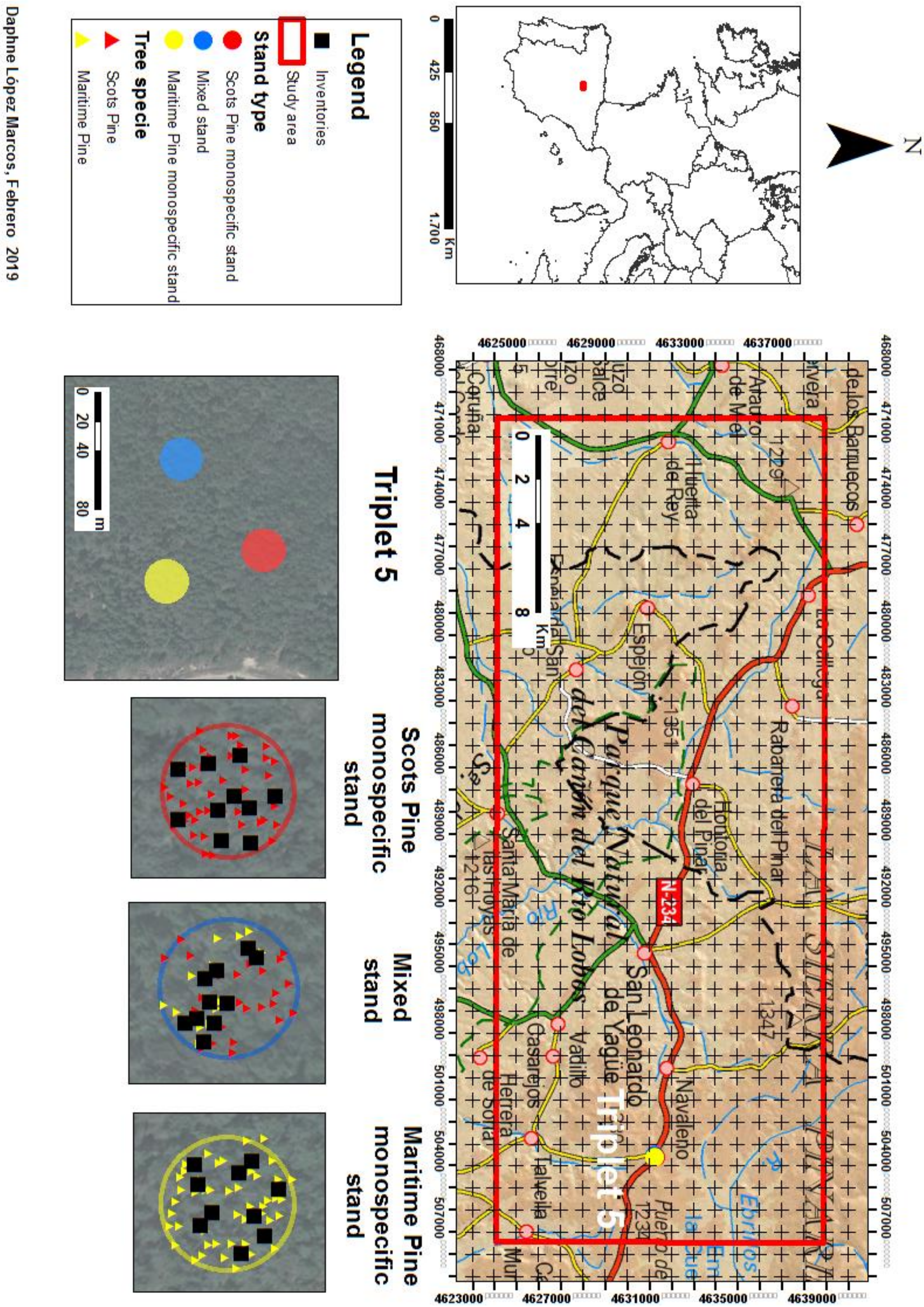


Figure 50. Location of the triplet 5, the three plots within the triplet, and the 10 quadrats for regeneration and vegetation sampling within each plot.

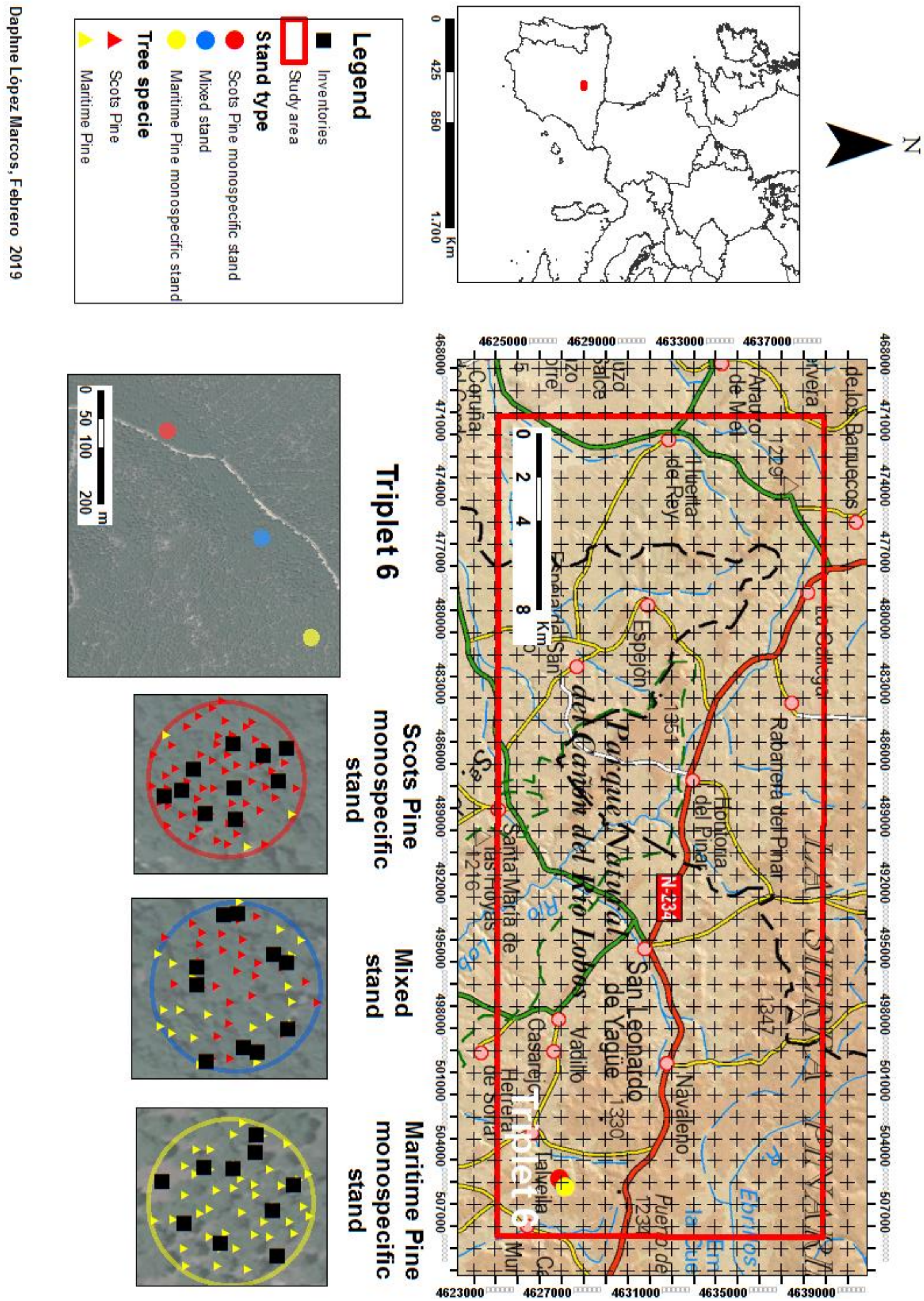


Figure 51 Location of the triplet 6, the three plots within the triplet, and the 10 quadrats for regeneration and vegetation sampling within each plot.

Climate

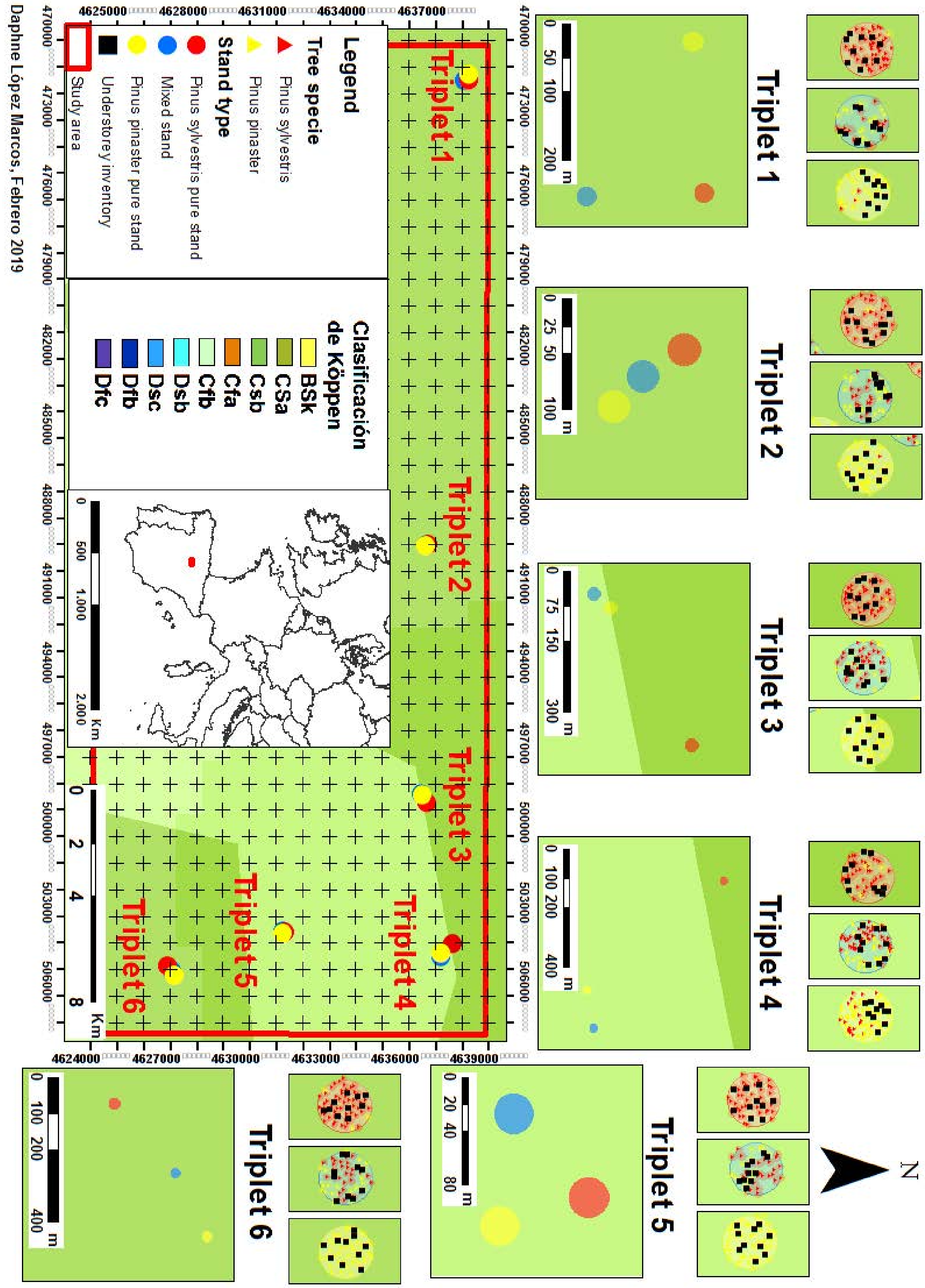


Figure 52. Climate of the study area according to Köppen (1936) classification for the Iberian Peninsula published by the 'Atlas Agroclimático de Castilla y León-ITACYL-AEMET'.

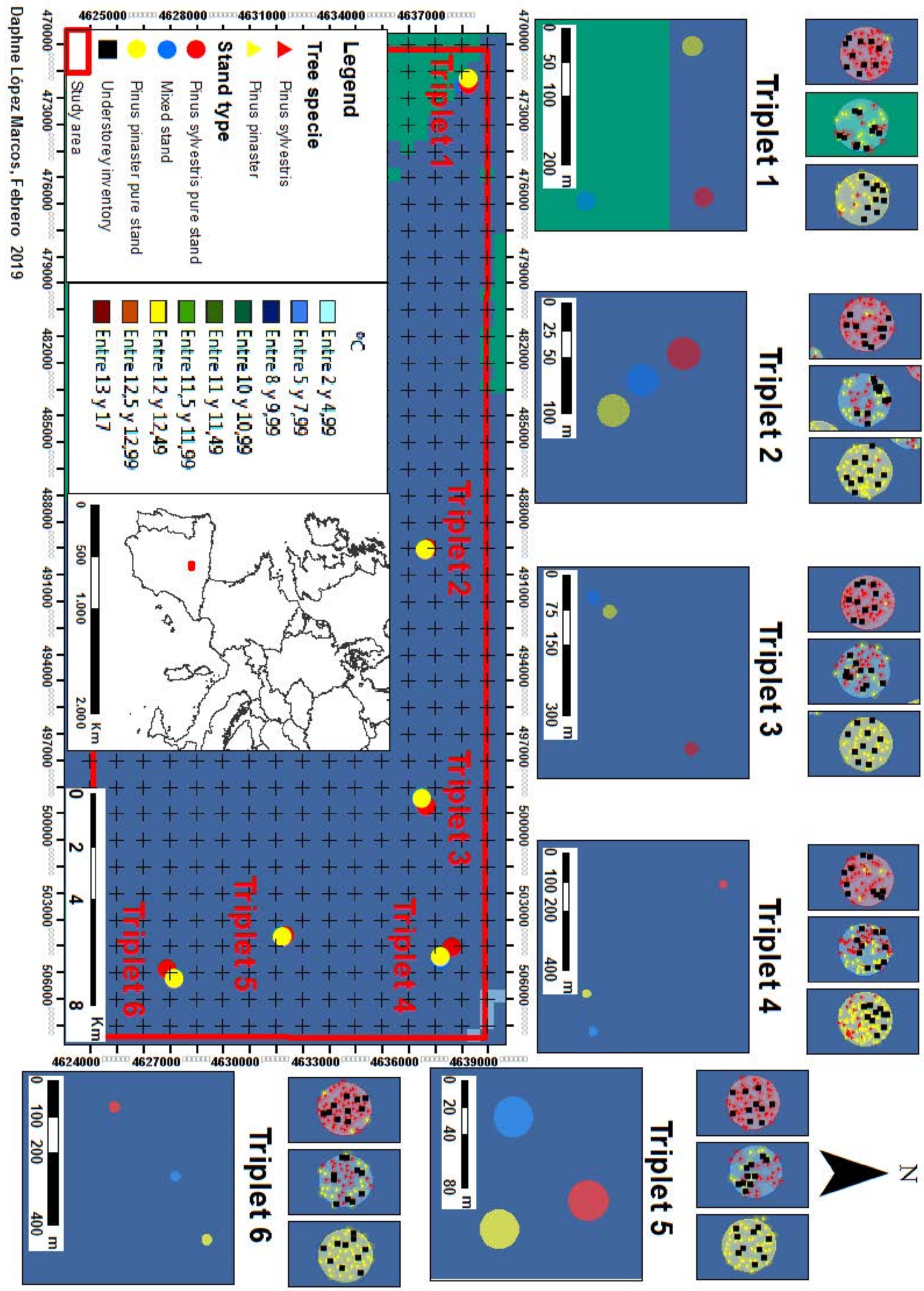


Figure 53. Mean annual temperature in the study area according to Köppen (1936) classification for the Iberian Peninsula published by the 'Atlas Agroclimático de Castilla y León-ITACYL-AEMET'.

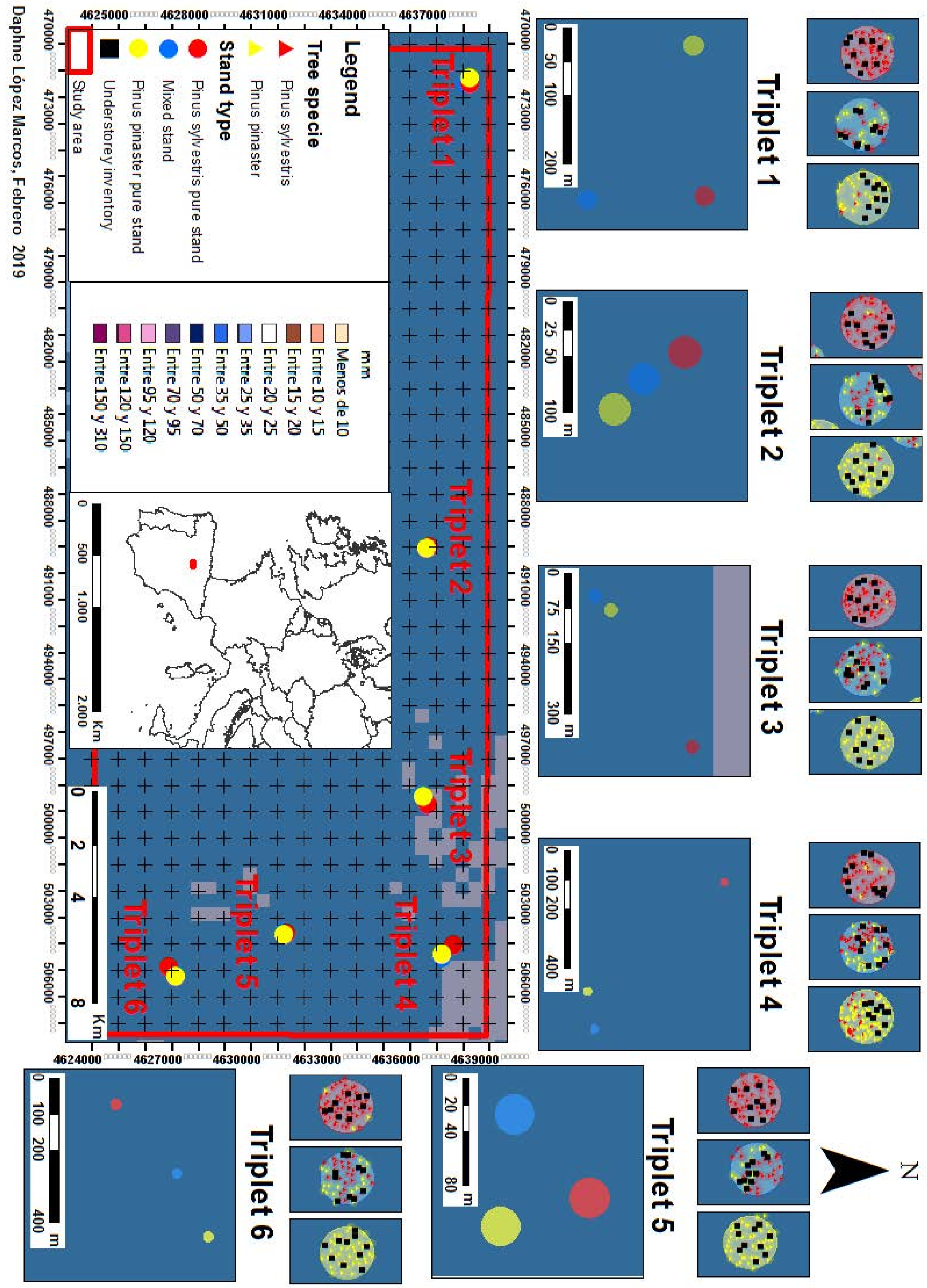


Figure 54. Mean annual rainfall in the study area according to the Köppen (1936) classification for the Iberian Peninsula published by the 'Atlas Agroclimático de Castilla y León-ITACYL-AEMET'.

Soils

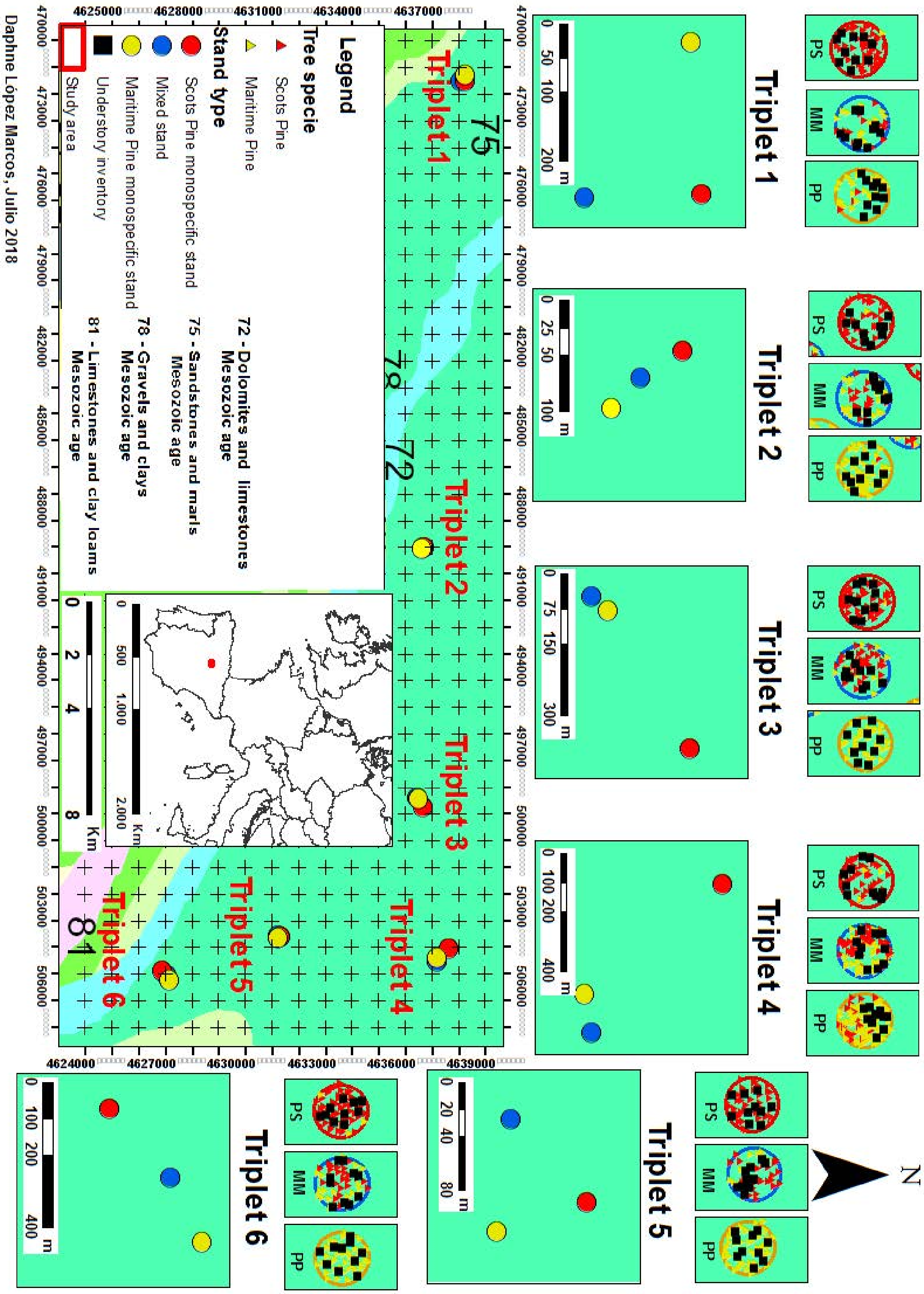


Figure 55. Geological map of the study area according to the classification published by the IGME (2015), (scale 1:1M).

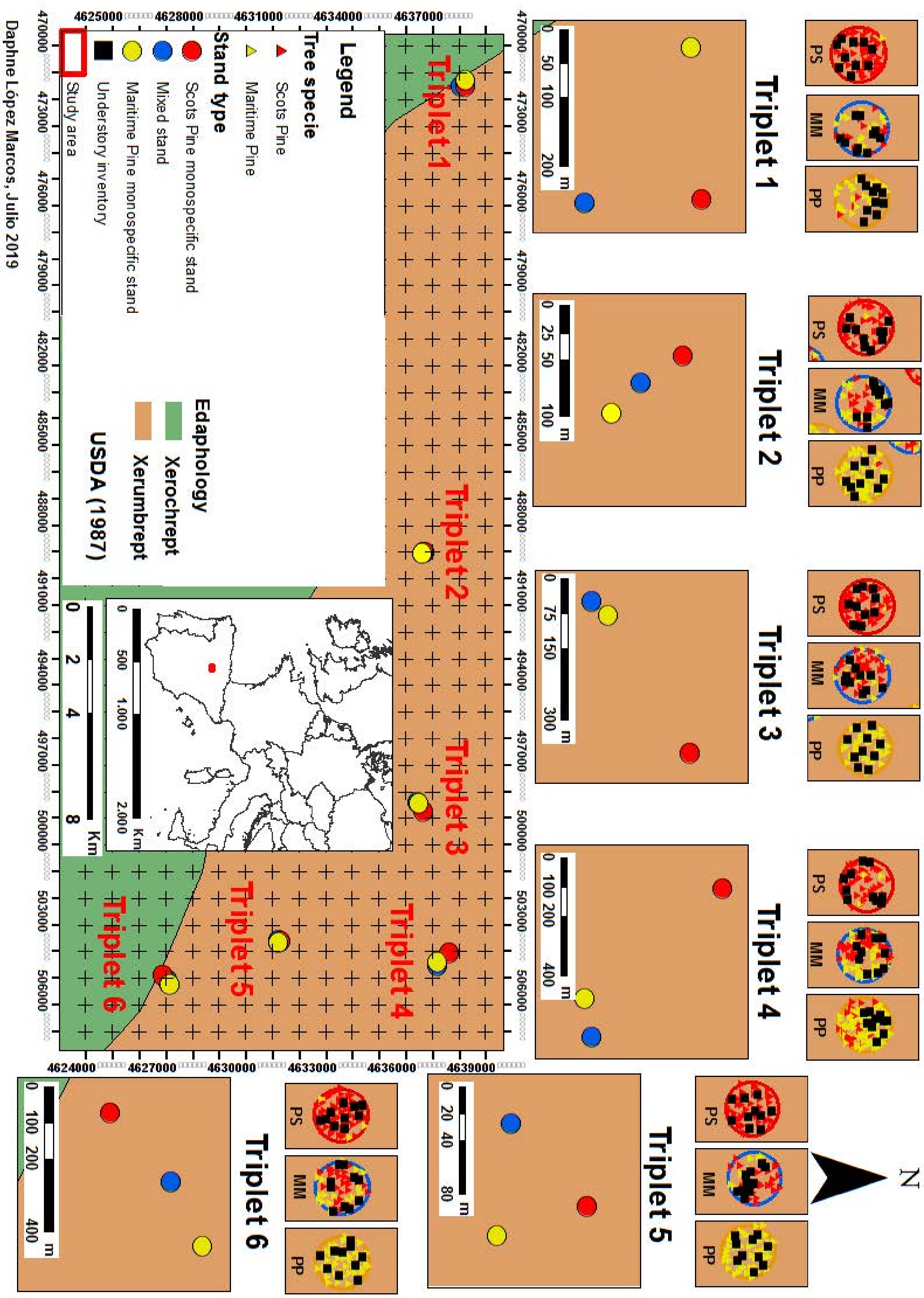


Figure 56. Map of soils in the study area according to IRNASA-CSIC (2012), scale 1/500.000.

Vegetation

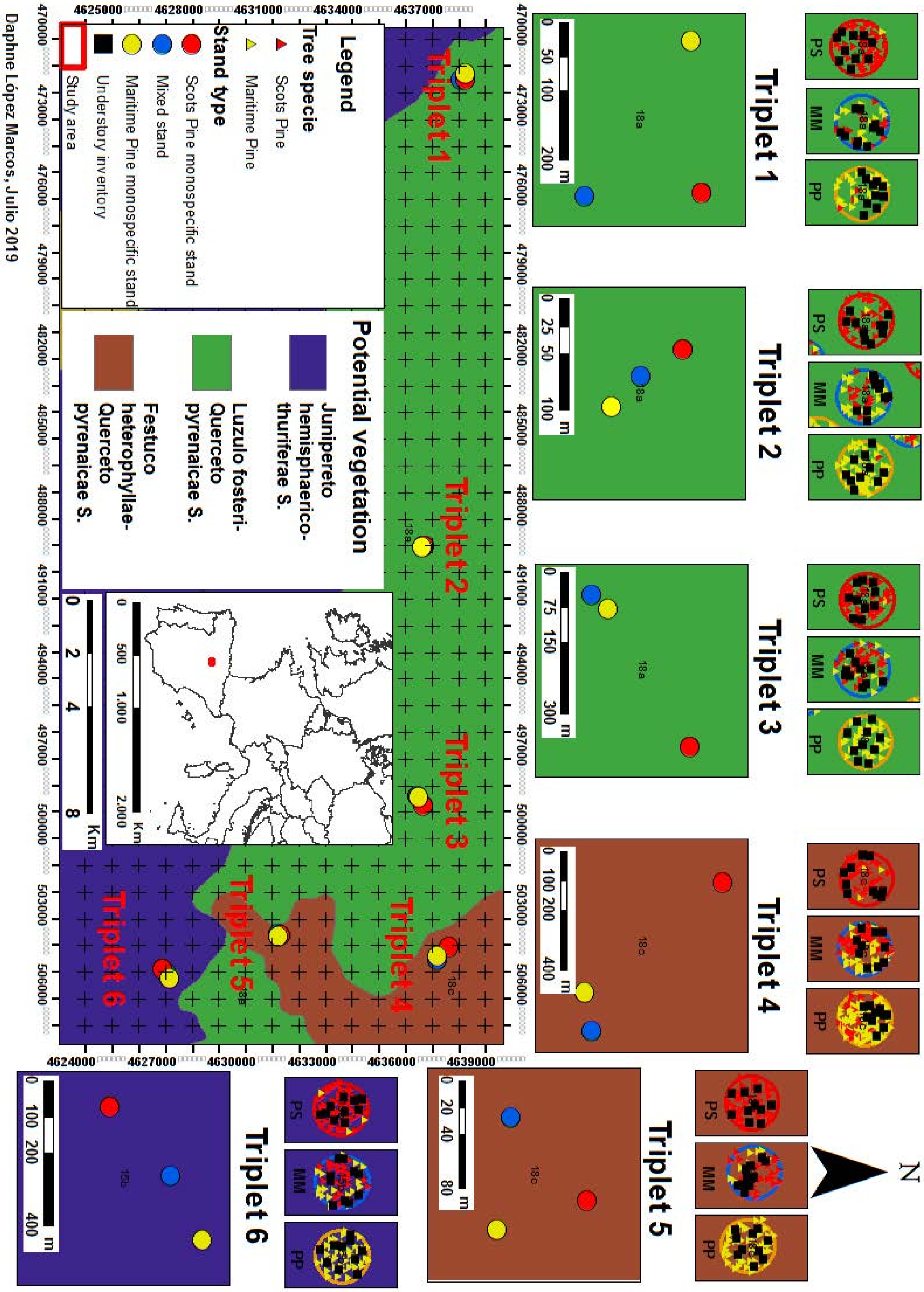


Figure 57. Potential vegetation of the study area according to the map of vegetation series of Spain (Rivas-Martínez 1987) scale 1/400.000.

Table 34. Current vegetation. General stand characteristics for monospecific stands of *Pinus sylvestris* (PS), monospecific stands of *Pinus pinaster* (PP) and mixed stands (MM), i.e. N: stems per hectare, G: basal area per hectare, Ho: dominant height, dq: quadratic mean diameter, Age: normal age.

		N (trees ha^{-1})			G (m^2 ha^{-1})			Dq (cm)			Ho (m)			Age (years)	
Triplet	Plot	Total	Scots	Maritime	Total	Scots	Maritime	Total	Scots	Maritime	Total	Scots	Maritime	Scots	Maritime
	PS	821.0	806.0	14.0	54.2	50.7	3.6	28.0±1.2	27.8±1.1	56.7±0.0	17.0±0.3	17.1±0.3	16.2±0.0	100	0
1	MM	523.0	241.0	283.0	53.0	19.9	33.1	32.3±1.6	32.3±2.0	40.3±2.2	18.0±0.4	17.5±0.6	18.5±0.3	118	113
	PP	566.0	57.0	509.0	59.4	1.2	58.2	36.2±1.7	15.8±2.2	38.6±1.3	17.3±0.5	10.8±1.8	18.0±0.3	0	118
	PS	509.3	495.1	14.1	49.2	47.0	2.2	34.4±1.1	32.3±1.0	44.7±0.0	19.3±0.3	19.3±0.3	19.9±0.0	151	0
2	MM	693.2	325.4	367.8	58.2	19.2	38.9	31.6±1.2	26.4±1.6	36.4±1.3	16.4±0.4	14.5±0.6	18.1±0.3	117	93
	PP	806.4	14.1	792.2	67.9	0.1	67.8	32.0±1.2	9.7±0.0	32.4±1.1	16.3±0.3	7.0±0.0	16.5±0.2	0	78
	PS	665.0	651.0	14.0	47.7	45.5	2.3	27.5±1.8	27.2±1.8	45.3±0.0	18.5±0.8	18.4±0.8	24.5±0.0	105	0
3	MM	693.0	495.0	198.0	63.5	33.0	30.5	32.0±1.8	27.3±1.8	43.5±2.4	20.9±0.7	19.8±0.8	23.7±0.5	100	95
	PP	538.0	0.0	538.0	68.6	0.0	68.6	39.6±1.3	0.0±0.0	39.6±1.3	20.5±0.2	0.0±0.0	20.5±0.2	0	105
	PS	636.6	580.0	56.6	48.9	40.7	8.2	30.4±1.2	29.3±1.0	45.4±5.8	22.1±0.2	22.1±0.2	22.2±1.3	78	0
4	MM	1330.0	764.0	566.0	55.3	23.2	32.1	20.2±1.2	16.6±1.5	25.0±1.6	13.1±0.5	12.3±0.7	14.2±0.6	78	79
	PP	1429.0	283.0	1146.0	69.4	3.3	66.0	22.6±1.1	9.5±1.8	26.0±0.9	12.4±0.4	7.3±0.9	13.6±0.3	0	80
	PS	651.0	651.0	0.0	54.9	54.9	0.0	32.4±1.2	32.4±1.2	0.0±0.0	21.8±0.3	21.8±0.3	0.0±0.0	121	0
5	MM	552.0	354.0	198.0	68.2	45.9	22.3	39.4±0.8	40.3±1.1	37.6±1.1	24.6±0.3	24.3±0.2	25.0±0.6	109	118
	PP	722.0	0.0	722.0	70.3	0.0	70.3	34.9±0.9	0.0±0.0	34.9±0.9	19.5±0.3	0.0±0.3	19.5±0.3	0	115
	PS	821.0	778.0	42.0	33.3	30.8	2.6	22.5±0.5	22.2±0.4	27.7±0.3	16.8±0.2	16.6±0.1	19.5±1.0	44	0
6	MM	679.0	396.0	283.0	33.3	13.0	20.2	24.2±0.9	20.2±0.6	29.8±1.1	14.8±0.2	14.0±0.3	15.9±0.2	44	49
	PP	594.2	0.0	594.2	37.5	0.0	37.5	28.2±0.7	0.0±0.0	28.2±0.7	15.6±0.2	0.0±0.0	15.6±0.2	0	49

Plots' description

*** Site description**: Author, Date; Weather; Soil climate (moisture and temperature soil regime and soil type according to Soil-Survey-Staff (2014)); Location (Province, Town, Place, Coordinates according to ETRS 1989 UTM Zone 30N, Altitude, Stepness and Orientation); Soil (Parent material and geological age according to IGME (2015) and Soil type according to Soil-Survey-Staff (2014)); and Vegetation (Potential vegetation according to Rivas-Martínez (1987) and Current vegetation according to WMS service of MAPAMA http://wms.mapama.es/sig/Biodiversidad); **Overstory description:** N (stems per hectare), G (basal area per hectare), DHB (quadratic mean diameter), Ho (dominant height), Age (normal age) and SI (site index) for *Pinus sylvestris* L. according to Rojo and Montero (1999) and for *Pinus pinaster* Aiton. according to Bravo et al. (2007) related at age 100 for total plot (plot) and only for *Pinus sylvestris* trees (Ps) or *Pinus pinaster* trees (Pp). **Understory vegetation:** cover percentage of Litter, Vascular plants and Bryophytes, and More abundant understory vegetation.

**** Climatic description** (rainfall and mean temperature in different months: J: January; F: February; M: March; A: April; My: May; Jn: June; Jl: July; A: August; S: September; O: October; N: November; D: December; X_{rain}: accumulated rainfall; $X_{temperature}$: anual mean temperature) according to 'Atlas Agroclimático de Castilla y León-ITACYL-AEMET'; **Leaf litter description**: Biomass (total litter biomass); Thickness (thickness of litter biomass); Composition (litter composition according to Van Delft et al. (2006), i.e. Fresh: % of fresh leaf litter; Fragmented :% of fragmented leaf litter and Humidified: % of humidified leaf litter); **Horizons' description**: Colour: wet matrix colour (Value/Chroma); Thickness: thickness of each horizon.

*****Analytic data**: Texture (sand/silt/clay: % of sand, silt and clay determined by the pipette method (MAPA 1994) according to Soil-Survey-Staff (2014); Stones: coarse soil material (> 2 mm); bulk and real density, pH (H_2O) and EC (electrical conductivity) according to (MAPA 1994); Pav (available phosphorus) according to (Olsen and Sommers 1982);TN (total nitrogen) and TOC (total carbon) analyzed with a LECO-CHN 2000 elemental analyzer; oxC (easily oxidizable carbon) according to Walkley (1947); Cmic (microbial biomass using the fumigation-extraction method (Vance et al. 1987); Cmin (mineralizable carbon according to Isermeyer (1952)); CEC (cation exchange capacity according to Mehlich (1953), exchangeable cations (Na^+, K^+, Ca^{++} and Mg^{++}) by means of extracting with 1N ammonium acetate (pH=7) (Schollenberger and Simon 1945), SB (sum of bases); FC (field capacity); PWP (permanent wilting point) and AW (available water) according to MAPA (1994) and WHC (water holding capacity accorging to López-Marcos et al. (2019)).

****** Map of stems position:** in these maps you can inside each plot (PS: big red circles - *Pinus sylvestris* monospecific stands; PP: big yellow circles - *Pinus pinaster* monospecific stands; MM: big blue circles - Mixed stands) see the position of the trees stem (circles of different sizes depending on the diameter of each tree: *Pinus sylvestris* in red and *Pinus pinaster* in yellow), the position of the understory vegetation inventories (1mx1m little black squares) and the position of the small-scale overstory inventories (4m radio black circles).

Triplet 1

Table 35. Pit description of plot PS01 (monospecific stand of *Pinus sylvestris* in triplet 01). Site, overstory and understory description, and pictures of the plot and the pit soil profile. *

Plot PS01		Triplet 01	Monospecific stand of *Pinus sylvestris* L.
Site description			
Author		Daphne López Marcos y Luis Alfonso Ramos Calvo	
Date		12/06/2016	
Weather		Sunny / Rain in the last 24 hours	
Soil climate	Moisture regime	Xeric	
	Temperature regime	Mesic	
Location	Province	Burgos	
	Town	Mamolar	
	Place	Mata Blanca	
	Coordinates (UTM) X	30T 471507	
	Coordinates (UTM) Y	4638240	
	Altitude	1146 m	
	Stepness	6.60%	
	Orientation	48.3°	
Soil	Parent material	Sandstones and Marls	
	Geologic age	Mesozoic	
	Soil type	Typic Dystroxerept	
Vegetation	Potential	*Luzulo forsteri-Querceto pyrenaicae S.*	
	Current	*Pinus sylvestris* L.	

Overstory description

	N (tres ha^{-1})			G (m^2 ha^{-1})			DHB (cm)			Ho (m)			Age (years)		SI	
	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	Ps	Pp	Ps	Pp
PS01	821	806	14	54.2	50.7	3.6	29.0	28.3	56.7	18.7	18.7	16.2	100	0	20	0

Understory vegetation

Cover (%)		More abundant understory vegetation
Litter	5	*Erica australis, Hypnum* spp.*, Juniperus oxycedrus* and *Deschampsia flexuosa*
Vascular plants	72	
Bryophytes	23	

Pictures

Plot	Pit soil profile
	

Table 36. Pit description of plot PS01 (monospecific stand of *Pinus sylvestris* L. in triplet 01): Climatic data, profile description including organic (leaf litter) and mineral horizons (Horizons). **

Climatic description													
Month	J	F	M	A	My	Jn	Jl	Ag	S	O	N	D	X
Rainfall (mm)	64	50	42	72	75	46	27	21	39	80	78	75	684
Temperature (ºC)	2.0	3.1	5.9	7.4	11.0	15.7	18.8	18.7	15.1	10.3	5.7	3.0	9.8

Leaf litter description					
Biomass (Mg ha^{-1})	Thickness (cm)	Composition (%)	Fresh	Fragmented	Humified
18.2	0.8		42	31	27

Horizons' description				
Horizon	Thickness (cm)	Colour		Description
		Wet	Dry	
Ah	0-10	10YR 2/2	10YR 4/2	Water status: slightly moist. Mottle: non-existent. Rock Fragments: few fine gravelly, Shape-spherical. Soil Texture: Loam. Soil Structure: moderate, granular. Consistence: friable, Slightly sticky and moderately plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: common fine roots and few coarse roots. No soil crusts. Horizon boundary: smooth and gradual.
AB	10-40	7.5YR4/6	10YR6/4	Water status: slightly moist. Mottle: non-existent. Rock Fragments: few fine gravelly, Shape-spherical. Soil Texture: Loam. Soil Structure: moderate, granular. Consistence: friable, Slightly sticky and plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: few fine roots and common coarse roots. No soil crusts. Horizon boundary: smooth and gradual.
Bw	40-60+	5YR4/6	7.5YR5/6	Water status: slightly moist. Mottle: non-existent. Rock Fragments: few fine gravelly, Shape-spherical. Soil Texture: Caly. Soil Structure: moderate, granular. Consistence: friable, Slightly sticky and plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: few fine roots and common coarse roots. No soil crusts.

Table 37. Pit description of plot PS01 (monospecific stand of *Pinus sylvestris* L. in triplet 01): analytic data of the mineral horizons. ***

Analytic data

Horizons	Texture (%)			Stones	Density (g cm^{-3})		Porosity
	Sand	Silt	Clay	(%)	Bulk	Real	(%)
Ah	50.67	36.11	9.97	2.25	0.50	1.77	72.02
AB	35.45	39.36	16.53	24.61	1.00	2.45	59.11
Bw	34.42	31.15	22.79	33.20	1.30	2.51	48.23

Horizons	pH (H_2O)	EC (dS m^{-1})	Pav (mg kg^{-1})	TN (mg g^{-1})	C properties (mg g^{-1})			
					TOC	oxC	Cmic	Cmin
Ah	4.2	157.5	7.0	2.61	78.2	88.2	0.11	0.99
AB	4.8	123.5	2.7	0.38	10.7	13.4	-	-
Bw	4.8	125.0	3.5	0.23	5.9	11.3	-	-

Horizons	Exchangeable cations (cmol^{+} kg^{-1})					
	CEC	Na^{+}	K^{+}	Ca^{++}	Mg^{++}	SB
Ah	26.2	1.0	0.3	6.1	1.3	8.7
AB	19.6	0.9	0.2	2.2	0.7	4.0
Bw	16.5	0.9	0.2	2.7	0.9	4.7

Horizons	Water properties			
	FC (%)	PWP (%)	AW (%)	WHC (g cm^{-2})
Ah	41.58	37.10	4.48	0.22
AB	32.12	12.33	19.79	4.49
Bw	19.22	6.85	12.37	1.07

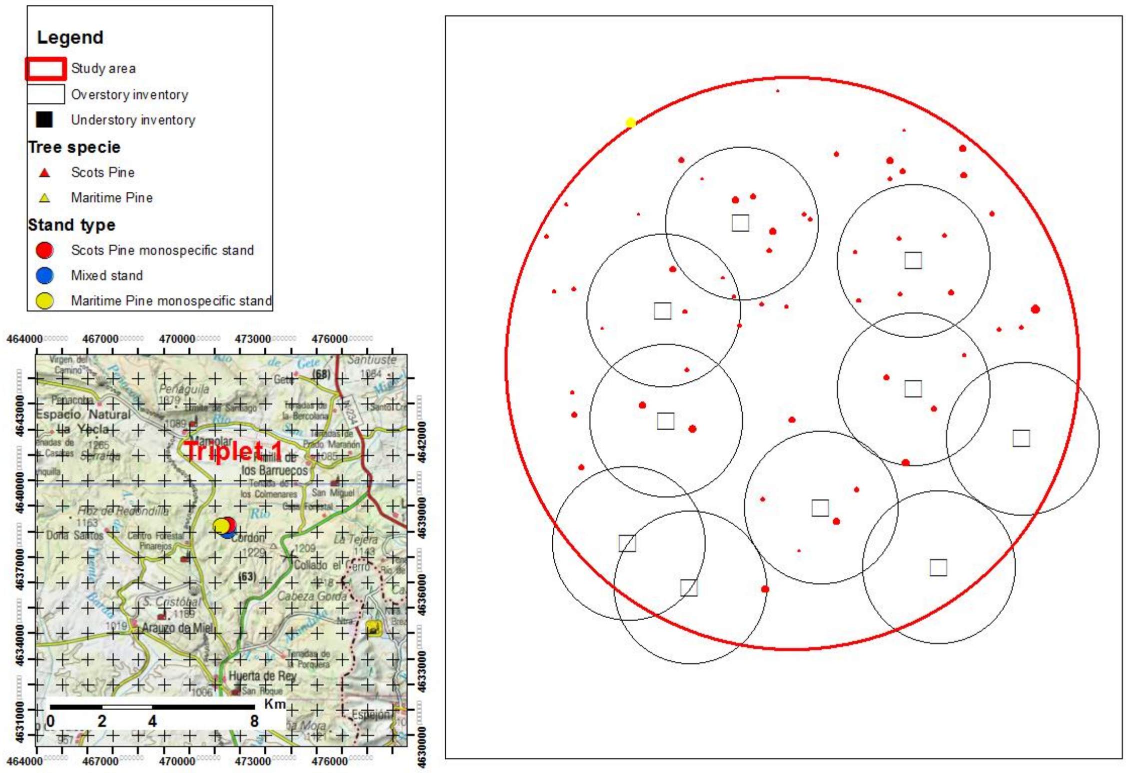


Figure 58. Map of stems position in plot PS01 (monospecific stand of *Pinus sylvestris* L. in triplet 01)****

Table 38. Pit description of plot PP01 (monospecific stand of *Pinus pinaster* Ait. in triplet 01). Site, overstory and understory description, and pictures of the plot and the pit soil profile. *

Plot PP01			Triplet 01	Monospecefic stand of *Pinus pinaster Aiton.*
Site description				
Author			Daphne López Marcos y Luis Alfonso Ramos Calvo	
Date			12/06/2016	
Weather			Sunny / Rain in the last 24 hours	
Soil climate	Moisture regime		Xeric	
	Temperature regime		Mesic	
Location	Province		Burgos	
	Town		Mamolar	
	Place		Mata Blanca	
	Coordinates (UTM)	X	30T 471283	
		Y	4638224	
	Altitude		1154 m	
	Stepness		6.20%	
	Orientation		23.4°	
Soil	Parent material		Sandstones and Marls	
	Geologic age		Mesozoic	
	Soil type		Typic Dystroxerept	
Vegetation	Potential		*Luzulo forsteri-Querceto pyrenaicae S*	
	Current		*Pinus pinaster* Ait.	

Overstory description

	N (trees ha^{-1})			G (m^2 ha^{-1})			DHB (cm)			Ho (m)			Age (years)		SI	
	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	Ps	pp	Ps	Pp
PP01	566	57	509	59.4	1.2	58.2	36.6	16.2	38.1	19.2	10.8	19.2	0	118	0	20

Understory vegetation

Cover (%)		More abundant understory vegetation
Litter	21	*Erica australis, Hypnum* spp. and *Deschampsia flexuosa*
Vascular plants	60	
Bryophytes	19	

Pictures

Plot	Pit soil profile
	

Table 39. Pit description of plot PP01 (monospecific stand of *Pinus pinaster* Ait. in triplet 01): Climatic data, profile description including organic (leaf litter) and mineral horizons (Horizons).**

Climatic description													
Month	J	F	M	A	My	Jn	Jl	Ag	S	O	N	D	X
Rainfall (mm)	64	50	42	72	75	46	27	21	39	80	78	75	684
Temperature (ºC)	2.0	3.1	5.9	7.4	11.0	15.7	18.8	18.7	15.1	10.3	5.7	3.0	9.8

Leaf litter description					
Biomass (Mg ha^{-1})	Thickness (cm)	Composition (%)	Fresh	Fragmented	Humified
8.6	0.5		35.0	29.0	36.0

Horizon description				
Horizon	Thickness (cm)	Colour Wet	Colour Dry	Description
Ah	0-15	10YR3/2	10YR5/3	Water status: slightly moist. Mottle: non-existent. Rock Fragments: few fine gravelly, Shape-spherical. Soil Texture: Loam. Soil Structure: moderate, granular. Consistence: friable, Slightly sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: common fine roots and few coarse roots. No soil crusts. Horizon boundary: smooth and gradual.
AB	15-30	10YR4/4	10YR6/4	Water status: slightly moist. Mottle: non-existent. Rock Fragments: few fine gravelly, Shape-spherical. Soil Texture: Loam. Soil Structure: moderate, granular. Consistence: friable, sticky and plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: few fine roots and common coarse roots. No soil crusts. Horizon boundary: smooth and gradual.
Bw	30-60+	5YR4/6	5YR5/6	Water status: slightly moist. Mottle: non-existent. Rock Fragments: few fine gravelly, Shape-spherical. Soil Texture: Clay. Soil Structure: moderate, blocky. Consistence: friable, very sticky and very plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: few fine roots and common coarse roots. No soil crusts.

Table 40. Pit description of plot PP01 (monospecific stand of *Pinus pinaster* Ait. in triplet 01): analytic data of the mineral horizons.***

Analytic data

Horizons	Texture (%)			Stones (%)	Density (g cm^{-3})		Porosity (%)
	Sand	Silt	Clay		Bulk	Real	
Ah	52.22	34.47	13.47	3.14	0.72	1.92	62.45
AB	47.62	36.67	14.06	34.12	1.07	2.29	53.47
Bw	14.86	31.32	52.14	38.09	1.15	2.65	56.71

Horizons	pH (H_2O)	EC (dS m^{-1})	Pav (mg kg^{-1})	TN (mg g^{-1})	C properties (mg g^{-1})			
					TOC	oxC	Cmic	Cmin
Ah	4.7	137.0	3.1	1.88	61.9	47.6	0.08	0.96
AB	5.2	105.5	2.8	0.64	21.6	23.1	-	-
Bw	4.8	133.0	1.7	0.25	5.4	11.6	-	-

Horizons	Exchangeable cations ($cmol^{+}$ kg^{-1})					
	CEC	Na^{+}	K^{+}	Ca^{++}	Mg^{++}	SB
Ah	21.3	0.9	0.2	4.9	1.4	7.4
AB	28.7	0.8	0.2	3.7	1.1	5.8
Bw	22.2	1.0	0.3	5.0	1.6	7.9

Horizons	Water properties			
	FC (%)	PWP (%)	AW (%)	WHC (g cm^{-2})
Ah	31.85	17.98	13.87	1.46
AB	29.34	11.29	18.04	1.90
Bw	23.83	16.93	6.90	0.98

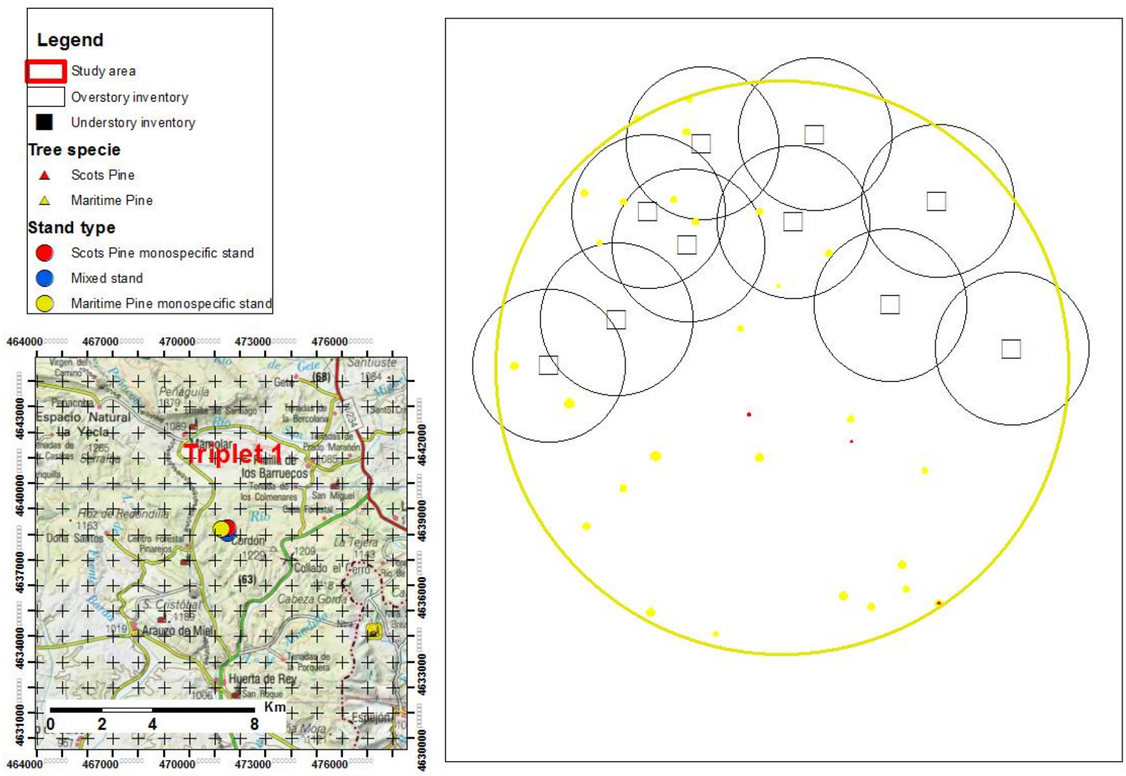


Figure 59. Map of stems position in plot PP01 (monospecefic stand of *Pinus pinaster* Ait. in triplet 01)****.

Table 41. Pit description of plot MM01 (mixed stand of *Pinus sylvestris* L. and *Pinus pinaster* Ait. in triplet 01). Site, overstory and understory description, and pictures of the plot and the pit soil profile. *

Plot MM01			Triplet 01	Mixed stand
Site description				
Author			Daphne López Marcos y Luis Alfonso Ramos Calvo	
Date			12/06/2016	
Weather			Sunny / Rain in the last 24 hours	
Soil climate	Moisture regime		Xeric	
	Temperature regime		Mesic	
Location	Province		Burgos	
	Town		Mamolar	
	Place		Mata Blanca	
	Coordinates (UTM)	X	30T 471283	
		Y	4638224	
	Altitude		1154 m	
	Stepness		6.20%	
	Orientation		23.4°	
Soil	Parent material		Sandstones and Marls	
	Geologic age		Mesozoic	
	Soil type		Typic Humixerept	
Vegetation	Potential		*Luzulo forsteri-Querceto pyrenaicae S.*	
	Current		*Pinus sylvestris* L. y *Pinus pinaster* Ait.	

Overstory description

Forest	N (trees ha^{-1})			G (m^2 ha^{-1})			DHB (cm)			Ho (m)			Age (years)		SI	
	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	Ps	Pp	Ps	pp
MM03	523	241	283	53.0	19.9	33.1	35.9	32.5	38.6	17.8	18.1	18.1	118	113	17	16

Understory vegetation

Cover (%)		More abundant understory vegetation
Litter	42.5	*Erica australis, Hypnum* spp. and *Deschampsia flexuosa*
Vascular plants	45	
Bryophytes	13	

Pictures

Plot	Pit soil profile
	

Table 42. Pit description of plot MM01 (mixed stand of *Pinus sylvestris* L. and *Pinus pinaster* Ait. in triplet 01): Climatic data, profile description including organic (leaf litter) and mineral horizons (Horizons).**

<table>
<tr><th colspan="14">Climatic description</th></tr>
<tr><td>Month</td><td>J</td><td>F</td><td>M</td><td>A</td><td>My</td><td>Jn</td><td>Jl</td><td>Ag</td><td>S</td><td>O</td><td>N</td><td>D</td><td>X</td></tr>
<tr><td>Rainfall (mm)</td><td>64</td><td>50</td><td>42</td><td>72</td><td>75</td><td>46</td><td>27</td><td>21</td><td>39</td><td>80</td><td>78</td><td>75</td><td>684</td></tr>
<tr><td>Temperature (ºC)</td><td>2.0</td><td>3.1</td><td>5.9</td><td>7.4</td><td>11.0</td><td>15.7</td><td>18.8</td><td>18.7</td><td>15.1</td><td>10.3</td><td>5.7</td><td>3.0</td><td>9.8</td></tr>
</table>

<table>
<tr><th colspan="6">Leaf litter description</th></tr>
<tr><td>Biomass (Mg ha^{-1})</td><td>Thickness (cm)</td><td rowspan="2">Composition (%)</td><td>Fresh</td><td>Fragmented</td><td>Humified</td></tr>
<tr><td>28.2</td><td>1.7</td><td>62.0</td><td>23.0</td><td>15.0</td></tr>
</table>

<table>
<tr><th colspan="5">Horizon description</th></tr>
<tr><td rowspan="2">Horizon</td><td rowspan="2">Thickness (cm)</td><td colspan="2">Colour</td><td rowspan="2">Description</td></tr>
<tr><td>Wet</td><td>Dry</td></tr>
<tr><td>Ah</td><td>0-35</td><td>10YR3/2</td><td>10YR5/3</td><td>Water status: slightly moist. Mottle: non-existent. Rock Fragments: few fine gravelly, Shape-spherical. Soil Texture: Loam. Soil Structure: moderate, granular. Consistence: friable, sticky and plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: common fine roots and few coarse roots. No soil crusts. Horizon boundary: smooth and gradual.</td></tr>
<tr><td>Bw</td><td>35-75 +</td><td>5YR5/8</td><td>7.5YR6/6</td><td>Water status: slightly moist. Mottle: non-existent. Rock Fragments: few fine gravelly, Shape-spherical. Soil Texture: Loam. Soil Structure: moderate, blocky. Consistence: friable, sticky and plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: few roots and common coarse roots. No soil crusts.</td></tr>
</table>

Table 43. Pit description of plot MM01 (mixed stand of *Pinus sylvestris* L. and *Pinus pinaster* Ait. in triplet 01): analytic data of the mineral horizons.***

Analytic data

Horizons	Texture (%)			Stones (%)	Density ($g\ cm^{-3}$)		Porosity (%)
	Sand	Silt	Clay		Bulk	Real	
Ah	43.49	46.29	10.73	15.79	1.12	2.77	59.60
Bw	24.49	33.37	31.01	34.80	1.52	2.44	37.76

Horizons	pH (H_2O)	EC ($dS\ m^{-1}$)	Pav ($mg\ kg^{-1}$)	TN ($mg\ g^{-1}$)	C properties ($mg\ g^{-1}$)			
					TOC	oxC	Cmic	Cmin
Ah	5.3	102.5	4.0	1.62	40.3	39.7	0.09	0,94
Bw	4.8	130.0	1.6	0.28	3.9	10.2	-	-

Horizons	Exchangeable cations ($cmol^+\ kg^{-1}$)					
	CEC	Na^+	K^+	Ca^{++}	Mg^{++}	SB
Ah	22.4	0.9	0.3	4.6	1.3	7.0
Bw	14.6	1.1	0.1	2.2	1.1	4.5

Horizons	Water properties			
	FC (%)	PWP (%)	AW (%)	WHC ($g\ cm^{-2}$)
Ah	31.33	11.48	19.85	6.55
Bw	26.81	8.10	18.72	2.78

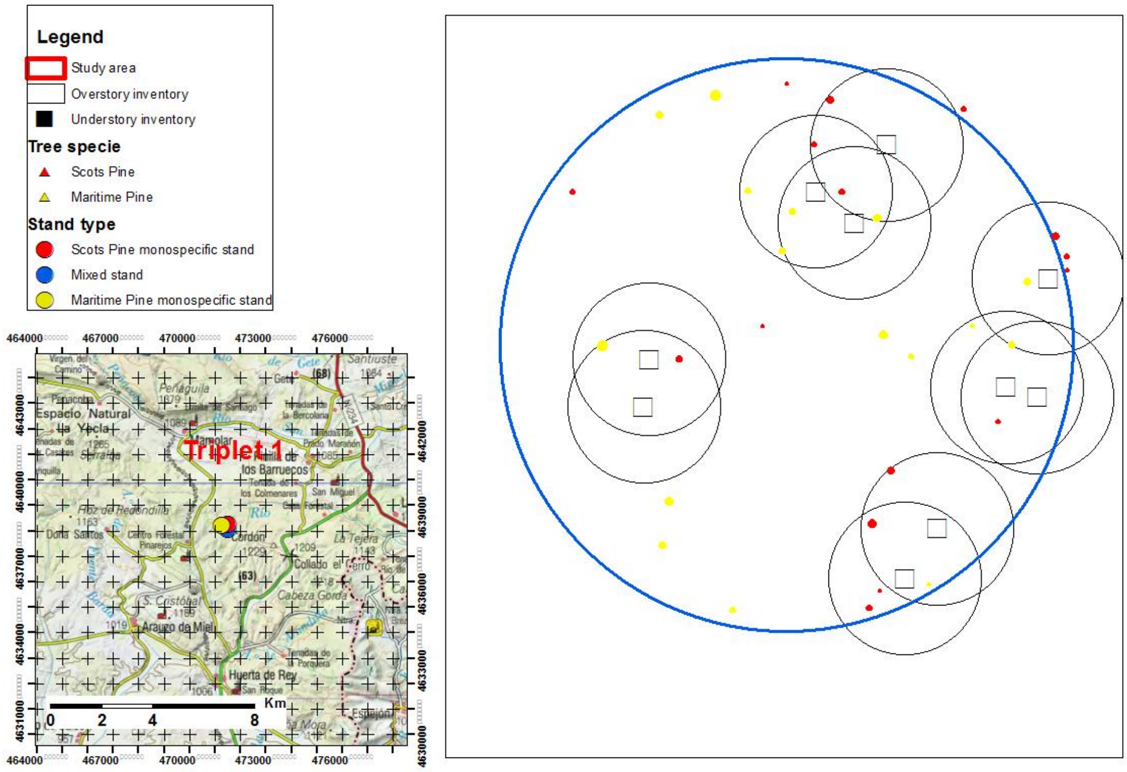


Figure 60. Map of stems position in plot MM01 (mixed stand of *Pinus sylvestris* L. and *Pinus pinaster* Ait. in triplet 01)****.

Triplet 2

Table 44. Pit description of plot PS02 (monospecific stand of *Pinus sylvestris* L. in triplet 02). Site, overstory and understory description, and pictures of the plot and the pit soil profile. *

Plot PS02			Triplet 02	Monospecific stand of *Pinus* sylvestris L.
Site description				
Author			Daphne López Marcos y Luis Alfonso Ramos Calvo	
Date			11/06/2016	
Weather			Sunny / Rain in the last 24 hours	
Soil climate	Moisture regime		Xeric	
	Temperature regime		Mesic	
Location	Province		Burgos	
	Town		Hontoria del Pinar	
	Place		Mata Robledo	
	Coordinates (UTM)	X	30T 489017	
		Y	4636684	
	Altitude		1173 m	
	Stepness		10,00%	
	Orientation		181°	
Soil	Parent material		Sandstones and Marls	
	Geologic age		Mesozoic	
	Soil type		Typic dystroxerept	
Vegetation	Potential		*Luzulo forsteri-Querceto pyrenaicae S.*	
	Current		*Pinus sylvestris* L.	

Overstory description

	N (trees ha^{-1})			G (m^2 ha^{-1})			DHB (cm)			Ho (m)			Age (years)		SI	
	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	Ps	Pp	Ps	Pp
PS02	509	495	14	49.24	47.02	2.22	35.1	34.8	44.6	20.2	20.24	19.9	151	0	20	0

Understory vegetation

Cover (%)		More abundant understory vegetation
Litter	56.8	*Pteridium aquilinum, Pinus sylvestris* (seedlings/saplings) and *Hypnum* spp.
Vascular plants	31.9	
Bryophytes	11.30	

Pictures

Plot	Pit soil profile
	

Table 45. Pit description of plot PS02 (monospecific stand of *Pinus sylvestris* L. in triplet 02): Climatic data, profile description including organic (leaf litter) and mineral horizons (Horizons). **

Climatic description													
Month	J	F	M	A	My	Jn	Jl	Ag	S	O	N	D	X
Rainfall (mm)	72	59	49	75	81	48	29	27	40	85	82	80	757
Temperature (ºC)	1.7	2.5	5.2	7.6	11.3	15.0	18.1	17.6	14.1	9.5	5.0	2.7	9.2

Leaf litter description					
Biomass (Mg ha^{-1})	Thickness (cm)	Composition (%)	Fresh	Fragmented	Humified
27.2	2.5		34.0	39.0	27.0

Horizon description				
Horizon	Thickness (cm)	Colour		Description
		Wet	Dry	
Ah	0-15	10YR3/2	10YR 4/2	Water status: slightly moist. Mottle: non-existent. Rock Fragments: few fine gravelly, Shape-spherical. Soil Texture: Sand. Soil Structure: moderate, granular. Consistence: friable, slightly sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: common fine roots and few coarse roots. No soil crusts. Horizon boundary: smooth and gradual.
AC	15-35	10YR5/4	10YR7/3	Water status: slightly moist. Mottle: non-existent. Rock Fragments: few fine gravelly, Shape-spherical. Soil Texture: Sand. Soil Structure: Weak, granular. Consistence: very friable, slightly sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: few fine roots and common coarse roots. No soil crusts. Horizon boundary: smooth and gradual.
C	35-65+	10YR4/6	10YR6/6	Water status: slightly moist. Mottle: non-existent. Rock Fragments: few fine gravelly, Shape-spherical. Soil Texture: Sand. Soil Structure: Weak, granular. Consistence: very friable, slightly sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: few fine roots and many coarse roots. No soil crusts.

Table 46. Pit description of plot PS02 (monospecific stand of *Pinus sylvestris* L. in triplet 02): analytic data of the mineral horizons. ***

Analytic data								
Horizons	Texture (%)			Stones (%)	Density (g cm^{-3})		Porosity (%)	
	Sand	Silt	Clay		Bulk	Real		
Ah	75.1	15.4	5.8	7.90	1.15	2.21	47.89	
AC	78.9	10.2	8.3	11.83	1.23	2.58	52.10	
C	77.3	10.0	10.5	8.39	1.18	2.36	50.17	
Horizons	pH (H_2O)	EC (dS m^{-1})	Pav (mg kg^{-1})	TN (mg g^{-1})	C properties (mg g^{-1})			
					TOC	oxC	Cmic	Cmin
Ah	3.9	173.0	4.1	2.04	49.06	36.4	0.09	0.93
AC	4.2	156.0	3.4	0.50	8.74	18.9	-	-
C	4.8	124.5	4.7	0.46	8.8	16.0	-	-
Horizons	Exchangeable cations ($cmol^+$ kg^{-1})							
	CEC	Na^+	K^+	Ca^{++}	Mg^{++}	SB		
Ah	23.2	0.9	0.1	3.2	0.5	4.7		
AC	11.0	0.9	0.1	1.0	0.4	2.3		
C	9.9	0.8	0.1	1.1	0.4	2.4		
Horizons	Water properties							
	FC (%)	PWP (%)	AW (%)	WHC (g cm^{-2})				
Ah	29.7	9.77	19.92	3.17				
AC	17.3	2.49	14.84	3.23				
C	15.4	2.76	12.61	2.04				

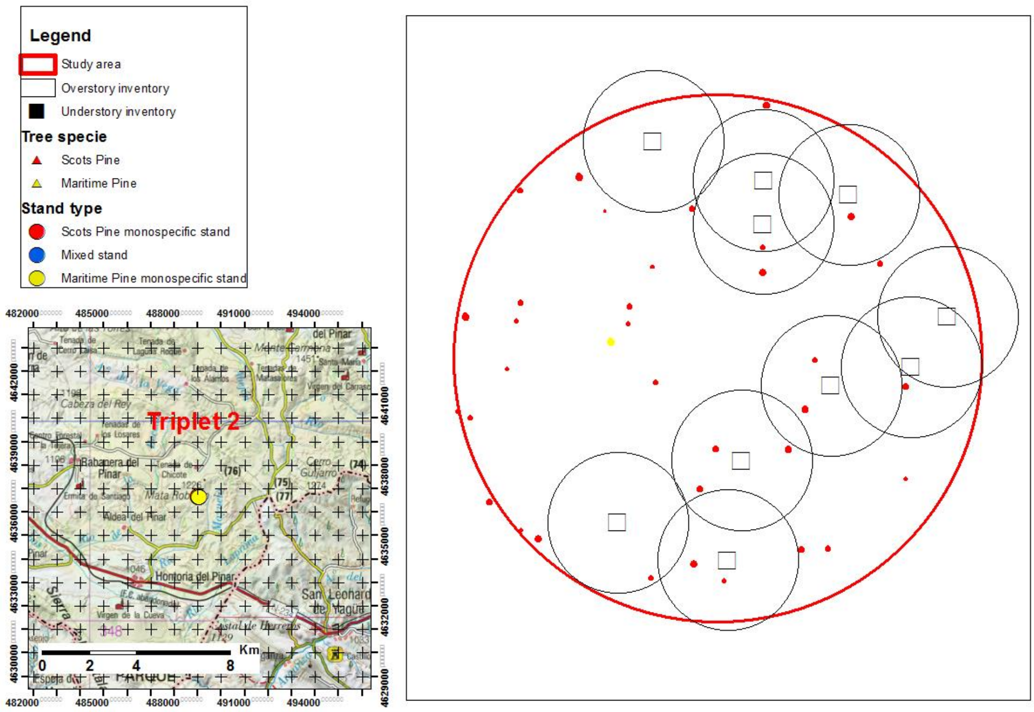


Figure 61. Map of stems position in plot PS02 (monospecific stand of *Pinus sylvestris* L. in triplet 02)****.

Table 47. Pit description of plot PP02 (monospecific stand of *Pinus pinaster* Aiton. in triplet 02). Site, overstory and understory description, and pictures of the plot and the pit soil profile. *

Plot PP02			Triplet 02	Monospecific stand of *Pinus* pinaster Aiton.
Site description				
Author			Daphne López Marcos y Luis Alfonso Ramos Calvo	
Date			11/06/2016	
Weather			Sunny / Rain in the last 24 hours	
Soil climate	Moisture regime		Xeric	
	Temperature regime		Mesic	
Location	Province		Burgos	
	Town		Hontoria del Pinar	
	Place		Mata Robledo	
	Coordinates (UTM)	X	30T 489069	
		Y	4636620,00	
	Altitude		1144 m	
	Stepness		7.00%	
	Orientation		166°	
Soil	Parent material		Sandstones and Marls	
	Geologic age		Mesozoic	
	Soil type		Typic humixerept	
Vegetation	Potential		*Luzulo forsteri-Querceto pyrenaicae S.*	
	Current		*Pinus pinaster* Ait.	

Overstory description

	N (trees ha^{-1})			G ($m^2 ha^{-1}$)			DHB (cm)			Ho (m)			Age (years)		SI	
	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	Ps	Pp	Ps	Pp
PP02	806	14	792	67.9	0.1	67.8	32.7	9.6	33.	17.94	7.0	17.9	0	78	0	20

Understory vegetation

Cover (%)			More abundant understory vegetation
Litter	76		*Cistus laurifolius, Erica australis, Calluna vulgaris* and *Deschampsia flexuosa*
Vascular plants	23		
Bryophytes	1		

Pictures

Plot	Pit soil profile
	

Table 48. Pit description of plot PP02 (monospecific stand of *Pinus pinaster* Ait. in triplet 02): Climatic data, profile description including organic (leaf litter) and mineral horizons (Horizons). **

<table>
<tr><th colspan="14">Climatic description</th></tr>
<tr><td>Month</td><td>J</td><td>F</td><td>M</td><td>A</td><td>My</td><td>Jn</td><td>Jl</td><td>Ag</td><td>S</td><td>O</td><td>N</td><td>D</td><td>X</td></tr>
<tr><td>Rainfall (mm)</td><td>72</td><td>59</td><td>49</td><td>75</td><td>81</td><td>48</td><td>29</td><td>27</td><td>40</td><td>85</td><td>82</td><td>80</td><td>757</td></tr>
<tr><td>Temperature (ºC)</td><td>1.7</td><td>2.5</td><td>5.2</td><td>7.6</td><td>11.3</td><td>15.0</td><td>18.1</td><td>17.6</td><td>14.1</td><td>9.5</td><td>5.0</td><td>2.7</td><td>9.2</td></tr>
</table>

<table>
<tr><th colspan="6">Leaf litter description</th></tr>
<tr><td>Biomass (Mg ha^{-1})</td><td>Thickness (cm)</td><td rowspan="2">Composition (%)</td><td>Fresh</td><td>Fragmented</td><td>Humified</td></tr>
<tr><td>21.70</td><td>2.50</td><td>32.00</td><td>19.00</td><td>49.00</td></tr>
</table>

<table>
<tr><th colspan="5">Horizon description</th></tr>
<tr><td rowspan="2">Horizon</td><td rowspan="2">Thickness (cm)</td><td colspan="2">Colour</td><td rowspan="2">Description</td></tr>
<tr><td>Wet</td><td>Dry</td></tr>
<tr><td>Ah</td><td>0-20</td><td>10YR2/1</td><td>10YR4/1</td><td>Water status: moist. Mottle: non-existent. Rock Fragments: many Shape-spherical grave. Soil Texture: Sand. Soil Structure: moderate, granular. Consistence: friable, slightly sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: common fine roots and few coarse roots. No soil crusts. Horizon boundary: smooth and gradual.</td></tr>
<tr><td>C</td><td>20-60+</td><td>10YR2/1</td><td>10YR7/4</td><td>Water status: moist. Mottle: non-existent. Rock Fragments: many Shape-spherical grave. Soil Texture: Sand. Soil Structure: weak, granular. Consistence: friable, slightly sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: few fine roots and commob coarse roots. No soil crusts.</td></tr>
<tr><td></td><td></td><td></td><td></td><td></td></tr>
</table>

Table 49. Pit description of plot PP02 (monospecific stand of *Pinus pinaster* Ait. in triplet 02): analytic data of the mineral horizons. ***

Analytic data

Horizons	Texture (%)			Stones (%)	Density (g cm^{-3})		Porosity (%)
	Sand	Silt	Clay		Bulk	Real	
Ah	63.93	16.27	11.37	31.84	0.93	2.20	57.73
C	71.93	10.30	12.96	21.66	1.40	2.12	33.83

Horizons	Ph (H_2O)	EC (dS/m)	Pav (mg kg^{-1})	TN (mg g^{-1})	C properties (mg g^{-1})			
					TOC	oxC	Cmic	Cmin
Ah	4.0	174.0	4.0	1.66	54.3	60.6	0.07	0.95
C	4.7	132.0	2.3	0.11	4.7	12.4	-	-

Horizons	Exchangeable cations ($cmol^{+}$ kg^{-1})					
	CEC	Na^{+}	K^{+}	Ca^{++}	Mg^{++}	SB
Ah	21.3	0.8	0.2	3.7	0.9	5.6
C	10.0	1.0	0.1	1.1	0.4	2.5

Horizons	Water properties			
	FC (%)	PWP (%)	AW (%)	WHC (g cm^{-2})
Ah	46.93	26.16	20.77	2.64
C	20.22	4.23	15.99	5.27

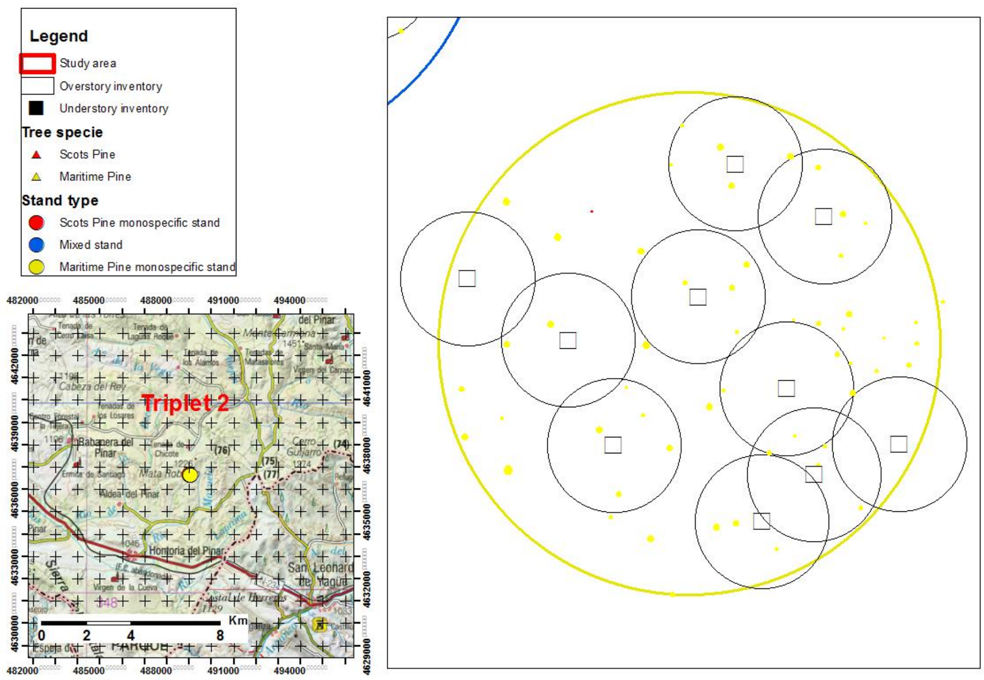


Figure 62. Map of stems position in plot PP02 (monospecific stand of *Pinus pinaster* Ait. in triplet 02)****.

Table 50. Pit description of plot MM02 (mixed stand of *Pinus sylvestris* L. and *Pinus pinaster* Ait. in triplet 02). Site, overstory and understory description, and pictures of the plot and the pit soil profile. *

Plot MM02			Triplet 02	Mixed stand
Site description				
Author			Daphne López Marcos y Luis Alfonso Ramos Calvo	
Date			11/06/2016	
Weather			Sunny / Rain in the last 24 hours	
Soil climate	Moisture regime		Xeric	
	Temperature regime		Mesic	
Location	Province		Burgos	
	Town		Hontoria del Pinar	
	Place		Mata Robledo	
	Coordinates (UTM)	X	30T 489042	
		Y	4636646,00	
	Altitude		1173 m	
	Stepness		10.00%	
	Orientation		181°	
Soil	Parentl material		Sandstones and Marls	
	Geologic age		Mesozoic	
	Soil type		Typic humixerept	
Vegetation	Potential		*Luzulo forsteri-Querceto pyrenaicae S.*	
	Current		*Pinus pinaster* Ait. and *Pinus silvestris* L.	

Overstory description

	N (trees ha^{-1})			G (m^2 ha^{-1})			DHB (cm)			Ho (m)			Age (years)		SI	
	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	Ps	Pp	Ps	Pp
MM02	693	325	367	58.2	19.2	39.0	32.7	27.4	36.7	19.6	15.9	19.6	117	93	20	20

Understory vegetation

Cover (%)		More abundant understory vegetation
Litter	81	*Pteridium aquilinum, Agrostis catellana* and *Pinus pinaster* (seedlings/saplings)
Vascular plants	19	
Bryophytes	1	

Pictures

Plot	Pit soil profile
	

Table 51. Pit description of plot MM02 (mixed stand of *Pinus sylvestris* L. and *Pinus pinaster* Ait. in triplet 02): Climatic data, profile description including organic (leaf litter) and mineral horizons (Horizons). **

Climatic description													
Month	J	F	M	A	My	Jn	Jl	Ag	S	O	N	D	X
Rainfall (mm)	72	59	49	75	81	48	29	27	40	85	82	80	757
Temperature (ºC)	1.7	2.5	5.2	7.6	11.3	15.0	18.1	17.6	14.1	9.5	5.0	2.7	9.2

Leaf litter description					
Biomass (Mg ha^{-1})	Thickness (cm)	Composition (%)	Fresh	Fragmented	Humified
27.20	2.50		34.00	39.00	27.00

Horizon description				
Horizon	Thickness (cm)	Colour		Description
		Wet	Dry	
Ah	0-23	10YR3/1	10YR5/2	Water status: moist. Mottle: non-existent. Rock Fragments: few, gravely, Shape-spherical. Soil Texture: Sand. Soil Structure: moderate, granular. Consistence: friable, slightly sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: common fine roots and few coarse roots. No soil crusts. Horizon boundary: smooth and gradual.
C	23-60+	10YR6/6	10YR7/4	Water status: moist. Mottle: non-existent. Rock Fragments: common, coarse gravely, Shape-spherical. Soil Texture: Sand. Soil Structure: weak, coarse granular. Consistence: friable, slightly sticky and plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: few fine roots and common coarse roots. No soil crusts.

Table 52. Pit description of plot MM02 (mixed stand of *Pinus sylvestris* L. and *Pinus pinaster* Ait. in triplet 02): analytic data of the mineral horizons. ***

Analytic data

Horizons	Texture (%)			Stones (%)	Density ($g\ cm^{-3}$)		Porosity (%)
	Sand	Silt	Clay		Bulk	Real	
Ah	65.86	10.94	12.58	5.21	1.11	2.18	48.95
C	68.68	14.04	14.92	8.33	1.30	2.48	47.74

Horizons	pH (H_2O)	EC ($dS\ m^{-1}$)	Pav ($mg\ kg^{-1}$)	TN ($mg\ g^{-1}$)	C properties ($mg\ g^{-1}$)			
					TOC	oxC	Cmic	Cmin
Ah	4.0	177.5	3.6	1.07	41.95	50.5	0.09	0.89
C	5.2	107.5	2.2	0.04	2.85	12.1	-	-

Horizons	Exchangeable cations ($cmol^+\ kg^{-1}$)					
	CEC	Na^+	K^+	Ca^{++}	Mg^{++}	SB
Ah	21.6	0.94	0.19	2.79	0.78	4.71
C	15.8	0.94	0.09	1.27	0.44	2.75

Horizons	Water properties			
	FC (%)	PWP (%)	AW (%)	WHC ($g\ cm^{-2}$)
Ah	40.25	24.97	15.28	3.71
C	18.68	2.58	16.10	5.17

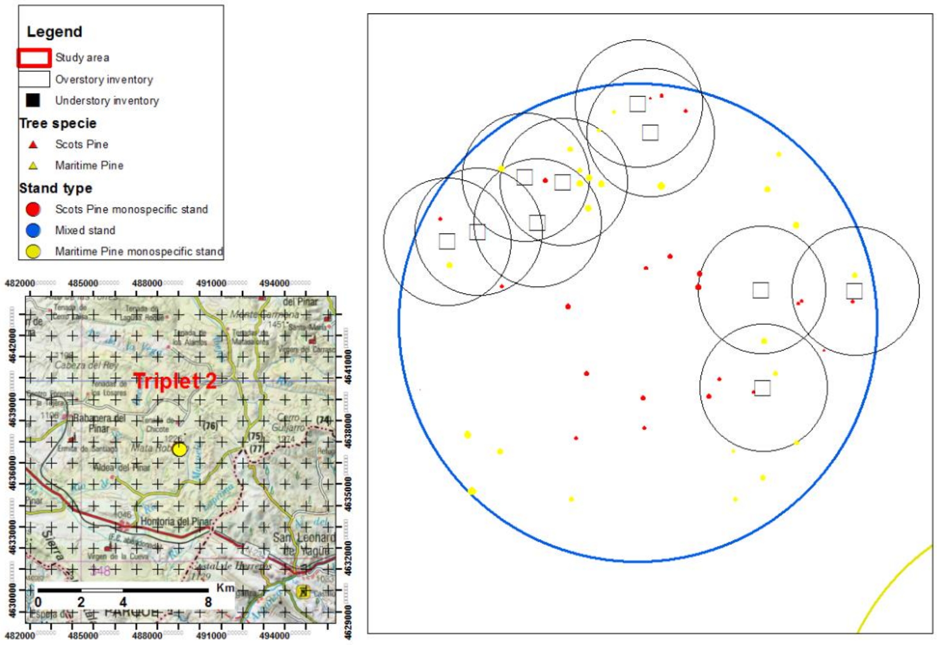


Figure 63. Map of stems position of plot MM02 (mixed stand of *Pinus sylvestris* L. and *Pinus pinaster* Ait. in triplet 02) ****

Triplet 3

Table 53. Pit description of plot PS03 (monospecific stand of *Pinus sylvestris* L. in triplet 03). Site, overstory and understory description, and pictures of the plot and the pit soil profile. *

Plot PS03			Triplet 03	Monospecific stand of *Pinus sylvestris* L.
Site description				
Author			Daphne López Marcos y Luis Alfonso Ramos Calvo	
Date			11/06/2016	
Weather			Sunny / Rain in the last 24 hours	
Soil climate	Moisture regime		Xeric	
	Temperature regime		Mesic	
Location	Province		Soria	
	Town		Navaleno	
	Place		Fuente del Pardo	
	Coordinates (UTM)	X	30T 498762	
		Y	4636644	
	Altitude		1277 m	
	Stepness		15,60%	
	Orientation		202°	
Soil	Parent material		Sandstones and Marls	
	Geologic age		Mesozoic	
	Soil type		Aquic humixerept	
Vegetation	Potential		*Luzulo forsteri-Querceto pyrenaicae S.*	
	Current		*Pinus sylvestris* L.	

Overstory description

	N (trees ha^{-1})			G (m^2 ha^{-1})			DHB (cm)			Ho (m)			Age (years)		SI	
	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	Ps	Pp	Ps	Pp
PS03	665	651	14	47.7	45.4	2.3	30.2	29.8	45.3	23.0	22.9	24.5	105	0	23	0

Understory vegetation

Cover (%)		More abundant understory vegetation
Litter	32	*Erica australis, Erica arborea, Deschampsia flexuosa* and *Pteridium aquilinum*
Vascular plants	68	
Bryophytes	0	

Pictures

Plot	Pit soil profile
	

Table 54. Pit description of plot PS03 (monospecific stand of *Pinus sylvestris* L. in triplet 03): Climatic data, profile description including organic (leaf litter) and mineral horizons (Horizons). **

Climatic description													
Month	J	F	M	A	My	Jn	Jl	Ag	S	O	N	D	X
Rainfall (mm)	79	64	60	84	86	53	31	30	44	97	89	90	801
Temperature (°C)	1.7	2.5	5.1	7.6	11.5	14.8	17.7	17.4	13.9	9.4	5.0	2.6	9.1

Leaf litter description					
Biomass (Mg ha^{-1})	Thickness (cm)	Composition (%)	Fresh	Fragmented	Humified
18.40	3.50		31.00	36.00	36.00

Horizon description				
Horizon	Thickness (cm)	Colour Wet	Colour Dry	Description
Ah	0-12	10YR2/	10YR4/1	Water status: moist. Mottle: non-existent. Rock Fragments: few, gravely, Shape-spherical. Soil Texture: Loam. Soil Structure: moderate, granular. Consistence: friable, slightly sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: many fine roots and few coarse roots. No soil crusts. Horizon boundary: smooth and gradual.
AC	12-30	10YR4/1	10YR6/1	Water status: moist. Mottle: non-existent. Rock Fragments: few, gravely, Shape-spherical. Soil Texture: Sand. Soil Structure: moderate, granular. Consistence: friable, sticky and plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: few fine roots and few coarse roots. No soil crusts. Horizon boundary: smooth and gradual.
Cg	30-60+	10YR6/1	10YR8/1	Water status: moist. Mottle: non-existent. Rock Fragments: few, gravely, Shape-spherical. Soil Texture: Sand. Soil Structure: weak, granular. Consistence: very friable, sticky and plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: few fine roots and many coarse roots. No soil crusts.

Table 55. Pit description of plot PS03 (monospecific stand of *Pinus sylvestris* L. in triplet 03): analytic data of the mineral horizons. ***

Analytic data

Horizons	Texture (%)			Stones (%)	Density ($g\ cm^{-3}$)		Porosity (%)
	Sand	Silt	Clay		Bulk	Real	
Ah	43.93	30.04	18.36	6.11	0.41	1.64	74.92
AC	57.71	26.44	12.17	20.24	1.40	2.50	44.25
Cg	59.56	20.67	10.63	22.27	1.58	2.55	37.76

Horizons	pH (H_2O)	EC ($dS\ m^{-1}$)	Pav ($mg\ kg^{-1}$)	TN ($mg\ g^{-1}$)	C properties ($mg\ g^{-1}$)			
					TOC	oxC	Cmic	Cmin
Ah	4.35	18.1	11.7	4.84	121.76	118.81	0.55	1.08
AC	4.77	15.6	7.9	0.92	29.31	17.45	-	-
Cg	4.7	5.2	7.1	0.19	5.8	7.5	-	-

Horizons	Exchangeable cations ($cmol^+\ kg^{-1}$)					
	CEC	Na^+	K^+	Ca^{++}	Mg^{++}	SB
Ah	36.10	1.15	0.45	12.14	2.57	16.30
AC	31.28	0.82	0.10	3.03	0.72	4.66
Cg	10.48	0.9	0.1	1.6	0.5	3.0

Horizons	Water properties			
	FC (%)	PWP (%)	AW (%)	WHC ($g\ cm^{-2}$)
Ah	92.20	27.95	64.25	2.98
AC	19.79	4.68	15.11	3.03
Cg	18.06	2.02	16.04	3.95

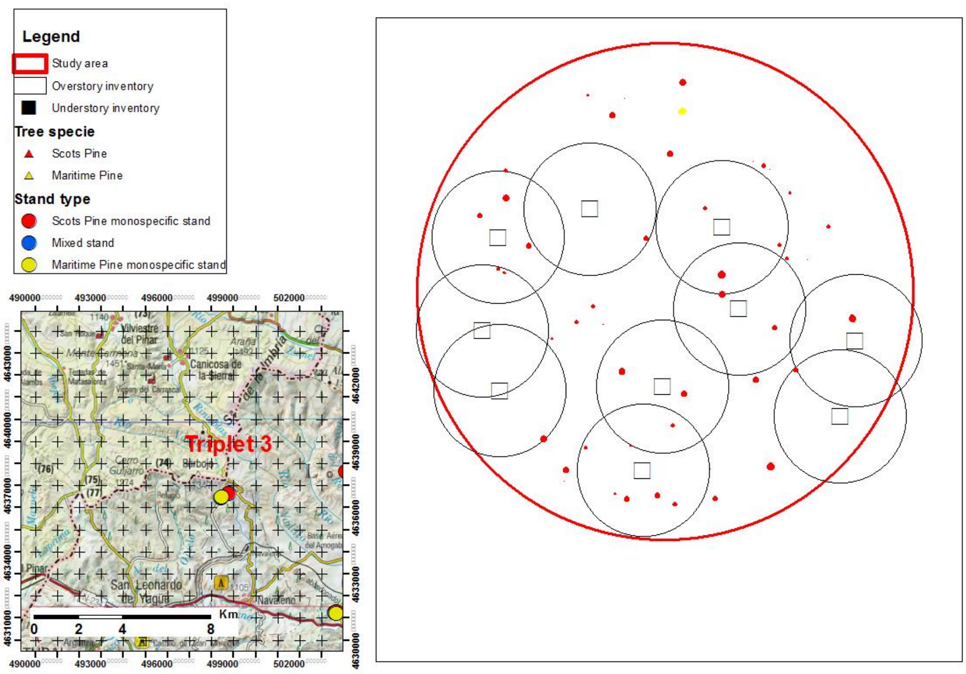


Figure 64. Map of stems position of plot PS03 (mMonospecific stand of *Pinus sylvestris* L. in triplet 03)****

Table 56. Pit description of plot PP03 (monospecific stand of *Pinus pinaster* Ait. in triplet 03). Site, overstory and understory description, and pictures of the plot and the pit soil profile. *

Plot PP03			Triplet 03	Monospecific stand of *Pinus pinaster* Aiton.
Site description				
Author			Daphne López Marcos y Luis Alfonso Ramos Calvo	
Date			11/06/2016	
Weather			Sunny / Rain in the last 24 hours	
Soil climate	Moisture regime		Xeric	
	Temperature regime		Mesic	
Location	Province		Soria	
	Town		Navaleno	
	Place		Fuente del Pardo	
	Coordinates (UTM)	X	30T 498471	
		Y	4636470	
	Altitude		1277 m	
	Stepness		0.19%	
	Orientation		200°	
Soil	Parent material		Sandstones and Marls	
	Geologic age		Mesozoic	
	Soil type		Typic humixerept	
Vegetation	Potential		*Luzulo forsteri-Querceto pyrenaicae S.*	
	Current		*Pinus pinaster* Ait.	

Overstory description

	N (trees ha^{-1})			G (m^2 ha^{-1})			DHB (cm)			Ho (m)			Age (years)		SI	
	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	Ps	Pp	Ps	Pp
PP03	538	0	538	68.6	0	68.6	40.3	0	40.3	21.8	0	21.8	0	105	0	20

Understory vegetation

Cover (%)		More abundant understory vegetation
Litter	86	*Erica arborea, Erica australis, Pinus pinaster* (seedlings/saplings), and *Cistus laurifolius*
Vascular plants	15	
Bryophytes	0	

Pictures

Plot	Pit soil profile
	

Table 57. Pit description of plot PP03 (monospecific stand of *Pinus pinaster* Ait. in triplet 03): Climatic data, profile description including organic (leaf litter) and mineral horizons (Horizons). **

Climatic description													
Month	J	F	M	A	My	Jn	Jl	Ag	S	O	N	D	X
Rainfall (mm)	79	64	60	84	86	53	31	30	44	97	89	90	801
Temperature (°C)	1.7	2.5	5.1	7.6	11.5	14.8	17.7	17.4	13.9	9.4	5.0	2.6	9.1

Leaf litter description					
Biomass (Mg ha^{-1})	Thickness (cm)	Composition (%)	Fresh	Fragmented	Humified
20.00	3.00		34.00	19.00	47.00

Horizon description				
Horizon	Thickness (cm)	Colour		Description
		Wet	Dry	
Ah	0-17	10YR3/1	10YR5/2	Water status: moist. Mottle: non-existent. Rock Fragments: many, gravely, Shape-spherical. Soil Texture: Sand. Soil Structure: weak, granular. Consistence: friable, slightly sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: many fine roots and few coarse roots. No soil crusts. Horizon boundary: smooth and gradual.
C	17-57+	10YR4/6	10YR6/6	Water status: moist. Mottle: non-existent. Rock Fragments: many, gravely, Shape-spherical. Soil Texture: Sand. Soil Structure: weak, granular. Consistence: friable, slightly sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: few fine roots and few coarse roots. No soil crusts.

Table 58. Pit description of plot PP03 (monospecific stand of *Pinus pinaster* Ait. In triplet 03): analytic data of the mineral horizons. ***

Analytic data

Horizons	Texture (%)			Stones (%)	Density ($g\ cm^{-3}$)		Porosity (%)
	Sand	Silt	Clay		Bulk	Real	
Ah	65.53	17.82	7.79	59.50	1.66	2.73	39.21
C	68.48	15.04	10.26	58.56	1.48	2.58	42.86

Horizons	pH (H_2O)	EC ($dS\ m^{-1}$)	Pav ($mg\ kg^{-1}$)	TN ($mg\ g^{-1}$)	C properties ($mg\ g^{-1}$)			
					TOC	oxC	Cmic	Cmin
Ah	5.04	118.5	7.3	1.46	45.53	32.94	0.09	0.95
C	4.80	130.0	7.7	0.20	5.53	6.19	-	-

Horizons	Exchangeable cations ($cmol^+\ kg^{-1}$)					
	CEC	Na^+	K^+	Ca^{++}	Mg^{++}	SB
Ah	19.93	0.85	0.17	3.41	0.83	5.26
C	10.83	0.82	0.06	0.95	0.35	2.18

Horizons	Water properties			
	FC (%)	PWP (%)	AW (%)	WHC ($g\ cm^{-2}$)
Ah	39.38	29.02	10.36	1.19
C	11.43	2.61	8.82	1.78

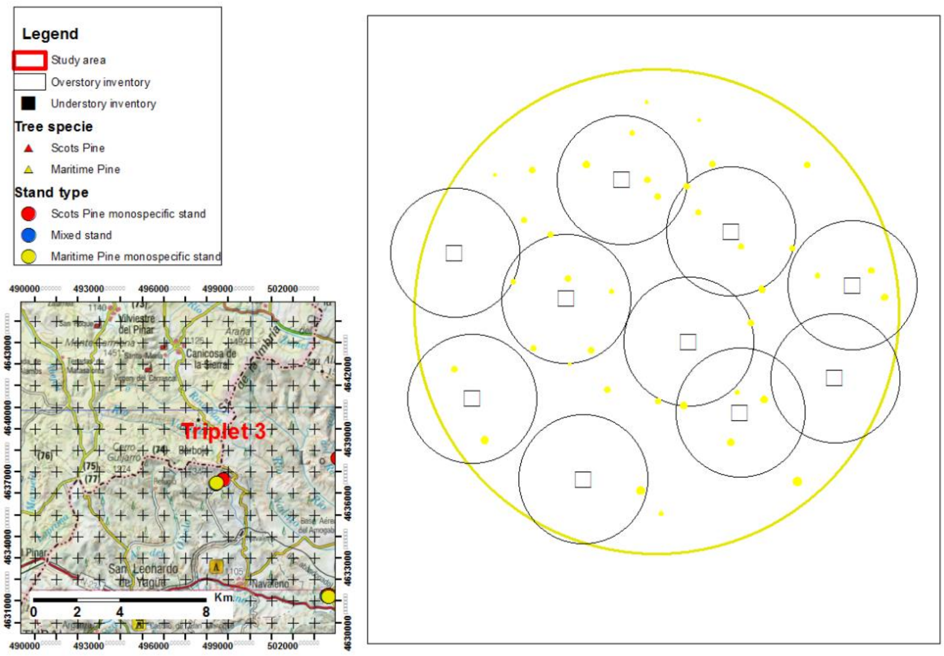


Figure 65. Map of stems position in plot PP03 (monospecific stand of *Pinus pinaster* Ait. in triplet 03)****.

Table 59. Pit description of plot MM03 (mixed stand of *Pinus sylvestris* L. and *Pinus pinaster* Ait. in triplet 03). Site, overstory and understory description, and pictures of the plot and the pit soil profile. *

Plot MM03			Triplet 03	Mixed stand
Site description				
Author			Daphne López Marcos y Luis Alfonso Ramos Calvo	
Date			11/06/2016	
Weather			Sunny / Rain in the last 24 hours	
Soil climate	Moisture regime		Xeric	
	Temperature regime		Mesic	
Location	Province		Soria	
	Town		Navaleno	
	Place		Fuente del Pardo	
	Coordinates (UTM)	X	30T 498440	
		Y	4636436	
	Altitude		1241 m	
	Stepness		18.70%	
	Orientation		200°	
Soil	Parent material		Sandstones and Marls	
	Geologic age		Mesozoic	
	Soil type		Typic humixerept	
Vegetation	Potential		*Luzulo forsteri-Querceto pyrenaicae S.*	
	Current		*Pinus sylvestris* L. and *Pinus pinaster* Ait.	

Overstory description

	N (trees ha^{-1})			G (m^2 ha^{-1})			DHB (cm)			Ho (m)			Age (years)		SI	
	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	Ps	Pp	Ps	Pp
MM03	693	495	198	63.5	33.0	30.5	34.1	29.1	44.3	25.0	22.6	24.8	100	95	23	23

Understory vegetation

Cover (%)		More abundant understory vegetation
Litter	49	*Erica australis, Deschampsia flexuosa, Hypnum* spp. and *Erica arborea*
Vascular plants	47	
Bryophytes	5	

Pictures

Plot	Pit soil profile
	

Table 60. Pit description of plot MM03 (mixed stand of *Pinus sylvestris* L. and *Pinus pinaster* Ait. in triplet 03): Climatic data, profile description including organic (leaf litter) and mineral horizons (Horizons). **

Climatic description													
Month	J	F	M	A	My	Jn	Jl	Ag	S	O	N	D	X
Rainfall (mm)	79	64	60	84	86	53	31	30	44	97	89	90	801
Temperature (ºC)	1.7	2.5	5.1	7.6	11.5	14.8	17.7	17.4	13.9	9.4	5.0	2.6	9.1

Leaf litter description					
Biomass (Mg ha^{-1})	Thickness (cm)	Composition (%)	Fresh	Fragmented	Humified
18.80	2.00		31.00	34.00	35.00

<table>
<tr><th colspan="5">Horizon description</th></tr>
<tr><th rowspan="2">Horizon</th><th rowspan="2">Thickness (cm)</th><th colspan="2">Colour</th><th rowspan="2">Description</th></tr>
<tr><th>Wet</th><th>Dry</th></tr>
<tr><td>Ah</td><td>0-17</td><td>10YR2/2</td><td>10YR4/1</td><td>Water status: moist. Mottle: non-existent. Rock Fragments: few, gravely, Shape-spherical. Soil Texture: Sand. Soil Structure: moderate, granular. Consistence: friable, slightly sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: many fine roots and few coarse roots. No soil crusts. Horizon boundary: smooth and gradual.</td></tr>
<tr><td>C</td><td>17-54+</td><td>10YR5/3</td><td>10YR6/3</td><td>Water status: moist. Mottle: non-existent. Rock Fragments: many, gravely, Shape-spherical. Soil Texture: Sand. Soil Structure: weak, granular. Consistence: very friable, slightly sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: few fine roots and many coarse roots.</td></tr>
<tr><td></td><td></td><td></td><td></td><td></td></tr>
</table>

Table 61. Pit description of plot MM03 (mixed stand of *Pinus sylvestris* L. and *Pinus pinaster* Ait. in triplet 03): analytic data of the mineral horizons. ***

Analytic data

Horizons	Texture (%)			Stones (%)	Density (g cm^{-3})		Porosity (%)
	Sand	Silt	Clay		Bulk	Real	
Ah	52.82	23.47	14.75	15.02	1.00	2.12	52.72
C	72.39	11.64	11.07	60.57	1.80	2.55	29.57

Horizons	Ph (H_2O)	EC (dS m^{-1})	Pav (mg kg^{-1})	TN (mg g^{-1})	C properties (mg g^{-1})			
					TOC	oxC	Cmic	Cmin
Ah	4.42	153.0	5.1	0.33	73.67	56.12	0.08	0.70
C	4.72	130.5	1.6	0.20	6.36	4.65	-	-

Horizons	Exchangeable cations (cmol+ kg^{-1})					
	CEC	Na^+	K^+	Ca^{++}	Mg^{++}	SB
Ah	24.18	0.94	0.21	4.18	0.91	6.24
C	11.87	0.85	0.08	1.14	0.38	2.44

Horizons	Water properties			
	FC (%)	PWP (%)	AW (%)	WHC (g cm^{-2})
Ah	32.19	28.20	3.99	0.58
C	7.42	1.89	5.52	1.29

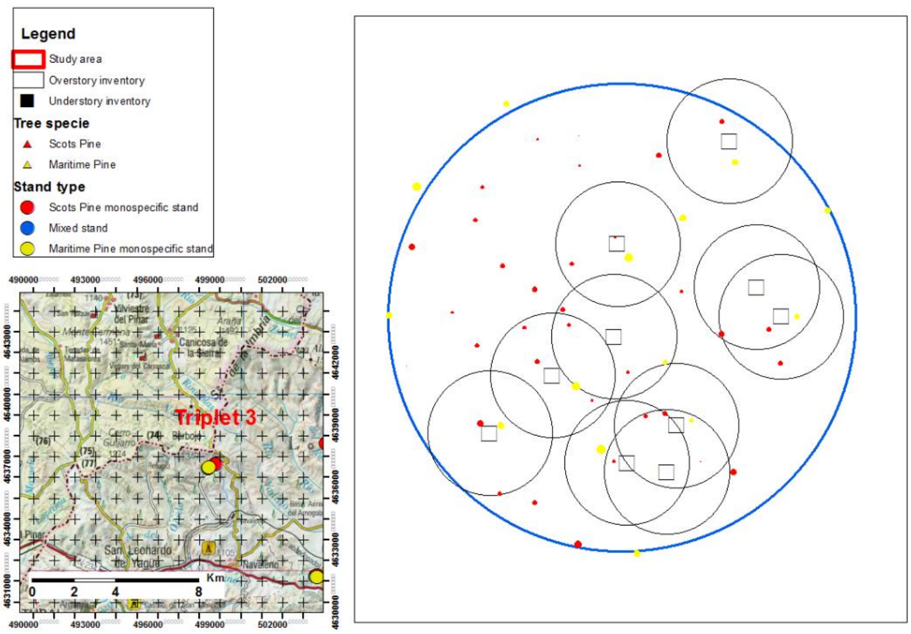


Figure 66. Map of stems position in plot MM03 (mixed stand of *Pinus sylvestris* L. and *Pinus pinaster* Ait. in triplet 03)****

Triplet 4

Table 62. Pit description of plot PS04 (monospecific stand of *Pinus sylvestris* L. in triplet 04). Site, overstory and understory description and pictures of the plot and the pit soil profile. *

Plot PS04			Triplet 04	Monospecific stand of *Pinus sylvestris* L.
Site description				
Author			Daphne López Marcos y Luis Alfonso Ramos Calvo	
Date			12/03/2016	
Weather			Sunny / Rain in the last 24 hours	
Soil climate	Moisture regime		Xeric	
	Temperature regime		Mesic	
Location	Province		Soria	
	Town		Soria	
	Place		Pajar de la molinera	
	Coordinates (UTM)	X	30T 0504090	
		Y	4637606	
	Altitude		1169 m	
	Stepness		14.00%	
	Orientation		255°	
Soil	Parent material		Sandstones and Marls	
	Geologic age		Mesozoic	
	Soil type		Typic dystroxerept	
Vegetation	Potential		*Festuco heterophyllae-Querceto pyrenaicae S.*	
	Current		*Pinus sylvestris* L.	

Overstory description

	N (trees ha^{-1})			G (m^2 ha^{-1})			DHB (cm)			Ho (m)			Age (years)		SI	
	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	Ps	Pp	Ps	Pp
PS04	634	580	57	48.9	40.7	8.2	31.3	29.9	43.0	22.9	22.6	21.2	78	0	26	0

Understory vegetation

Cover (%)		More abundant understory vegetation
Litter	30	*Hypnum* spp., *Erica arborea, Quercus pyrenaica* (seedlings/saplings) and *Erica australis*
Vascular plants	50	
Bryophytes	20	

Pictures

Plot	Pit soil profile
	

Table 63. Pit description of plot PS04 (monospecific stand of *Pinus sylvestris* L. in triplet 04): Climatic data, profile description including organic (leaf litter) and mineral horizons (Horizons). **

Climatic description													
Months	J	F	M	A	My	Jn	Jl	Ag	S	O	N	D	X
Rainfall (mm)	80	65	57	85	83	53	31	29	42	90	90	90	833
Temperature (ºC)	1.8	2.6	5.1	7.9	11.8	14.7	17.5	17.2	13.8	9.4	5.0	2.6	8.8

Leaf litter description					
Biomass (Mg ha^{-1})	Thickness (cm)	Composition (%)	Fresh	Fragmented	Humified
17.80	2.00		44.00	32.00	24.00

Horizon description				
Horizon	Thickness (cm)	Colour Wet	Colour Dry	Description
Ah	0-8	10YR3/1	10YR5/2	Water status: slightly moist. Mottle: non-existent. Rock Fragments: few, gravely, Shape-spherical. Soil Texture: Loam. Soil Structure: moderate, granular. Consistence: friable, sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: many fine roots and few coarse roots. No soil crusts. Horizon boundary: smooth and gradual.
AB	8-30	10YR3/2	10YR6/6	Water status: slightly moist. Mottle: non-existent. Rock Fragments: few, gravely, Shape-spherical. Soil Texture: Loam. Soil Structure: weak, granular. Consistence: friable, slightly sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: common fine roots and many coarse roots. No soil crusts. Horizon boundary: smooth and gradual.
C	30-60+	10YR5/8	10YR7/4	Water status: slightly moist. Mottle: 5-10% 0.5-1cm spots. wet red (2.5Y 5/8) and light red dry (2.5Y 7/8). Rock Fragments: few, gravely, Shape-spherical. Soil Texture: Loam. Soil Structure: moderate, granular. Consistence: friable, sticky and plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: few fine roots and many coarse roots. No soil crusts.

Table 64. Pit description of plot PS04 (monospecific stand of *Pinus sylvestris* L. in triplet 04): analytic data of the mineral horizons. ***

Analytic data

Horizons	Texture (%)			Stones (%)	Density (g cm-3)		Porosity (%)
	Sand	Silt	Clay		Bulk	Real	
Ah	55.73	21.41	14.38	9.04	0.98	1.31	25.18
AB	47.99	41.27	12.40	25.68	1.37	2.44	43.86
C	34.93	34.74	21.77	25.56	1.46	2.55	42.66

Horizons	pH (H_2O)	EC (dS m^{-1})	Pav (mg kg^{-1})	TN (mg g^{-1})	C properties (mg g^{-1})			
					TOC	oxC	Cmic	Cmin
Ah	4.63	74.1	5.9	1.77	46.84	35.88	0.09	0.95
AB	5.37	25.0	3.8	0.61	13.00	7.51	-	-
C	4.98	23.7	3.4	0.40	4.84	4.27	-	-

Horizons	Exchangeable cations (cmol+ kg^{-1})					
	CEC	Na^+	K^+	Ca^{++}	Mg^{++}	SB
Ah	21.43	0.76	0.38	4.61	1.05	6.80
AB	18.03	0.77	0.14	2.03	0.61	3.54
C	13.86	0.69	0.16	1.56	0.84	3.26

Horizons	Water properties			
	FC (%)	PWP (%)	AW (%)	WHC (g cm^{-2})
Ah	46.42	25.31	21.11	1.51
AB	23.16	3.91	19.25	4.31
C	23.62	8.51	15.11	3.29

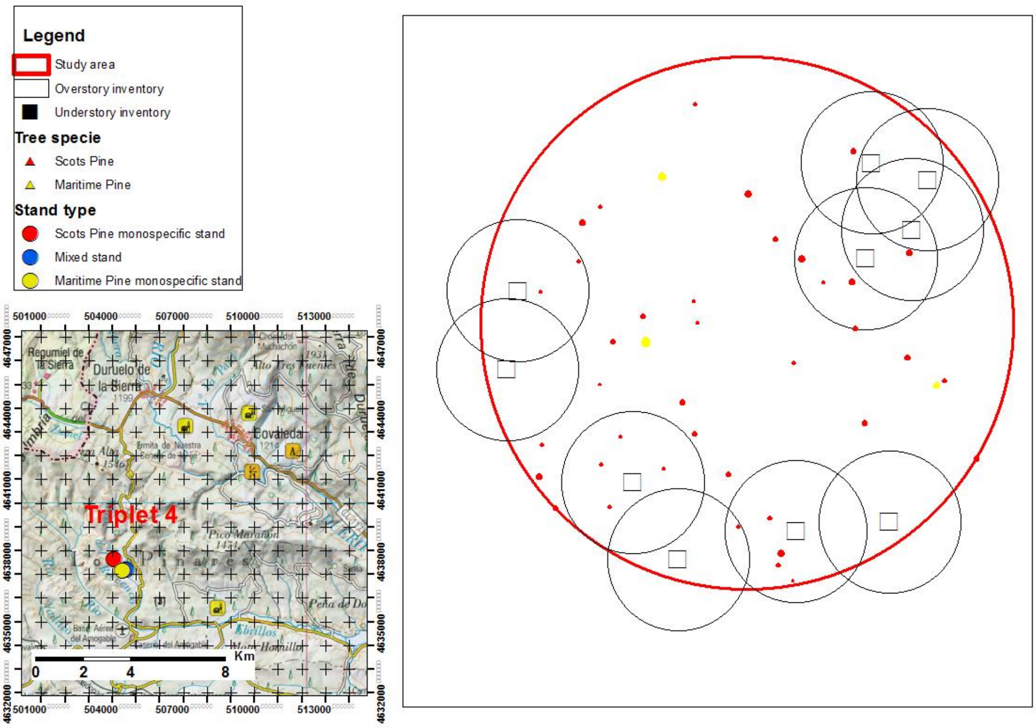


Figure 67. Map of stems position in plot PS04 (monospecific stand of *Pinus sylvestris* L. in triplet 04)****.

Table 65. Pit description of plot PP04 (monospecific stand of *Pinus pinaster* Ait. in triplet 04). Site, overstory and understory description, and pictures of the plot and the pit soil profile. *

Plot PP04			Triplet 04	Monospecific stand of *Pinus pinaster Aiton.*
Site description				
Author			Daphne López Marcos y Luis Alfonso Ramos Calvo	
Date			12/03/2016	
Weather			Sunny / Rain in the last 24 hours	
Soil climate	Moisture regime		Xeric	
	Temperature regime		Mesic	
Location	Province		Soria	
	Town		Soria	
	Place		Pajar de la molinera	
	Coordinates (UTM)	X	30T 0504456	
		Y	4637191	
	Altitude		1165 m	
	Stepness		0.20%	
	Orientation		208°	
Soil	Parent material		Sandstones and Marls	
	Geologic age		Mesozoic	
	Soil type		Typic dystroxerept	
Vegetation	Potential		*Festuco heterophyllae-Querceto pyrenaicae S.*	
	Current		*Pinus pinaster* Ait.	

Overstory description

	N (trees ha^{-1})			G (m^2 ha^{-1})			DHB (cm)			Ho (m)			Age (years)		SI	
	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	Ps	Pp	Ps	Pp
PP04	1429	283	1146	69.4	3.3	66	24.9	12.3	27.1	15.6	12.3	15.6	0	80	0	16

Understory vegetation

Cover (%)			More abundant understory vegetation
Litter	39		*Erica australis, Hypnum* spp. and *Poligala vulgaris*
Vascular plants	54		
Bryophytes	7		

Pictures

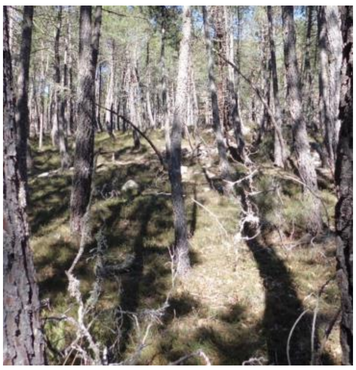
Plot	Pit soil profile
	

Table 66. Pit description of plot PP04 (monospecific stand of *Pinus pinaster* Ait. in triplet 04): Climatic data, profile description including organic (leaf litter) and mineral horizons (Horizons). **

Climatic description												
Month	J	F	M	A	My	Jn	Jl	Ag	S	O	N	D	X
Rainfall (mm)	80	65	57	85	83	53	31	29	42	90	90	90	833
Temperature (°C)	1.8	2.6	5.1	7.9	11.8	14.7	17.5	17.2	13.8	9.4	5.0	2.6	8.8

Leaf litter description					
Biomass (Mg ha^{-1})	Thickness (cm)	Composition (%)	Fresh	Fragmented	Humified
20.80	2.00		29.00	28.00	43.00

Horizon description				
Horizon	Thickness (cm)	Colour		Description
		Wet	Dry	
Ah	0-8	10YR3/1	10YR6/2	Water status: slightly moist. Mottle: non-existent. Rock Fragments: few, gravely, Shape-spherical. Soil Texture: Sand. Soil Structure: moderate, granular. Consistence: friable, sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: many fine roots and few coarse roots. No soil crusts. Horizon boundary: smooth and gradual.
AC	8-34	10YR3/2	10YR6/6	Water status: slightly moist. Mottle: non-existent. Rock Fragments: few, gravely, Shape-spherical. Soil Texture: Sand. Soil Structure: weak, granular. Consistence: friable, sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: common fine roots and many coarse roots. No soil crusts. Horizon boundary: smooth and gradual.
C	34-60+	10YR5/8	10YR7/4	Water status: slightly moist. Mottle: non-existent. Rock Fragments: few, gravely, Shape-spherical. Soil Texture: Sand. Soil Structure: weak, granular. Consistence: very friable, sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: few fine roots and many coarse roots. No soil crusts

Table 67. Pit description of plot PP04 (monospecific stand of *Pinus pinaster* Ait. in triplet 04): analytic data of the mineral horizons. ***

Analytic data

Horizons	Texture (%) Sand	Texture (%) Silt	Texture (%) Clay	Stones (%)	Density ($g\ cm^{-3}$) Bulk	Density ($g\ cm^{-3}$) Real	Porosity (%)
Ah	68.44	24.11	10.72	5.62	1.21	1.76	69.12
AC	60.74	27.45	15.89	9.29	1.31	2.74	47.68
C	57.22	38.02	15.66	12.75	1.20	2.55	47.32

Horizons	pH (H_2O)	EC ($dS\ m^{-1}$)	Pav ($mg\ kg^{-1}$)	TN ($mg\ g^{-1}$)	C properties ($mg\ g^{-1}$) TOC	oxC	Cmic	Cmin
Ah	4.80	94.6	1.7	4.20	49.82	53.74	0.09	0.90
AC	5.15	39.3	0.5	1.97	8.43	12.83	-	-
C	5.01	28.0	0.4	1.17	4.33	7.28	-	-

Horizons	Exchangeable cations ($cmol^+\ kg^{-1}$) CEC	Na^+	K^+	Ca^{++}	Mg^{++}	SB
Ah	14.12	0.64	0.14	1.98	0.56	3.32
AC	12.57	0.72	0.12	1.02	0.33	2.19
C	10.06	0.69	0.07	0.98	0.30	2.05

Horizons	Water properties FC (%)	PWP (%)	AW (%)	WHC ($g\ cm^{-2}$)
Ah	23.26	19.88	3.39	0.31
AC	10.98	9.21	1.76	0.54
C	14.69	11.75	2.94	0.49

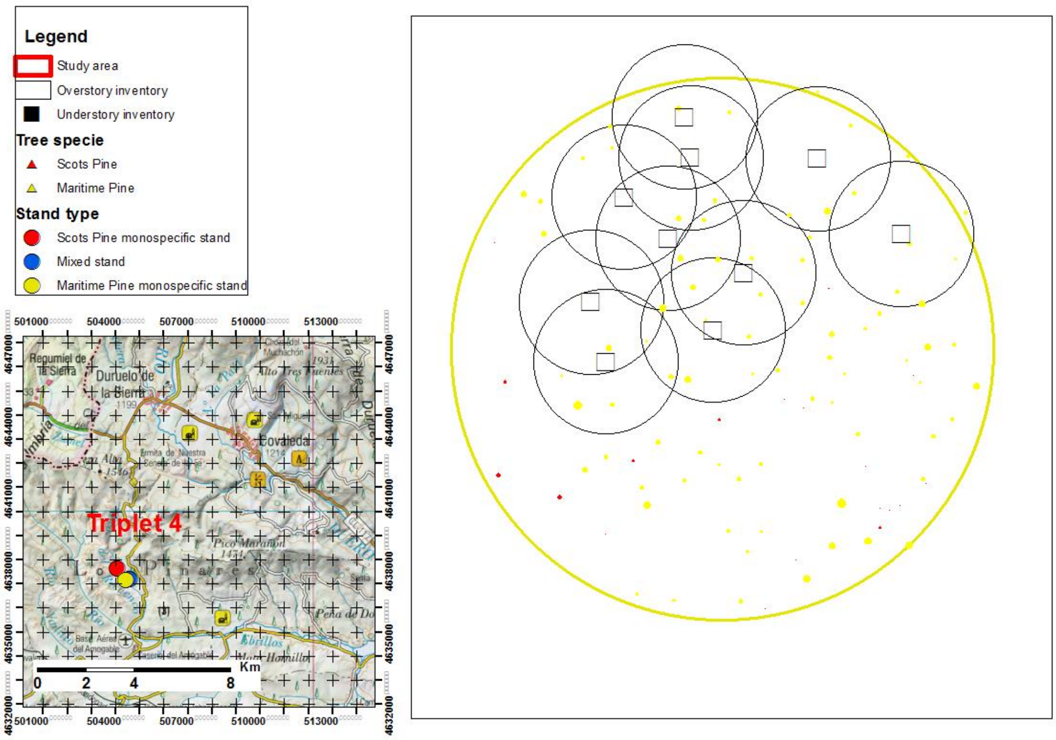


Figure 68. Map of stems position in plot PP04 (monospecific stand of *Pinus pinaster* Ait. in triplet 04)****.

Table 68. Pit description of plot MM04 (mixed stand of *Pinus sylvestris* L. and *Pinus pinaster* Ait. in triplet 04). Site, overstory and understory description, and pictures of the plot and the pit soil profile. *

Plot MM04			Triplet 04	Mixed stand
Site description				
Author			Daphne López Marcos y Luis Alfonso Ramos Calvo	
Date			12/03/2016	
Weather			Sunny / Rain in the last 24 hours	
Soil climate	Moisture regime		Xeric	
	Temperature regime		Mesic	
Location	Province		Soria	
	Town		Soria	
	Place		Pajar de la molinera	
	Coordinates (UTM)	X	30T 0504595	
		Y	4637174	
	Altitude		1206 m	
	Stepness		0.09%	
	Orientation		155°	
Soil	Parent material		Sandstones and Marls	
	Geologic age		Mesozoic	
	Soil type		Typic dystroxerept	
Vegetation	Potential		*Festuco heterophyllae-Querceto pyrenaicae S.*	
	Current		*Pinus sylvestris* L. and *Pinus pinaster* Ait.	

Overstory description

	N (trees ha^{-1})			G (m^2 ha^{-1})			DHB (cm)			Ho (m)			Age (years)		SI	
	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	Ps	Pp	Ps	Pp
MM04	1330	764	566	55.3	23.2	32.1	23	19.7	26.9	19.3	17.9	18.8	78	79	20	20

Understory vegetation

Cover (%)		More abundant understory vegetation
Litter	39	*Erica australis, Quercus pyrenaica* (seedlings/saplings), *Erica arborea* and *Hypnum* spp.
Vascular plants	53	
Bryophytes	8	

Pictures

Plot

Pit soil profile

Table 69. Pit description of plot MM04 (Mixed stand of *Pinus sylvestris* L. and *Pinus pinaster* Aiton. of triplet 04): Climatic data, profile description including organic (leaf litter) and mineral (Horizons). **

Climatic description												
Month	J	F	M	A	My	Jn	Jl	Ag	S	O	N	D	X
Rainfall (mm)	80	65	57	85	83	53	31	29	42	90	90	90	833
Temperature (ºC)	1.8	2.6	5.1	7.9	11.8	14.7	17.5	17.2	13.8	9.4	5.0	2.6	8.8

Leaf litter description					
Biomass (Mg ha^{-1})	Thickness (cm)	Composition (%)	Fresh	Fragmented	Humified
18.80	1.50		31.00	34.00	35.00

Horizon description				
Horizon	Thickness (cm)	Colour		Description
		Wet	Dry	
Ah	0-20	10YR4/1	10YR6/2	Water status: slightly moist. Mottle: non-existent. Rock Fragments: many, gravely, Shape-spherical. Soil Texture: Sand. Soil Structure: moderate, granular. Consistence: friable, sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: many fine roots and few coarse roots. No soil crusts. Horizon boundary: smooth and gradual.
C	20-50	10YR5/8	10YR6/6	Water status: slightly moist. Mottle: non-existent. Rock Fragments: few, gravely, Shape-spherical. Soil Texture: Sand. Soil Structure: weak, granular. Consistence: very friable, slightly sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: few fine roots and many coarse roots. No soil crusts. Horizon boundary: wavy and abrupt (lithic contact).

Table 70. Pit description of plot MM04 (mixed stand of *Pinus sylvestris* L. and *Pinus pinaster* Ait. in triplet 04): analytic data of the mineral horizons. ***

Analytic data

Horizons	Texture (%)			Stones (%)	Density (g cm^{-3})		Porosity (%)
	Sand	Silt	Clay		Bulk	Real	
Ah	76.96	14.32	5.35	15.12	0.88	2.25	60.92
C	71.44	13.95	10.64	35.15	1.33	2.54	47.70

Horizons	pH (H_2O)	EC (dS m^{-1})	Pav (mg kg^{-1})	TN (mg g^{-1})	C properties (mg g^{-1})			
					TOC	oxC	Cmic	Cmin
Ah	5.16	38.6	3.9	1.39	23.41	15.12	0.08	0.70
C	5.20	24.7	3.3	0.74	5.63	4.46	-	-

Horizons	Exchangeable cations (cmol$^+$ kg^{-1})					
	CEC	Na^+	K^+	Ca^{++}	Mg^{++}	SB
Ah	18.74	0.80	0.20	1.35	0.36	2.71
C	16.31	0.76	0.06	0.86	0.30	1.98

Horizons	Water properties			
	FC (%)	PWP (%)	AW (%)	WHC (g cm^{-2})
Ah	12.10	7.74	4.36	0.65
C	8.91	4.75	4.16	1.07

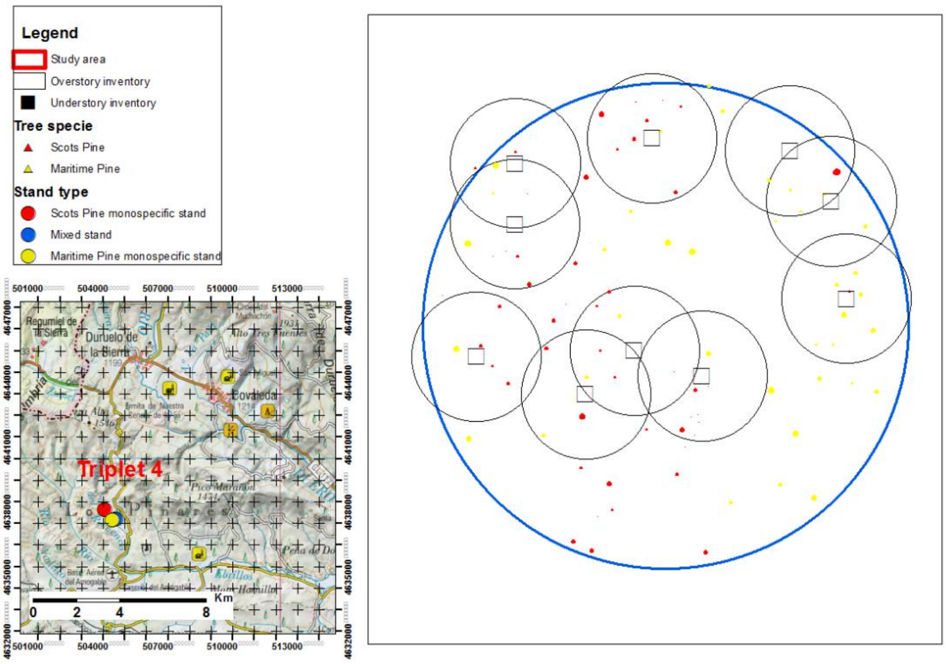


Figure 69 Map of stems position in plot MM04 (mixed stand of *Pinus sylvestris* L. and *Pinus pinaster* Ait. in triplet 04)****.

Triplet 5

Table 71. Pit description of plot PS05 (monospecific stand of *Pinus sylvestris* L. in triplet 05). Site, overstory and understory description, and pictures of the plot and the pit soil profile. *

Plot PS05			Triplet 05	Monospecific stand of *Pinus sylvestris* L.
Site description				
Author			Daphne López Marcos y Luis Alfonso Ramos Calvo	
Date			12/03/2016	
Weather			Sunny / Rain in the last 24 hours	
Soil climate	Moisture regime		Xeric	
	Temperature regime		Mesic	
Location	Province		Soria	
	Town		Soria	
	Place		Mojon Pardo	
	Coordinates (UTM)	X	30T 0503658	
		Y	4631296	
	Altitude		1145 m	
	Stepness		0.01%	
	Orientation		250°	
Soil	Parent material		Sandstones and Marls	
	Geologic age		Mesozoic	
	Soil type		Typic humixerept	
Vegetation	Potential		*Festuco heterophyllae-Querceto pyrenaicae S.*	
	Current		*Pinus sylvestris* L.	

Overstory description

	N (trees ha^{-1})			G (m^2 ha^{-1})			DHB (cm)			Ho (m)			Age (years)		SI	
	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	Ps	Pp	Ps	Pp
PS05	651	651	0	54.9	54.9	0	32.8	32.8	0	23	23	0	121	0	23	0

Understory vegetation

Cover (%)		More abundant understory vegetation
Litter	60	*Hypnum* spp., *Erica australis* and *Pinus sylvestris* (seedlings/saplings)
Vascular plants	18	
Bryophytes	24	

Pictures

Plot	Pit soil profile
	

Table 72. Pit description of plot PS05 (Monospecific stand of *Pinus sylvestris* L. of triplet 05): Climatic data, profile description including organic (leaf litter) and mineral (Horizons) horizons. **

Climatic description												
Month	J	F	M	A	My	Jn	Jl	Ag	S	O	N	D	X
Rainfall (mm)	78	64	56	84	84	53	31	31	42	92	89	89	810
Temperature (ºC)	1.5	2.5	4.8	7.7	11.5	14.	17.1	17.1	13.5	9.1	5.1	2.4	8.7

Leaf litter description					
Biomass (Mg ha^{-1})	Thickness (cm)	Composition (%)	Fresh	Fragmented	Humified
21.00	1.50		51.00	29.00	19.00

Horizon description				
Horizon	Thickness (cm)	Colour Wet	Colour Dry	Description
Ah	0-15	10YR2/1	10YR4/2	Water status: very wet. Mottle: non-existent. Rock Fragments: few, gravely, Shape-spherical. Soil Texture: Loam. Soil Structure: moderate, granular. Consistence: friable, sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: many fine roots and few coarse roots. No soil crusts. Horizon boundary: smooth and gradual.
AB	15-40	10YR5/3	10YR6/3	Water status: very wet. Mottle: non-existent. Rock Fragments: few, gravely, Shape-spherical. Soil Texture: Loam. Soil Structure: weak, granular. Consistence: very friable, sticky and plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: few fine roots and common coarse roots. No soil crusts. Horizon boundary: smooth and gradual.
C	40-60+	10YR5/8	10YR7/4	Water status: very wet. Mottle: non-existent. Rock Fragments: many, gravely, Shape-spherical. Soil Texture: sandy. Soil Structure: weak, granular. Consistence: very friable, sticky and plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: few fine roots and many coarse roots. No soil crusts.

Table 73. Pit description of plot PS05 (monospecific stand of *Pinus sylvestris* L. in triplet 05): analytic data of the mineral horizons. ***

Analytic data

Horizons	Texture (%)			Stones	Density ($g\ cm^{-3}$)		Porosity
	Sand	Silt	Clay	(%)	Bulk	Real	(%)
Ah	55.18	21.38	13.36	2.68	0.61	1.52	59.80
AB	53.21	23.32	11.99	11.68	1.11	2.40	53.61
C	49.16	26.32	16.34	16.09	1.29	2.54	49.23

Horizons	pH (H_2O)	EC ($dS\ m^{-1}$)	Pav ($mg\ kg^{-1}$)	TN ($mg\ g^{-1}$)	C properties ($mg\ g^{-1}$)			
					TOC	oxC	Cmic	Cmin
Ah	4.05	102.1	7.4	3.23	84.60	72.00	0.39	0.79
AB	4.75	35.2	3.9	0.66	13.19	10.09	-	-
C	5.3	20.4	3.1	0.61	4.12	2.67	-	-

Horizons	Exchangable cations ($cmol^{+}\ kg^{-1}$)					
	CEC	Na^{+}	K^{+}	Ca^{++}	Mg^{++}	SB
Ah	18.46	0.82	0.33	4.44	0.82	6.41
AB	12.93	0.69	0.48	1.01	0.32	2.49
C	10.06	0.77	0.14	1.31	0.42	2.64

Horizons	Water properties			
	FC (%)	PWP (%)	AW (%)	WHC ($g\ cm^{-2}$)
Ah	46.57	26.86	19.71	1.76
AB	23.93	4.92	19.00	4.68
C	21.24	3.74	17.50	1.89

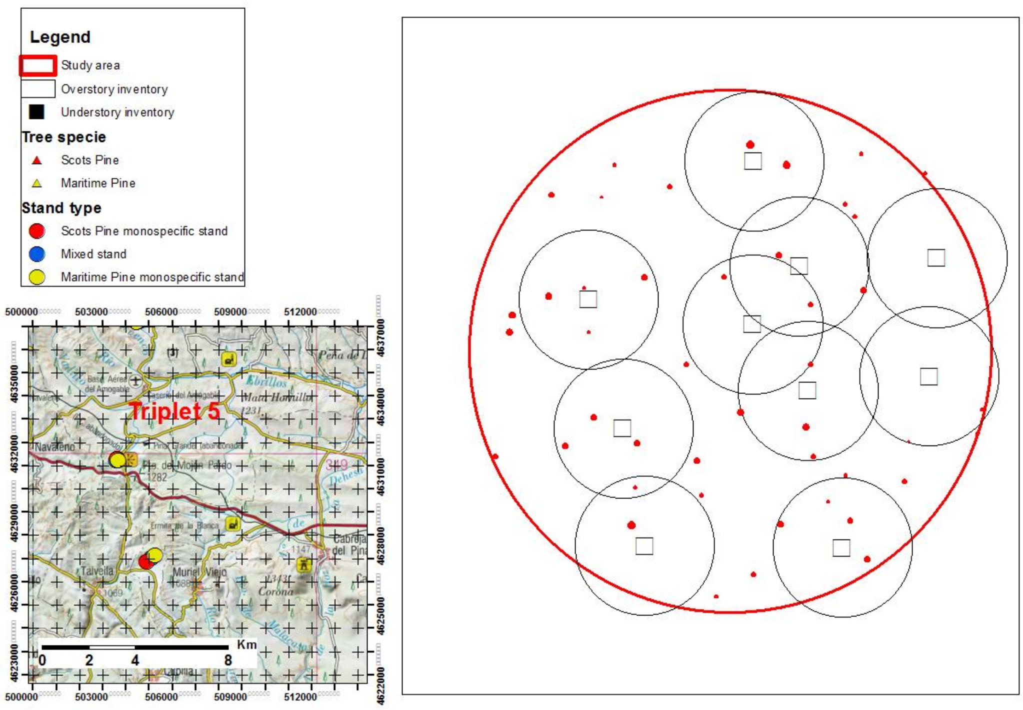


Figure 70. Map of stems position in plot PS05 (monospecific stand of *Pinus sylvestris* L. in triplet 05)****.

Table 74. Pit description of plot PP05 (monospecific stand of *Pinus pinaster* Ait. in triplet 05). Site, overstory and understory description, and pictures of the plot and the pit soil profile. *

Plot PP05		Triplet 05	Monospecific stand of *Pinus pinaster Aiton.*
Site description			
Author			Daphne López Marcos y Luis Alfonso Ramos Calvo
Date			12/03/2016
Weather			Sunny / Rain in the last 24 hours
Soil climate	Moisture regime		Xeric
	Temperature regime		Mesic
Location	Province		Soria
	Town		Soria
	Place		Mojon Pardo
	Coordinates (UTM)	X	30T 0503674
		Y	4631248
	Altitude		1145 m
	Stepness		0.01%
	Orientation		250°
Soil	Parent material		Sandstones and Marls
	Geologic age		Mesozoic
	Soil type		Typic humixerept
Vegetation	Potential		*Festuco heterophyllae-Querceto pyrenaicae S.*
	Current		*Pinus pinaster* Ait.

Overstory description

	N (trees ha^{-1})			G (m^2 ha^{-1})			DHB (cm)			Ho (m)			Age (years)		SI	
	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	Ps	Pp	Ps	Pp
PP05	722	0	722	70.3	0	70.3	35.2	0	35.2	21.4	0	21.4	0	115	0	20

Understory vegetation

Cover (%)		More abundant understory vegetation
Litter	44	*Erica australis, Arctostaphillos uva-ursi* and *Hypnum* spp.
Vascular plants	54	
Bryophytes	3	

Pictures

Plot	Pit soil profile
	

Table 75. Pit description of plot PP05 (monospecific stand of *Pinus pinaster* Ait. in triplet 05): Climatic data, profile description including organic (leaf litter) and mineral horizons (Horizons). **

Climatic description												
Month	J	F	M	A	My	Jn	Jl	Ag	S	O	N	D	X
Rainfall (mm)	78	64	56	84	84	53	31	31	42	92	89	89	810
Temperature (°C)	1.5	2.5	4.8	7.7	11.5	14.3	17.1	17.1	13.5	9.1	5.1	2.4	8.7

Leaf litter description					
Biomass (Mg ha^{-1})	Thickness (cm)	Composition (%)	Fresh	Fragmented	Humified
14.50	1.50		29.00	28.00	43.00

Horizon description				
Horizon	Thickness (cm)	Colour Wet	Colour Dry	Description
Ah	0-20	10YR2/1	10YR5/1	Water status: slightly moist. Mottle: non-existent. Rock Fragments: few, coarse gravely, Shape-spherical. Soil Texture: Sand. Soil Structure: moderate, granular. Consistence: friable, sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: many fine roots and few coarse roots. No soil crusts. Horizon boundary: smooth and gradual.
AC	20-30	10YR4/2	10YR6/2	Water status: slightly moist. Mottle: non-existent. Rock Fragments: many, gravely, Shape-spherical. Soil Texture: Sand. Soil Structure: moderate, granular. Consistence: friable, sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: few fine roots and common coarse roots. No soil crusts. Horizon boundary: smooth and gradual.
C	30-52+	10YR2/2	10YR6/4	Water status: slightly moist. Mottle: non-existent. Rock Fragments: many, gravely, Shape-spherical. Soil Texture: Sand. Soil Structure: weak, granular. Consistence: friable, sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: few fine roots and few coarse roots. No soil crusts.

Table 76. Pit description of plot PP05 (monospecific stand of *Pinus pinaster* Ait. in triplet 05): analytic data of the mineral horizons. ***

Analytic data

Horizons	Texture (%)			Stones (%)	Density (g cm^{-3})		Porosity (%)
	Sand	Silt	Clay		Bulk	Real	
Ah	64.80	15.80	10.58	12.01	0.86	2.15	60.17
AC	58.63	24.48	11.47	52.86	1.22	2.45	50.25
C	61.46	22.72	8.48	65.63	1.17	2.35	50.07

Horizons	pH (H_2O)	EC (dS m^{-1})	Pav (mg kg^{-1})	TN (mg g^{-1})	C properties (mg g^{-1})			
					TOC	oxC	Cmic	Cmin
Ah	4.45	41.0	5.8	1.35	54.38	39.67	0.14	0.85
AC	4.91	24.7	3.9	0.50	9.76	8.54	-	-
C	4.41	25.0	3.4	0.51	13.29	10.01	-	-

Horizons	Exchangeable cations (cmol^{+} kg^{-1})					
	CEC	Na^{+}	K^{+}	Ca^{++}	Mg^{++}	SB
Ah	14.58	0.75	0.15	2.75	0.70	4.35
AC	10.06	0.70	0.30	0.81	0.30	2.11
C	4.73	0.70	0.25	0.76	0.27	1.98

Horizons	Water properties			
	FC (%)	PWP (%)	AW (%)	WHC (g cm^{-2})
Ah	27.70	11.50	16.20	2.44
AC	15.47	5.95	9.52	0.55
C	13.44	4.12	9.32	0.75

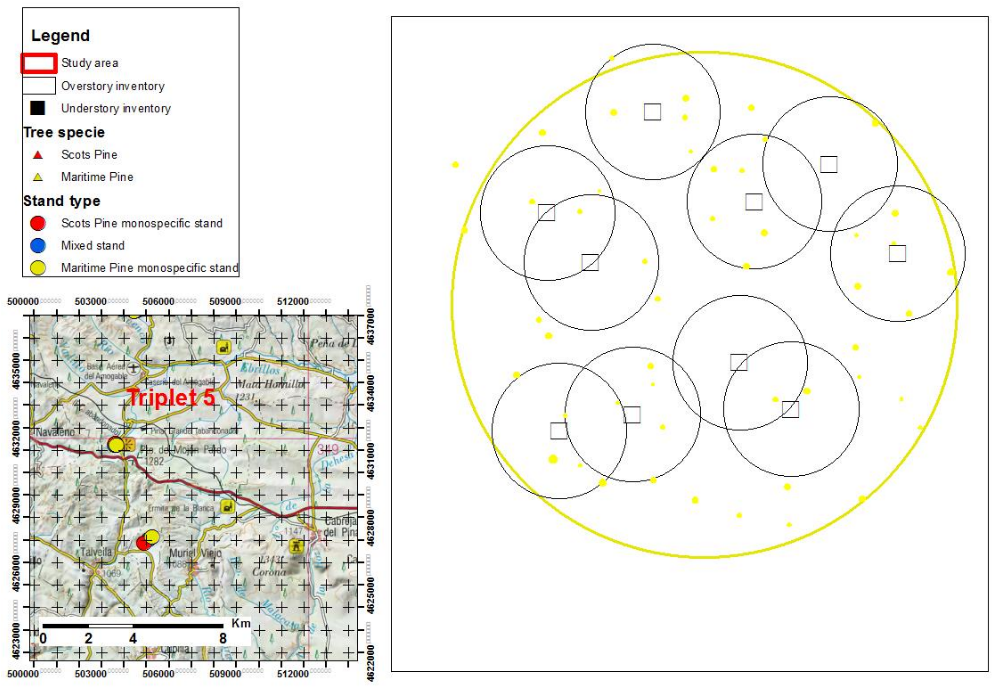


Figure 71. Map of stems position in plot PP05 (monospecific stand of *Pinus pinaster* Ait. in triplet 05)****.

Table 77. Pit description of plot MM05 (mixed stand of *Pinus sylvestris* L. and *Pinus pinaster* Ait. in triplet 05). Site, overstory and understory description, and pictures of the plot and the pit soil profile. *

Plot MM05			Triplet 05	Mixed stand
Site description				
Author			Daphne López Marcos y Luis Alfonso Ramos Calvo	
Date			12/03/2016	
Weather			Sunny / Rain in the last 24 hours	
Soil climate	Moisture regime		Xeric	
	Temperature regime		Mesic	
Location	Province		Soria	
	Town		Soria	
	Place		Mojon Pardo	
	Coordinates (UTM)	X	30 T 503581	
		Y	4631237	
	Altitude		1159 m	
	Stepness		0.04%	
	Orientation		100.4°	
Soil	Parent material		Sandstones and Marls	
	Geologic age		Mesozoic	
	Soil type		Typic dystroxerept	
Vegetation	Potential		*Festuco heterophyllae-Querceto pyrenaicae S.*	
	Current		*Pinus sylvestris* L. and *Pinus pinaster* Ait.	

Overstory description

	N (trees ha^{-1})			G (m^2 ha^{-1})			DHB (cm)			Ho (m)			Age (years)		SI	
	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	Ps	Pp	Ps	Pp
MM05	552	354	198	68.2	45.9	22.3	39.7	40.6	37.9	24.3	24.3	25.8	109	118	23	23

Understory vegetation

Cover (%)		More abundant understory vegetation
Litter	66	*Hypnun* spp., *Aira cariophilea* and *Potentilla montana*
Vascular plants	12	
Bryophytes	23	

Pictures

Plot	Pit soil profile

Table 78. Pit description of plot MM05 (mixed stand of *Pinus sylvestris* L. and *Pinus pinaster* Ait. in triplet 05): Climatic data, profile description including organic (leaf litter) and mineral horizons (Horizons). **

Climatic description												
Month	J	F	M	A	My	Jn	Jl	Ag	S	O	N	D	X
Rainfall (mm)	78	64	56	84	84	53	31	31	42	92	89	89	810
Temperature (°C)	1.5	2.5	4.8	7.7	11.5	14.3	17.1	17.1	13.5	9.1	5.1	2.4	8.7

Leaf litter description					
Biomass(Mg ha^{-1})	Thickness (cm)	Composition (%)	Fresh	Fragmented	Humified
10.50	1.50		26.00	32.00	42.00

Horizon description				
Horizon	Thickness (cm)	Colour Wet	Colour Dry	Description
Ah	0-12	10YR2/1	10YR4/1	Water status: very wet. Mottle: non-existent. Rock Fragments: many, gravely, Shape-spherical. Soil Texture: Loam. Soil Structure: moderate, granular. Consistence: friable, sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: many fine roots and few coarse roots. No soil crusts. Horizon boundary: smooth and gradual.
AC	12-24	10YR4/4	10YR6/3	Water status: very wet. Mottle: non-existent. Rock Fragments: many, gravely, Shape-spherical. Soil Texture: Sand. Soil Structure: weak, granular. Consistence: friable, slightly sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: few fine roots and common coarse roots. No soil crusts. Horizon boundary: smooth and gradual.
C	24-50+	10YR4/6	10YR6/6	Water status: very wet. Mottle: non-existent. Rock Fragments: many, gravely, Shape-spherical. Soil Texture: Sand. Soil Structure: weak, granular. Consistence: friable, slightly sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: few fine roots and manny coarse roots. No soil crusts.

Table 79. Pit description of plot MM05 (mixed stand of *Pinus sylvestris* L. and *Pinus pinaster* Ait. in triplet 05): analytic data of the mineral horizons. ***

Analytic data

Horizons	Texture (%)			Stones	Density (g cm^{-3})		Porosity
	Sand	Silt	Clay	(%)	Bulk	Real	(%)
Ah	51.44	23.51	18.24	11.70	0.71	2.20	67.86
AC	47.09	22.49	16.60	15.27	1.24	2.57	51.94
C	45.03	21.81	17.52	17.88	1.44	2.31	37.68

Horizons	pH (H_2O)	EC (dS m^{-1})	Pav (mg kg^{-1})	TN (mg g^{-1})	C properties (mg g^{-1})			
					TOC	oxC	Cmic	Cmin
Ah	4.38	158.0	5.4	1.78	55.88	34.69	0.11	0.76
AC	4.47	152.5	5.0	0.80	19.57	4.75	-	-
C	4.5	149.0	6.1	0.24	4.08	4.10	-	-

Horizons	Exchangeable cations (cmol$^+$ kg^{-1})					
	CEC	Na$^+$	K$^+$	Ca^{++}	Mg^{++}	SB
Ah	14.74	0.75	0.19	3.26	0.66	4.86
AC	10.03	0.82	0.14	1.39	0.42	2.77
C	7.04	0.73	0.21	1.21	0.44	2.59

Horizons	Water properties			
	FC (%)	PWP (%)	AW (%)	WHC (g cm^{-2})
Ah	44.73	7.83	36.90	2.76
AC	23.86	4.27	19.59	2.46
C	13.13	4.61	8.52	2.62

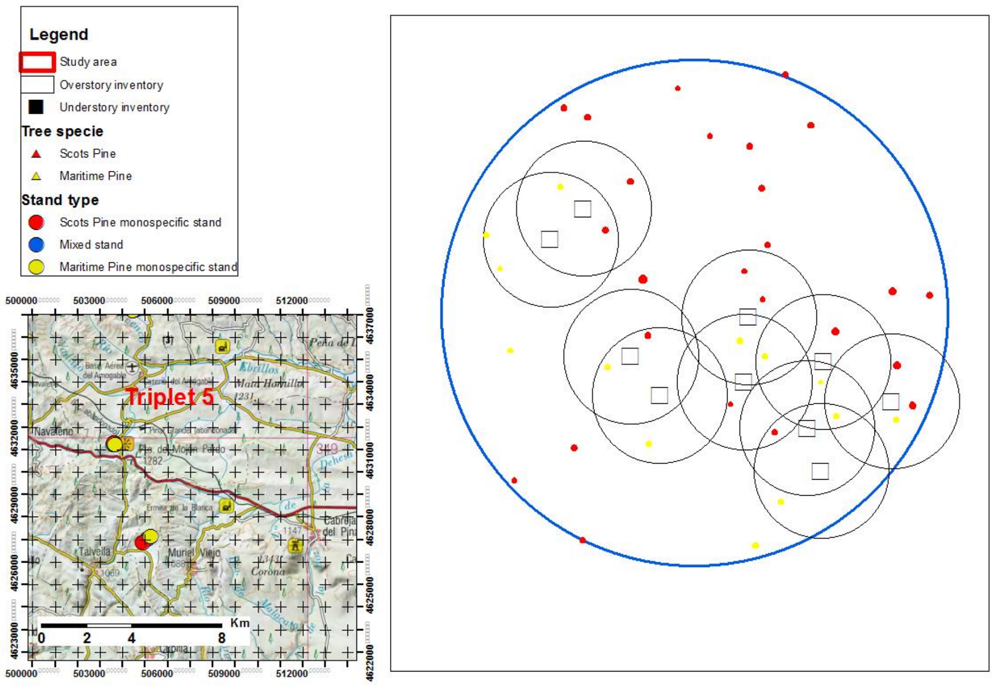


Figure 72. Map of stems position in plot MM05 (mixed stand of *Pinus sylvestris* L. and *Pinus pinaster* Ait. in triplet 05)****

Triplet 6

Table 80. Pit description of plot PS06 (monospecific stand of *Pinus sylvestris* L. in triplet 06). Site, overstory and understory description, and pictures of the plot and the pit soil profile. *

Plot PS06			Triplet 06	Monospecific stand of *Pinus sylvestris* L.
Site description				
Author			Daphne López Marcos y Luis Alfonso Ramos Calvo	
Date			12/03/2016	
Weather			Sunny / Rain in the last 24 hours	
Soil climate	Moisture regime		Xeric	
	Temperature regime		Mesic	
Location	Province		Soria	
	Town		Cabrejas del Pinar	
	Place		Cueva de Matarubias	
	Coordinates (UTM)	X	30T 0504876	
		Y	4626851	
	Altitude		1093 m	
	Stepness		2.00%	
	Orientation		306°	
Soil	Parent material		Sandstones and Marls	
	Geologic age		Mesozoic	
	Soil type		Typic dystroxerept	
Vegetation	Potential		*Junipereto hemisphaerico-thuriferae S.*	
	Current		*Pinus sylvestris* L.	

Overstory description

	N (trees ha^{-1})			G (m^2 ha^{-1})			DHB (cm)			Ho (m)			Age (years)		SI	
	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	Ps	Pp	Ps	Pp
PS06	821	778	42	33.3	30.8	2.6	22.7	22.4	27.7	18.5	17.8	19.5	44	0	26	0

Understory vegetation

Cover (%)		More abundant understory vegetation
Litter	59	*Pinus sylvestris* (seedlings/saplings) and *Cistus laurifolius.*
Vascular plants	31	
Bryophytes	1	

Pictures

Plot	Pit soil profile
	

Table 81. Pit description of plot PS06 (monospecific stand of *Pinus sylvestris* L. in triplet 06): Climatic data, profile description including organic (leaf litter) and mineral horizons (Horizons). **

Climatic description													
Month	J	F	M	A	My	Jn	Jl	Ag	S	O	N	D	X
Rainfall (mm)	75	62	53	80	82	50	30	30	41	89	84	85	786
Temperature (°C)	1.9	2.9	5.5	8.0	11.8	15.2	18.1	17.9	14.3	9.8	5.3	2.8	9.4

Leaf litter description					
Biomass (Mg ha^{-1})	Thickness (cm)	Composition (%)	Fresh	Fragmented	Humified
28.30	4.00		30.00	34.00	36.00

Horizon description				
Horizon	Thickness (cm)	Colour		Description
		Wet	Dry	
Ah	0-28	10YR6/3	10YR7/2	Water status: slightly moist. Mottle: non-existent. Rock Fragments: few, gravely, Shape-spherical. Soil Texture: Sand. Soil Structure: weak, granular. Consistence: friable, sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: many fine roots and few coarse roots. No soil crusts. Horizon boundary: smooth and gradual.
C	28-65+	10YR5/6	10YR4/1	Water status: slightly moist. Mottle: non-existent. Rock Fragments: few, gravely, Shape-spherical. Soil Texture: Sand. Soil Structure: weak, granular. Consistence: very friable, sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: few fine roots and many coarse roots. No soil crusts.

Table 82. Pit description of plot PS06 (monospecific stand of *Pinus sylvestris* L. in triplet 06): analytic data of the mineral horizons. ***

Analytic data

Horizons	Texture (%)			Stones (%)	Density ($g\ cm^{-3}$)		Porosity (%)
	Sand	Silt	Clay		Bulk	Real	
Ah	80.64	8.56	8.36	13.03	1.13	2.41	53.20
C	73.57	12.20	11.16	5.53	1.39	2.46	43.63

Horizons	pH (H_2O)	EC ($dS\ m^{-1}$)	Pav ($mg\ kg^{-1}$)	TN ($mg\ g^{-1}$)	C properties ($mg\ g^{-1}$)			
					TOC	oxC	Cmic	Cmin
Ah	4.45	28.5	4.2	0.66	18.03	19.03	0.05	0.82
C	4.60	15.9	3.4	0.45	6.06	5.33	-	-

Horizons	Exchangeable cations ($cmol^+\ kg^{-1}$)					
	CEC	Na^+	K^+	Ca^{++}	Mg^{++}	SB
Ah	22.6	0.9	0.1	2.4	0.5	3.8
C	16.3	0.8	0.1	1.5	0.4	2.8

Horizons	Water properties			
	FC (%)	PWP (%)	AW (%)	WHC ($g\ cm^{-2}$)
Ah	15.01	6.45	8.56	2.35
C	9.16	3.06	6.11	1.76

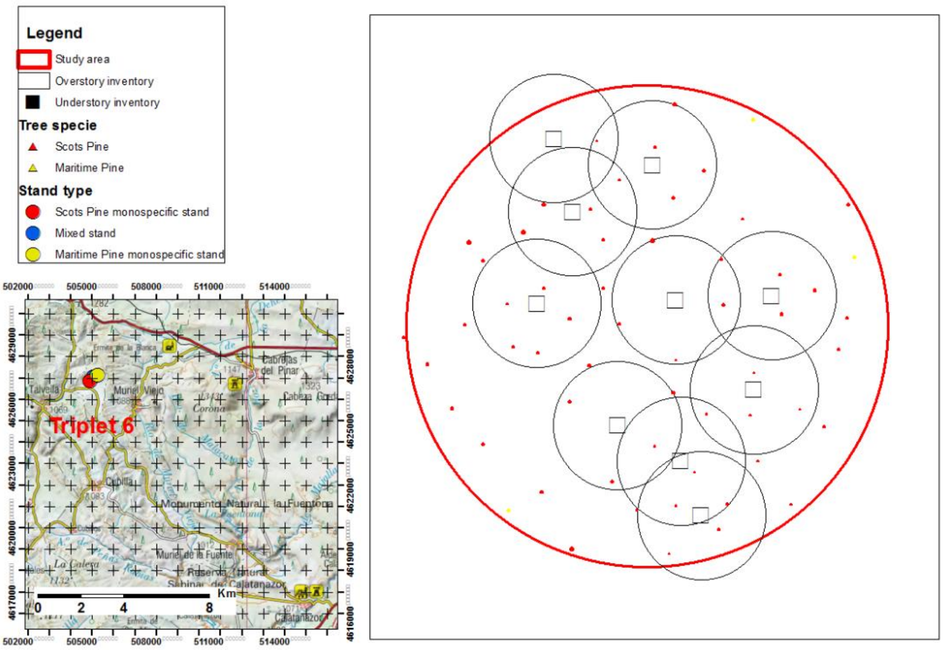


Figure 73. Map of stems position of plot PS06 (monospecific stand of *Pinus sylvestris* L. in triplet 06)****.

Table 83. Pit description of plot PP06 (monospecific stand of *Pinus pinaster* Ait. in triplet 06). Site, overstory and understory description, and pictures of the plot and the pit soil profile. *

Plot PP06			Triplet 06	Monospecific stand of *Pinus pinaster Aiton.*
Site description				
Author			Daphne López Marcos y Luis Alfonso Ramos Calvo	
Date			12/03/2016	
Weather			Sunny / Rain in the last 24 hours	
Soil climate	Moisture regime		Xeric	
	Temperature regime		Mesic	
Location	Province		Soria	
	Town		Cabrejas del Pinar	
	Place		Cueva de Matarubias	
	Coordinates (UTM)	X	30T 505260	
		Y	4627130	
	Altitude		1116 m	
	Stepness		12.00%	
	Orientation		222°	
Soil	Parent material		Sandstones and Marls	
	Geologic age		Mesozoic	
	Soil type		Typic dystroxerept	
Vegetation	Potential		*Junipereto hemisphaerico-thuriferae S.*	
	Current		*Pinus pinaster* Ait.	

Overstory description

	N (trees ha^{-1})			G (m^2 ha^{-1})			DHB (cm)			Ho (m)			Age (years)		SI	
	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	Ps	Pp	Ps	Pp
PP06	594	0	594	37.5	0	37.5	28.4	0	28.4	16.9	0	16.9	0	49	0	23

Understory vegetation

Cover (%)			More abundant understory vegetation
Litter	56		*Calluna vulgaris, Pinus pinaster* (seedlings/saplings), *Arctostaphillos uva-ursi* and *Erica australis*
Vascular plants	42		
Bryophytes	2		

Pictures

Plot	Pit soil pofile
	

Table 84. Pit description of plot PP06 (monospecific stand of *Pinus pinaster* Ait. in triplet 06): Climatic data, profile description including organic (leaf litter) and mineral horizons (Horizons). **

Climatic description													
Month	J	F	M	A	My	Jn	Jl	Ag	S	O	N	D	X
Rainfall (mm)	75	62	53	80	82	50	30	30	41	89	84	85	786
Temperature (ºC)	1.9	2.9	5.5	8.0	11.8	15.2	18.1	17.9	14.3	9.8	5.3	2.8	9.4

Leaf litter description					
Biomass (Mg ha^{-1})	Thickness (cm)	Composition (%)	Fresh	Fragmented	Humified
6.20	2.00		49.00	25.00	26.00

Horizon description				
Horizon	Thickness (cm)	Colour		Description
		Wet	Dry	
Ah	0-12	10YR4/1	10YR6/2	Water status: slightly moist. Mottle: non-existent. Rock Fragments: few, gravely, Shape-spherical. Soil Texture: Sand. Soil Structure: weak, granular. Consistence: friable, slightly sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: few fine roots and many coarse roots. No soil crusts. Horizon boundary: smooth and gradual.
C	12-50+	10YR6/4	10YR7/3	Water status: slightly moist. Mottle: non-existent. Rock Fragments: few, gravely, Shape-spherical. Soil Texture: Sand. Soil Structure: weak, granular. Consistence: very friable, slightly sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: few fine roots and many coarse roots. No soil crusts.

Table 85. Pit description of plot PP06 (monospecific stand of *Pinus pinaster* Ait. in triplet 06): analytic data of the mineral horizons. ***

Analytic data

Horizons	Texture (%)			Stones (%)	Density (g cm^{-3})		Porosity (%)
	Sand	Silt	Clay		Bulk	Real	
Ah	85.29	8.91	4.98	6.44	1.21	2.63	53.89
C	84.45	8.28	6.13	9.07	1.41	2.65	46.78

Horizons	pH	EC (dS m^{-1})	Pav (mg kg^{-1})	TN (mg g^{-1})	C properties (mg g^{-1})			
					TOC	oxC	Cmic	Cmin
Ah	4.90	129.0	4.1	0.33	11.10	4.38	0.05	0.83
C	5.16	111.0	1.6	0.25	3.21	3.52	-	-

Horizons	Exchangeable cations ($cmol^+ kg^{-1}$)					
	CEC	Na^+	K^+	Ca^{++}	Mg^{++}	SB
Ah	13.4	0.9	0.1	1.8	0.5	3.2
C	16.0	0.8	0.1	1.1	0.4	2.4

Horizons	Water properties			
	FC (%)	PWP (%)	AW (%)	WHC (g cm^{-2})
Ah	24.71	1.18	23.53	3.20
C	18.69	1.03	17.66	8.60

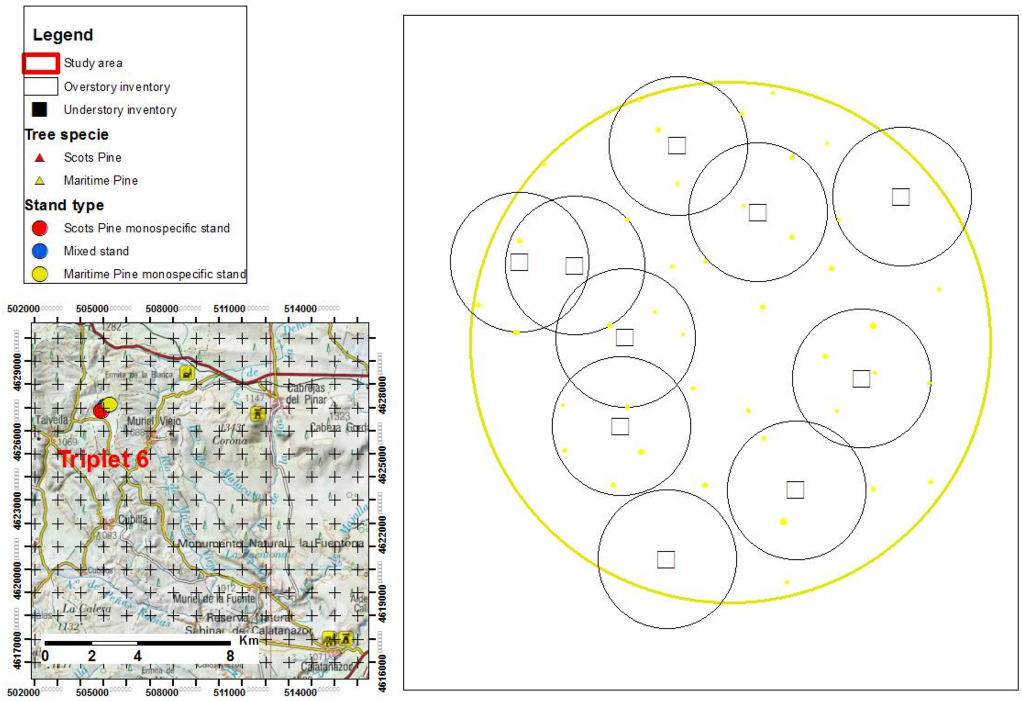


Figure 74. Map of stems position in plot PP06 (monospecific stand of *Pinus pinaster* Ait. in triplet 06)****.

Table 86. Pit description of plot MM06 (mixed stand of *Pinus sylvestris* L. and *Pinus pinaster* Ait. in triplet 06). Site, overstory and understory description, and pictures of the plot and the pit soil profile. *

Plot MM06			Triplet 06	Mixed stand
Site description				
Author			Daphne López Marcos y Luis Alfonso Ramos Calvo	
Date			12/03/2016	
Weather			Sunny / Rain in the last 24 hours	
Soil climate	Moisture regime		Xeric	
	Temperature regime		Mesic	
Location	Province		Soria	
	Town		Cabrejas del Pinar	
	Place		Cueva de Matarubias	
	Coordinates (UTM)	X	30T 505084	
		Y	4627042	
	Altitude		1119 m	
	Stepness		11.00%	
	Orientation		184°	
Soil	Parent material		Sandstones and Marls	
	Geologic age		Mesozoic	
	Soil type		Typic dystroxerept (Soil Taxonomy, 2015)	
Vegetation	Potential		*Junipereto hemisphaerico-thuriferae S*	
	Current		*Pinus sylvestris L. and Pinus pinaster* Ait.	

Overstory description

	N (trees ha^{-1})			G (m^2 ha^{-1})			DHB (cm)			Ho (m)			Age (years)		SI	
	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	plot	Ps	Pp	Ps	Pp	Ps	Pp
MM06	679	396	283	33.3	13	20.2	25	20.5	30.2	16.1	15	16.1	44	49	23	23

Understory vegetation

Cover (%)		More abundant understory vegetation
Litter	34	*Arctostaphillos uva-ursi, Erica australis* and *Calluna vulgaris*
Vascular plants	59	
Bryophytes	2	

Pictures

Plot	Pit soil profile
	

Table 87. Pit description of plot MM06 (mixed stand of *Pinus sylvestris* L. and *Pinus pinaster* Ait. in triplet 06): Climatic data, profile description including organic (leaf litter) and mineral horizons (Horizons). **

Climatic description													
Month	J	F	M	A	My	Jn	Jl	Ag	S	O	N	D	X
Rainfall (mm)	75	62	53	80	82	50	30	30	41	89	84	85	786
Temperature (ºC)	1.9	2.9	5.5	8.0	11.8	15.2	18.1	17.9	14.3	9.8	5.3	2.8	9.4

Leaf litter description					
Biomass (Mg ha^{-1})	Thickness (cm)	Composition (%)	Fresh	Fragmented	Humified
17.60	2.00		50.00	19.00	31.00

<table>
<tr><th colspan="5">Horizon description</th></tr>
<tr><th rowspan="2">Horizon</th><th rowspan="2">Thickness (cm)</th><th colspan="2">Colour</th><th rowspan="2">Description</th></tr>
<tr><th>Wet</th><th>Dry</th></tr>
<tr><td>Ah</td><td>0-30</td><td>10YR3/1</td><td>10YR6/1</td><td>Water status: slightly moist. Mottle: non-existent. Rock Fragments: few, gravely, Shape-spherical. Soil Texture: Sand. Soil Structure: weak, granular. Consistence: friable, slightly sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: common fine roots and few coarse roots. No soil crusts. Horizon boundary: smooth and gradual.</td></tr>
<tr><td>C</td><td>30-70+</td><td>10YR5/6</td><td>10YR8/3</td><td>Water status: slightly moist. Mottle: non-existent. Rock Fragments: few, gravely, Shape-spherical. Soil Texture: Sand. Soil Structure: weak, granular. Consistence: very friable, slightly sticky and slightly plastic. Pores: common, fine and interstitial. No anthropic activity apparent. Roots: few fine roots and common coarse roots. No soil crusts.</td></tr>
<tr><td></td><td></td><td></td><td></td><td></td></tr>
</table>

Table 88. Pit description of plot MM06 (mixed stand of *Pinus sylvestris* L. and *Pinus pinaster* Ait. in triplet 06): analytic data of the mineral horizons. ***

Analytic data

Horizons	Texture (%)			Stones (%)	Density ($g\ cm^{-3}$)		Porosity (%)
	Sand	Silt	Clay		Bulk	Real	
Ah	71.72	14.15	9.30	47.93	1.10	2.23	50.50
C	78.05	14.14	5.25	11.88	1.49	2.63	43.19

Horizons	pH (H_2O)	EC ($dS\ m^{-1}$)	Pav ($mg\ kg_{-1}$)	TN ($mg\ g^{-1}$)	C properties ($mg\ g^{-1}$)			
					TOC	oxC	Cmic	Cmin
Ah	4.6	145.5	7.5	55.46	42.7	42.7	0.06	0.91
C	5.0	119.0	0.5	4.39	2.6	3.4	-	-

Horizons	Exchangeable cations ($cmol^+\ kg^{-1}$)					
	CEC	Na^+	K^+	Ca^{++}	Mg^{++}	SB
Ah	17.4	0.9	0.2	3.9	0.8	5.8
C	10.5	0.9	0.1	1.1	0.4	2.5

Horizons	Water properties			
	FC (%)	PWP (%)	AW (%)	WHC ($g\ cm^{-2}$)
Ah	41.92	5.20	36.72	6.33
C	14.06	0.95	13.11	5.17

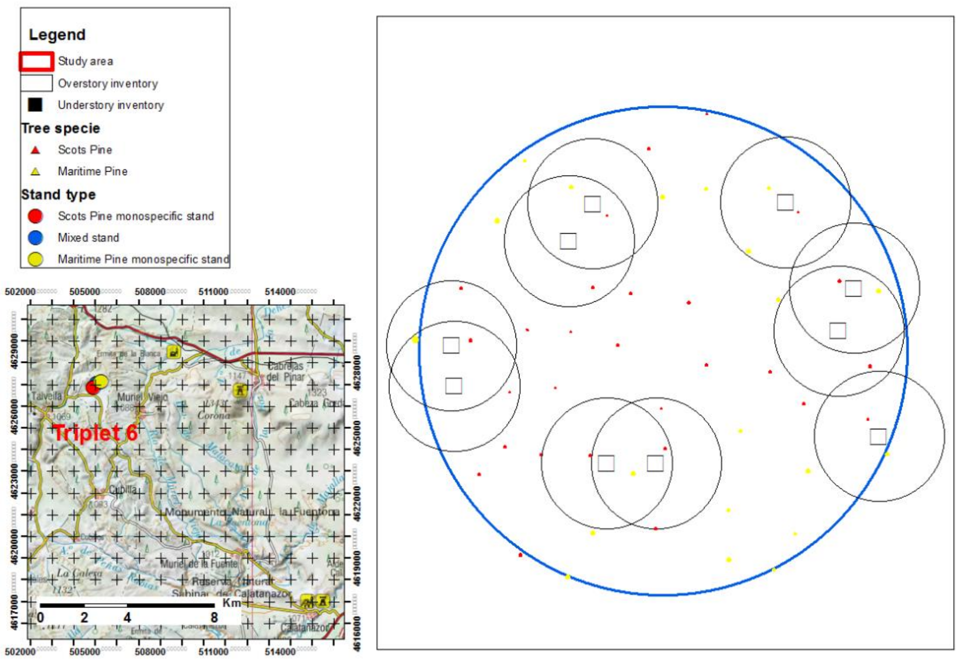


Figure 75. Map of stems position in plot MM06 (mixed stand of *Pinus sylvestris* L. and *Pinus pinaster* Ait. in triplet 06)****.

List of Acronyms

Acronym	Description
	Overstory
%PP	Percentage of Maritime pine basal area
%PS	Percentage of Scots pine basal area
Age	Normal age (years)
dg	Quadratic mean diameter (cm)
DHB	Diameter at breast height (cm)
G	Basal area per hectare (m^2 ha^{-1})
GPP	Maritime pine basal area per hectare (m^2 ha^{-1})
GPS	Scots pine basal area per hectare (m^2 ha^{-1})
Ho	Dominant height (m)
ipD	Distances from a random point to the nearest tree as Hopkin´s (1954)
iiD	Distances from such a tree to its nearest neighbor as Hopkin´s (1954).
MM	Mixture plot of Scots and Maritime pine
N	Density (stems per hectare; trees ha^{-1})
PP	Maritime pine monospecific plots
pp	*Pinus pinaster* Ait. stems
PS	Scots pine monospecific plots
ps	*Pinus sylvestris* L. stems
SI	Site index for *Pinus sylvestris* L. according to Rojo and Montero (1996) and for *Pinus pinaster* Ait. according to Bravo et al. (2007) related at age 100 for total plot
	Understory
Agca	*Agrostis castellana* Boiss. & Reut.
Aica	*Aira caryophyllea* L.
Armo	*Arenaria montana* L.
Aruv	*Arctostaphylos uva-ursi* (L.) Spreng.
Asal	*Asphodelus albus* Mill.
Cavu	*Calluna vulgaris* (L.) Hull
Cila	*Cistus laurifolius* L.
Cover	Percentage of plant cover (%)

Acronym	Description
	Overstory
CR	Critically endangered species according to UICN (2012)
Defl	*Deschampsia flexuosa* (L.) Trin.
EN	Endangered species according to UICN (2012)
Erar	*Erica arborea* L.
Erau	*Erica australis* L.
Gasa	*Galium saxatile* L.
Gero	*Geranium robertianum* L.
Hyra	*Hypochoeris radicata* L.
Hysp	*Hypnum* spp.
Ilaq	*Ilex aquifolium* L.
Juco	*Juncus conglomeratus* L.
Juox	*Juniperus oxycedrus* L.
Lesp	Leucobrium sp.
Loco	*Lotus corniculatus* L.
Mepa	*Melampyrum pratense* L.
Pipi	*Pinus pinaster* Ait. (seedlings/saplings)
Pisy	*Pinus sylvestris* L. (seedlings/saplings)
Pomo	*Potentilla montana* Brot.
Povu	*Polygala vulgaris* L.
Ptaq	*Pteridium aquilinum* (L.) Kuhn
Qufa	*Quercus faginea* Lam. (seedlings/saplings)
Qupy	*Quercus pyrenaica* Willd. (seedlings/saplings)
S	Richness (Colwell 2009)
Sami	*Sanguisorba minor* Scop.
Sima	*Simethis mattiazzii* (Vand.) Sacc.
SpI	Species of special interest according the regional o national laws
Vamy	*Vaccinium myrtillus* L.
Vimo	*Viola montcaunica* Pau
VU	Vulnerable species according to UICN (2012)

Soil	
%clay	Soil clay content according to USDA criteria determined by the pipette method (MAPA 1994)
%CR	Percentage of coarse roots
%EFHi	Percentage of earth fraction of each horizon
%FR	Percentage of fine roots
%sand	Soil sand content according to USDA criteria determined by the pipette method (MAPA 1994)
%silt	Soil silt contents according to USDA criteria determined by the pipette method (MAPA 1994)
AW	Available water according to MAPA (1994)
bD	Soil bulk density (g cm^{-3})
bD_{Hi}	Bulk density of each horizon
B_{FF}	Forest floor biomass (Mg ha^{-1})
B_{FgL}	Biomass of partially decomposed litter or fragmented fraction (Mg ha^{-1})
B_{FsL}	Biomass of almost undecomposed litter or fresh fraction (Mg ha^{-1})
B_{HmL}	Biomass of mostly decomposed organic matter or humified fraction (Mg ha^{-1})
C	Carbon
$Cstock_{0\text{-}10cm}$	Total organic carbon stock in the topsoil (0-10 cm depth); Mg ha^{-1}
$Cstock_{0\text{-}40cm}$	Total organic carbon stock in the whole mineral soil profile (0-40cm depth); Mg ha^{-1}
$Cstock_{10\text{-}20cm}$	Total organic carbon stock in the 10-20 cm depth mineral soil (Mg ha^{-1})
$Cstock_{20\text{-}30cm}$	Total organic carbon stock in the 20-30 cm depth mineral soil (Mg ha^{-1})
$Cstock_{30\text{-}40cm}$	Total organic carbon stock in the 30-40 cm depth mineral soil (Mg ha^{-1})
$Cstock_{FF}$	Total organic carbon stock of the Forest floor (Mg ha^{-1})
$Cstock_{FgL}$	Total organic carbon stock of the partially decomposed litter or fragmented fraction (Mg ha^{-1})
$Cstock_{FsL}$	Total organic carbon stock of the almost undecomposed litter or fresh fraction (Mg ha^{-1})
$Cstock_{HmL}$	Total organic carbon stock of the mostly decomposed organic matter or humified fraction (Mg ha^{-1})
$Cstock_{SOIL}$	Total organic carbon stock of the mineral soil (Mg ha^{-1})

Ca^{+2}	Exchangeable calcium according to Schollenberger and Simon (1945); $cmol_c\ kg^{-1}$
$Ca^{+2}{}_{0\text{-}10cm}$	Exchangeable calcium in the topsoil (0-10 cm depth); $cmol_c\ kg^{-1}$
$Ca^{+2}{}_{10\text{-}20cm}$	Exchangeable calcium in the 10-20 cm mineral soil layer ($cmol_c\ kg^{-1}$)
$Ca^{+2}{}_{20\text{-}30cm}$	Exchangeable calcium in the 20-30 cm mineral soil layer ($cmol_c\ kg^{-1}$)
$Ca^{+2}{}_{30\text{-}40cm}$	Exchangeable calcium in the 30-40 cm mineral soil layer ($cmol_c\ kg^{-1}$)
$Ca^{+2}stock$	Exchangeable calcium stock in the whole mineral soil profile (0-50cm depth); $Mg\ ha^{-1}$
$Ca^{+2}\ stock_{Hi}$	Exchangeable calcium stock of each horizon ($Mg\ ha^{-1}$)
CEC	Cation exchange capacity according to Mehlich (1953); $cmol_c\ kg^{-1}$
Cmic	Microbial biomass using the fumigation-extraction method according Vance et al. (1987); $mg\ g^{-1}$
Cmin	Mineralizable carbon according to Isermeyer (1952); $mg\ g^{-1}$
CN	Total organic carbon and total nitrogen ratio
CN_{FF}	Total organic carbon and total nitrogen ratio in the forest floor
CN_{FgL}	Total organic carbon and total nitrogen ratio of the almost undecomposed litter or fresh fraction
CN_{FgL}	Total organic carbon and total nitrogen ratio of the partially decomposed litter or fragmented fraction
CN_{HmL}	Total organic carbon and total nitrogen ratio of the mostly decomposed organic matter or humified fraction
Cstock	Total organic carbon stock in the whole mineral soil profile (0-50cm depth); $Mg\ ha^{-1}$
$Cstock_{Hi}$	Total organic carbon stock of each horizon ($Mg\ ha^{-1}$)
EC	Electrical conductivity according to MAPA (1994); dS/m
EF	Soil earth fraction (<2mm); %
FC	Field capacity (water remaining in a soil after it has been thoroughly saturated for two days and allowed to drain freely); %
FF	Forest floor
FgL	Partially decomposed litter or fragmented fraction according to Van Delft et al. (2006)
FsL	Almost undecomposed litter or fresh fraction according to Van Delft et al. (2006)

HmL	Mostly decomposed organic matter or humified fraction according to Van Delft et al. (2006)
K^+	Exchangeable potassium according to Schollenberger and Simon (1945); $cmol_c\ kg^{-1}$
$K^+_{0\text{-}10cm}$	Exchangeable potassium in the topsoil (0-10 cm depth); $cmol_c\ kg^{-1}$
$K^+_{10\text{-}20cm}$	Exchangeable potassium in the 10-20 cm mineral soil lyer ($cmol_c\ kg^{-1}$)
$K^+_{20\text{-}30cm}$	Exchangeable potassium in the 20-30 cm mineral soil layer ($cmol_c\ kg^{-1}$)
$K_{30\text{-}40cm}$	Exchangeable potassium in the 30-40 cm mineral soil layer ($cmol_c\ kg^{-1}$)
K^+stock	Exchangeable potassium stock in the whole mineral soil profile (0-50cm depth); Mg ha^{-1}
K^+stock_{Hi}	Exchangeable potassium stock of each horizon (Mg ha^{-1})
Mg^{+2}	Exchangeable magnesium according to Schollenberger and Simon (1945); $cmol_c\ kg^{-1}$
$Mg^{+2}_{0\text{-}10cm}$	Exchangeable magnesium in the topsoil (0-10 cm depth); $cmol_c\ kg^{-1}$
$Mg^{+2}_{10\text{-}20cm}$	Exchangeable magnesium in the 10-20 cm mineral soil layer ($cmol_c\ kg^{-1}$)
$Mg^{+2}_{20\text{-}30cm}$	Exchangeable magnesium in the 20-30 cm mineral soil layer ($cmol_c\ kg^{-1}$)
$Mg^{+2}_{30\text{-}40cm}$	Exchangeable magnesium in the 30-40 cm mineral soil lyer ($cmol_c\ kg^{-1}$)
Mg^{+2}stock	Exchangeable magnesium stock in the whole mineral soil profile (0-50cm depth); Mg ha^{-1}
$Mg^{+2}stock_{Hi}$	Exchangeable magnesium stock of each horizon (Mg ha^{-1})
Na^+	Exchangeable sodium according to Schollenberger and Simon (1945); $cmol_c\ kg^{-1}$
$Na^+_{0\text{-}10cm}$	Exchangeable sodium in the topsoil (0-10 cm depth); $cmol_c\ kg^{-1}$
$Na^+_{10\text{-}20cm}$	Exchangeable sodium in the 10-20 cm mineral soil layer ($cmol_c\ kg^{-1}$)
$Na^+_{20\text{-}30cm}$	Exchangeable sodium in the 20-30 cm mineral soil layer ($cmol_c\ kg^{-1}$)
$Na^+_{30\text{-}40cm}$	Exchangeable sodium in the 30-40 cm mineral soil layer ($cmol_c\ kg^{-1}$)
Na+ stock	Exchangeable sodium stock in the whole mineral soil profile (0-50cm depth); Mg ha^{-1}
Na^+stock_{Hi}	Exchangeable sodium stock of each horizon (Mg ha^{-1})
Nstock	Total nitrogen stock in the whole mineral soil profile (0-50cm depth); Mg ha^{-1}
$Nstock_{Hi}$	Total nitrogen stock of each horizon(Mg ha^{-1})
oxC	Easily oxidizable carbon according to Walkley (1947)
oxC_{Hi}	Easily oxidizable carbon of each horizon (Mg ha^{-1})

oxCstock	Easily oxidizable carbon stockin the whole mineral soil profile (0-50cm depth); Mg ha^{-1}
avP	Available phosphorus according to Olsen and Sommers (1982); ppm
Pavstock	Available phosphorus stock in the whole mineral soil profile (0-50 cm depth); Mg ha^{-1}
$Pavstock_{Hi}$	Available phosphorus stock of each horizon (Mg ha^{-1})
pH (H_2O)	pH according to MAPA (1994)
PWP	Permanenten wilting point (soil water content retained at 1500 kPa using Eijkelkamp pF Equipment); %
SB	Sum of bases (sum of the Ca^{+2}, Mg^{+2}, K^{+} and Na^{+} concentrations); $cmol_c$ kg^{-1}
SB_{0-10cm}	Sum of bases in the topsoil (0-10 cm depth); $cmol_c$ kg^{-1}
$SB_{10-20cm}$	Sum of bases in the 10-20 cm mineral soil layer ($cmol_c$ kg^{-1})
$SB_{20-30cm}$	Sum of bases in the 20-30 cm mineral soil layer ($cmol_c$ kg^{-1})
$SB_{30-40cm}$	Sum of bases in the 30-40 cm mineral soil layer ($cmol_c$ kg^{-1})
SOC	Soil organic carbon
Stones	Coarse soil material (>2mm); %
Thi	Thickness of each horizon (cm)
TN	Total nitrogen analyzed by dry combustion using a LECO CHN-2000 elemental analyzer(mg g^{-1})
TOC	Total organic carbon by dry combustion using a LECO CHN-2000 elemental analyzer (mg g^{-1})
TOC_{0-10cm}	Total organic carbon in the topsoil (0-10 cm depth); mg g^{-1}
$TOC_{10-20cm}$	Total organic carbon in the 10-20 cm mineral soil layer (mg g^{-1})
$TOC_{20-30cm}$	Total organic carbon in the 20-30 cm mineral soil layer (mg g^{-1})
TOC_{30-0cm}	Total organic carbon in the 30-40 cm mineral soil layer (mg g^{-1})
WHC	Water holding capacity in the whole mineral soil profile (0-50 cm); g water cm^{-2}
WHC_{Hi}	Water holding capacity of each horizon (g water cm^{-2})

Data analysis	
AIC	Akaike Information Criterion (Akaike 1973)
DCA	Detrended Correspondence Analysis (Oksanen 2016)
HOF models	Huisman–Olff–Fresco models (Huisman et al. 1993)
LMM	Linear Mixed Models (Pinheiro and Bates 2000)
RDA	Redundancy analysis (Oksanen 2016)
REML	Restricted Maximum Likelihood method (Richards 2005)
SEMs	Structural Equation Models (Rosseel 2012)
Others	
IGME	Instituto Geológico y Minero de España
Cfb	Temperate without dry season and warm summer climate
Csb	Temperate with dry summer climate
iuFOR	Sustainable Forest Research Management Institute
m a.s.l	Metres abovethe sea level
UVa	University of Valladolid

"mais je fais ma part"