



# Overyielding in mixed pine forests with belowground complementarity: impacts on understory

Daphne López-Marcos<sup>1,2</sup> · María-Belén Turrión<sup>1,2</sup> · Felipe Bravo<sup>1,3</sup> · Carolina Martínez-Ruiz<sup>1,2</sup>

Received: 23 July 2020 / Revised: 24 December 2020 / Accepted: 5 February 2021 / Published online: 24 February 2021  
© The Author(s), under exclusive licence to Springer-Verlag GmbH, DE part of Springer Nature 2021

## Abstract

The impact of biodiversity loss on the functioning of forest ecosystems has become a central issue in ecology. Most reports of the positive effects of tree mixture on the biodiversity–productivity relationship focus on mixtures that combine tree species with contrasting traits. Nevertheless, little is known about how coniferous mixtures of the same genus affect forest productivity, what mechanisms are involved, and how the understory is affected. Here, we assessed the effect of mixed versus monospecific stands of *Pinus sylvestris* L. and *P. pinaster* Ait. on productivity, its impact on the understory, and its relationship with soil water and fertility, based on research with six triplets (6 triplets × 3 forest stands × 1 plot = 18 plots) in North-Central Spain. Each triplet consisted of two plots dominated either by *P. sylvestris* or *P. pinaster* and of one mixed plot that contained both species. Productivity, at the stand and neighborhood levels, and the understory richness, and soil water and fertility at the stand level were analyzed. A positive effect of pine mixture on productivity was observed at the smaller spatial scale, and it had no negative effect on the understory richness. The greater space-use efficiency (higher tree density and basal area) of both *Pinus* species in the admixtures was related to soil water and fertility niche complementarity. The fundamental role of scale in determining the relationship between species richness and ecosystem functioning in forests is highlighted.

---

Communicated by Miren del Rio.

---

✉ Daphne López-Marcos  
daphne.lopez@uva.es

María-Belén Turrión  
bturrión@agro.uva.es

Felipe Bravo  
fbravo@pvs.uva.es

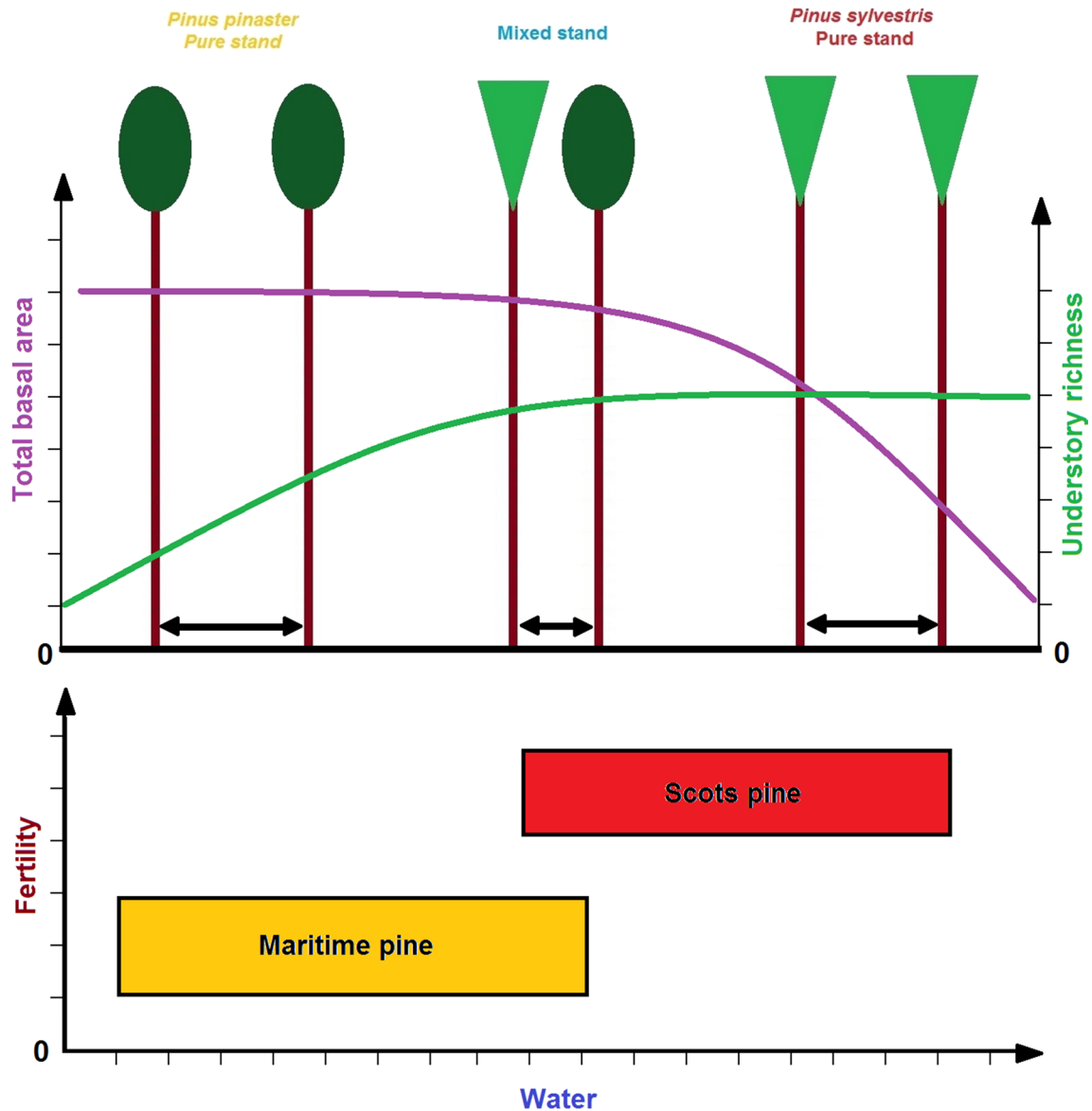
Carolina Martínez-Ruiz  
caromar@agro.uva.es

<sup>1</sup> Sustainable Forest Management Research Institute UVA-INIA, Avda. Madrid 50, 34071 Palencia, Spain

<sup>2</sup> Dpto. de Ciencias Agroforestales, E.T.S. de Ingenierías Agrarias, Universidad de Valladolid, Campus La Yutera, Avda. Madrid 50, 34071 Palencia, Spain

<sup>3</sup> Dpto. de Producción Vegetal Y Recursos Forestales, E.T.S. de Ingenierías Agrarias, Universidad de Valladolid, Campus La Yutera, Avda. Madrid 50, 34071 Palencia, Spain

## Graphic abstract



**Keywords** Neighborhood spatial scale · Understorey richness · Soil niche complementarity · 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 (Knocke 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; Vilà et al. 2007; Pretzsch et al. 2012; Gamfeldt et al. 2013). Biodiversity promotes 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. 1997; Luo et al. 2019) seems to be the best potential explanation for species packing and a key mechanism by which the productivity of species mixtures is enhanced compared to the respective monocultures (Hooper and Dukes 2004),

i.e., overyielding (Madriral-González et al. 2016). Through niche complementarity, competing species change their pattern of resource use (Hector and Hooper 2002) that reduces competition and promotes coexistence between species, which 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; Madriral-González et al. 2016), it has been also described in forests; both in the exploitation of above- (Forrester and Albrecht 2014; Forrester et al. 2018) and belowground resources (Brassard et al. 2013; Seidel et al. 2013), such as the influence of rooting architecture (Van de Peer et al. 2018) or different roots depth in the soil water and nutrients total acquisition (Forrester et al. 2010; Reyer et al. 2010; Pretzsch et al. 2013).

Forest management is commonly applied in small units, typically called a stand (Bravo-Oviedo et al. 2014), covering more than 0.5 ha according to Lanz et al. (2010), and defined by a relative homogeneity in age, structure, composition, and site conditions, and with sufficient area to permit independent treatments as the thinning (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 mixtures change with the spatial scale (Bravo-Oviedo et al. 2014). Multiple studies in forests have analyzed the biodiversity–productivity relationship at the scale of tree communities (Grossman et al. 2017; Van de Peer et al. 2018), although positive biodiversity–productivity relationship was only demonstrated at smaller scales (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 spatial scales in mixed forests is welcome (Rodríguez-Calcerrada et al. 2011), as this is what will be considered in this study.

Mixed forests can be considered as a network of locally interacting individuals of different species (Vandermeer 1989; Michalet et al. 2015). 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). The outcome of such small-scale interactions can be positive (e.g., niche complementarity) or negative (e.g., competition for resources), and it can shift with time (Fichtner et al. 2018) and, for instance, with the availability of the limiting resource. 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 composition and richness can 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). 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 lower light availability (Dorman et al. 2020). However, managers and ecologists traditionally have paid little 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 retention (Liu et al. 2017), the assessment of the repercussion of the mixed forest overyielding on the understory is necessary.

In recent years, numerous experiments have explored the biodiversity–productivity relationship in forests, from a global scale (Jactel et al. 2018) to a small scale (Nguyen et al. 2012; Fichtner et al. 2018), including mixed forests (Forrester et al. 2004, 2005, 2006) but also comparing monospecific vs mixed forests (Pretzsch et al. 2012; Thurm and Pretzsch 2016; Riofrío et al. 2017a). Nevertheless, the biodiversity–productivity relationship in monospecific vs. mixed forests that combine tree species of the same genus remains virtually unknown (but see Forrester and Smith 2012 for *Eucalyptus* species) even more so for coniferous mixtures of the same genus (but see Riofrío et al. 2017a). This is so despite these mixtures being frequent in many environments, such as the admixtures of *Pinus sylvestris* L. (Scots pine) and *Pinus pinaster* Ait. (Maritime pine) in Spain, or the admixtures of *Eucalyptus* species in the southern hemisphere, growing in pure and mixed stands either naturally or as a result of species selection for afforestation (Serrada et al. 2008; Forrester and Smith 2012). Both *Pinus* species show similar crown architecture (Poorter et al. 2012) and slight differences in shade tolerance (Sánchez-Gómez et al. 2006; Gaudio et al. 2011) but differ in water-stress tolerance (Andivia et al. 2020). *P. pinaster* is the dominant species in Mediterranean forests and can survive severe droughts, whereas *P. sylvestris* is the most widely distributed species of pine in the world and commonly grows in humid environments (Bogino and Bravo 2014).

New findings on this pine mixture in the same experimental device were the crucial role of the crown complementarity as a mechanism for enhancing ecosystem productivity (Riofrío et al. 2017a, 2019) or the effect of the mixture on the growth efficiency increasing productivity with regard to pure stands (Cattaneo et al. 2020). However, the increased productivity in these mixtures was already suspected to be partially due to the complementarity in the use of belowground resources, since the highest soil organic carbon stocks were found there due to the greater thickness of the first mineral soil horizon (López-Marcos et al. 2018). The aims of this study were: (1) to test the influence of the spatial scale of

study to detect the greater overstory yield in the mixtures; (2) to understand the mechanisms involved in determining the overstory yield; and (3) to analyze the overstory yield effect on the understory richness in mixed versus monospecific pine forests. We hypothesize that: (1) the heterogeneity in the mixture of both *Pinus* species promotes higher overstory yield at a smaller spatial scale; (2) the higher overstory yield in mixed stands is partially caused by the belowground niche complementarity; and (3) the overstory overyielding in the mixtures reduces the understory richness.

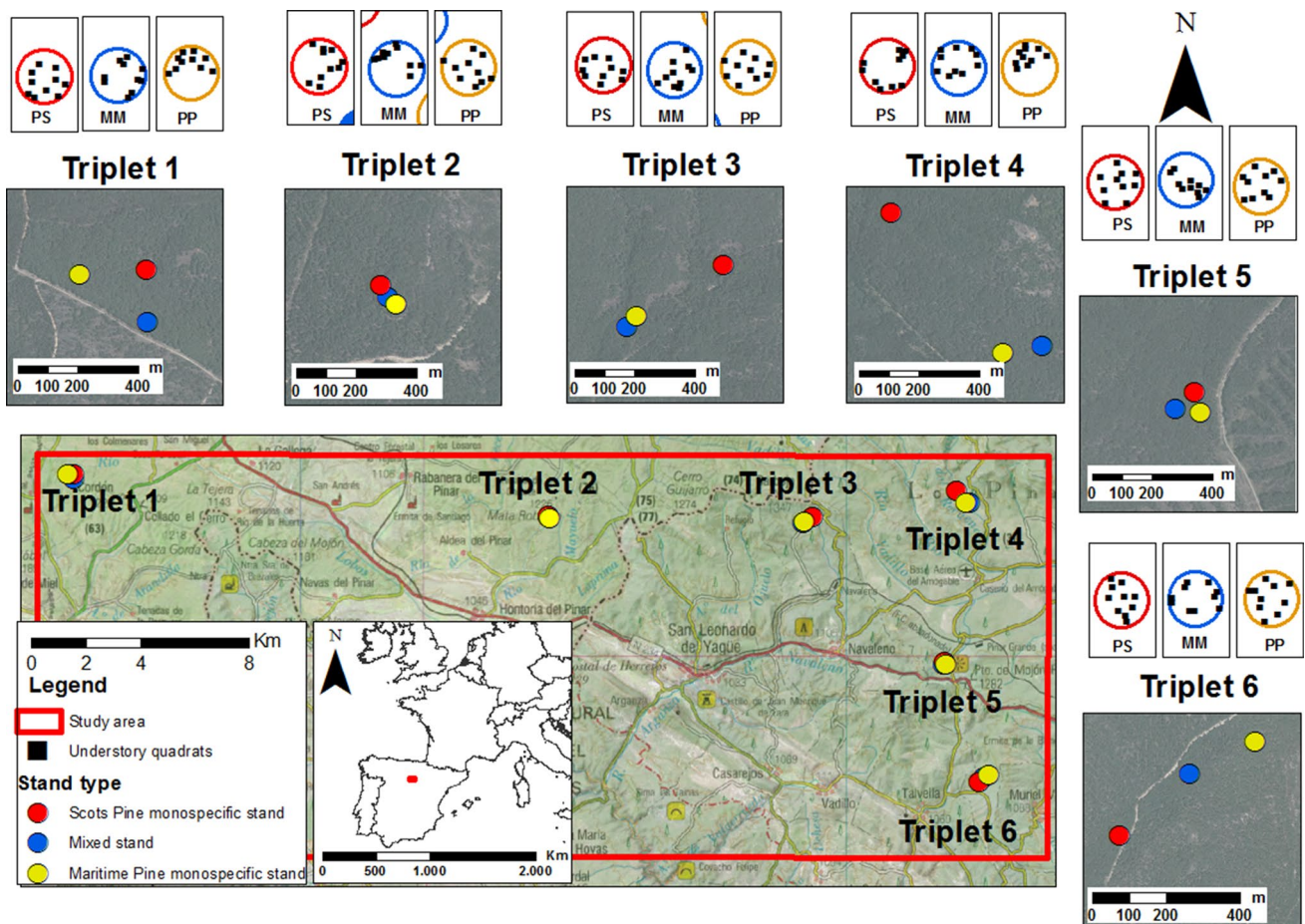
## Materials and methods

### Study sites

The research was carried out in eighteen forest plots (6 triplets  $\times$  3 forest stands (2 monospecific + 1 mixed)  $\times$  1 plot) located in the Northern Iberian Range, in North-Central Spain ( $41^{\circ} 47' 35''$  N and  $41^{\circ} 53' 41''$  N latitude, and  $2^{\circ}$

$56' 12''$  W and  $3^{\circ} 20' 46''$  W longitude; Fig. 1). 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 (Nafria-García et al. 2013). Altitude varies from 1093 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 Dystrochrept or Typic Humixerept (sensu Soil-Survey-Staff 2014). The sandy soil texture is dominant, and the pH varies from extremely acid to strongly acid (see López-Marcos et al. 2018, 2021). Nearby vegetation, highly degraded by anthropogenic action, is characterized by Pyrenean oak (*Quercus pyrenaica* Willd.) forests or communities dominated by junipers.

Each triplet consisted of three circular plots of 15 m radius, two dominated either by *P. sylvestris* or *P. pinaster*



**Fig. 1** 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* monospe-

cific plots, PP; blue circles: mixed plots of both *Pinus* species, MM), and the understory quadrats (small black squares) within each plot

and one mixed plot that contained both species, located less than 1 km from each other so that the environmental conditions were homogeneous within the triplet (Fig. 1). Also, the stand characteristics as age, density, basal area, and management are intended to be similar within the triplet, although they could differ among distinct triplets (see 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%. The age of the selected plots ranged between 44 and 151 years, the density between 509 and 1429 trees ha<sup>-1</sup>, the basal area between 33.3 and 70.30 m<sup>2</sup> ha<sup>-1</sup>, and the dominant height between 15.60 and 25.04 m (López-Marcos et al. 2018). Traditionally, forest management consists of strip clear-cutting with plowing and planting or sowing when necessary, and moderate thinning from below (Riofrío et al. 2019) benefiting *P. sylvestris* (López-Marcos et al. 2019). The stands have had no silvicultural intervention or damage in the last ten years. 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 et al. 2020; López-Marcos et al. 2018, 2019, 2020, 2021).

### Overstory sampling

The number and diameter of all stems > 7.5 cm in diameter for every *Pinus* species were computed at the stand level, i.e., within each circular plot of 15 m radius, and at the neighborhood level, i.e., within each circular 4 m radius subplot centered in each quadrat of understory sampling according to Rodríguez-Calcerrada et al. (2011). There were 18 plots of 15 m radius, one per stand type and triplet, and 180 subplots of 4 m radius, 10 per stand type and triplet.

Tree density, total basal area, and the basal area of each *Pinus* species were calculated at both spatial scales; basal area as indicated in ‘Appendix 1.’ At the smaller spatial 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.

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 at the stand level following Hopkins (1954): (1) the distance from a random point (the center of the quadrat for understory sampling) to the nearest tree (piD), and (2) the distance from that tree to its nearest neighbor (iiD). The Hopkins’ coefficient of aggregation (1954) was then calculated for determining the spatial

distribution pattern of trees in each stand type. This test assumes that a population is randomly distributed whether the distance from a random point 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 ( $p < 0.05$ ).

### Understory sampling

Within each plot, 10 quadrats (1 m × 1 m) were randomly located, i.e., 6 triplets × 3 forest stands (2 monospecific + 1 mixed) × 1 plot × 10 quadrats = 180 quadrats, 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 Raunkiaer’s life-forms (1934), following Aizpiru et al. (2007), into the following categories: therophytes, hemicryptophytes, geophytes, chamaephytes, and phanerophytes (see López-Marcos et al. 2019).

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 Raunkiaer’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 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 ca. 20 m in height, and the understory being only ca. 20 cm in height, and never higher than 1 m (López-Marcos et al. 2019).

### 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, 2021). Two undisturbed soil samples were collected from each pit’s mineral soil horizon with steel cylinders (98.2 cm<sup>3</sup>) 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 ( $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ ,  $\text{K}^+$ ,  $\text{Na}^+$ ) that were extracted with 1 N ammonium acetate at  $\text{pH} = 7$  (Schollenberger and Simon 1945) and determined using an atomic absorption/emission spectrometer.

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

## Data analyses

Differences among stands in total basal area and density, at two spatial scales, were analyzed using linear mixed models (LMM; Pinheiro and Bates 2000) with the restricted maximum likelihood method (REML; Richards 2005), and triplet as the random term. Also, differences among stands in piD and iiD were analyzed 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 understand why the greatest basal area found at the smaller spatial scale in mixed stands in comparison with the monospecific stands of *P. sylvestris* did not have a negative effect on the understory richness. Data used come from the 180 subplots of 4 m radius at the neighborhood level (10 per stand type and triplet). 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). Here, we hypothesized that there was probably no direct effect of the total basal area on the understory richness but through the complementarity in the use of belowground resources (water, WHC, and fertility, SBstock) by both *Pinus* species. Thus, we needed to divide the effect of the basal area of each species to test to what extent the complementarity in the use of soil resources contributes to maintaining higher values of understory richness in the admixtures than expected given the basal area recorded (as a proxy of light availability) and soil fertility and moisture conditions of the mixed stands (see López-Marcos et al. 2019). We also hypothesized that hemicryptophytes greatly contribute to the understory

richness through the effect of soil fertility and water on them (López-Marcos et al. 2019). We knew that the basal areas of *P. sylvestris* and *P. pinaster* were negatively correlated, as the basal area of *P. pinaster* and WHC, the understory richness increased as soil moisture increased, and the hemicryptophytes cover increased as the soil fertility increased being the highest for intermediate values of WHC (see López-Marcos et al. 2019). We suspected that the basal area of *P. sylvestris* was positively correlated with soil fertility (see Fig. 6), and the hemicryptophytes cover was positively correlated with the understory richness (López-Marcos et al. 2019). SEMs model simplification method was based on Akaike Information Criterion (AIC) deleting all the nonsignificant 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.

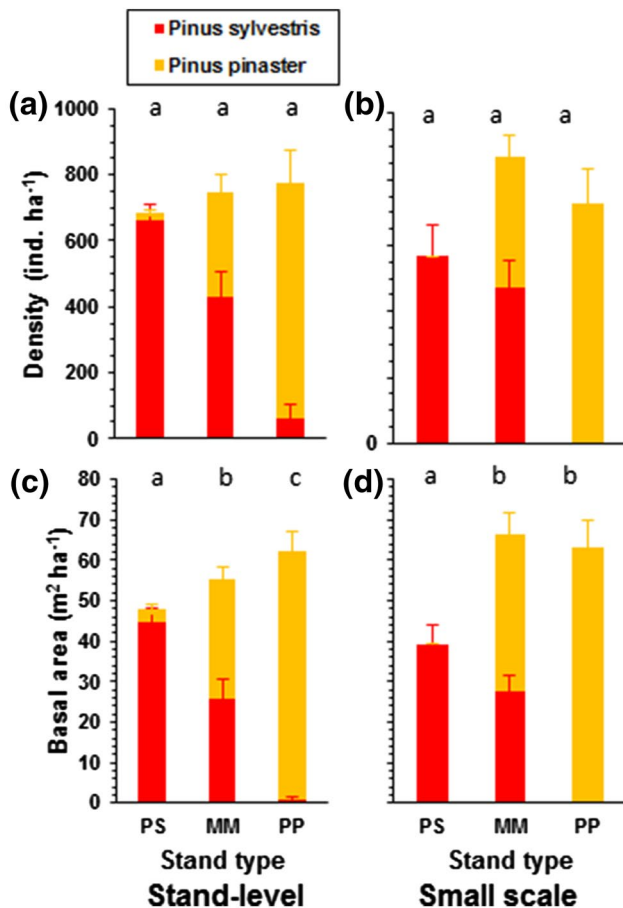
The response pattern of both *Pinus* species along the significant soil properties (i.e., WHC and SBstock), as well as of the understory richness along the percentage of *P. pinaster* basal area were modeled by Huisman–Olf–Fresco (HOF) models (Huisman et al. 1993). These are a hierarchical set of five 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 ( $\mu$ ) 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

### Overstorey density and basal area at two spatial scales

No difference of total density was found among stands at any spatial scale (Fig. 2a, b, ‘Appendix 2’). Nevertheless, at the stand level (Fig. 2a) density seemed to increase from PS



**Fig. 2** a Density (ind. ha<sup>-1</sup>; mean+SE) and c basal area (m<sup>2</sup> ha<sup>-1</sup>; mean+SE) at stand level (i.e., within the circular plots of 15 m radius); and b density and d basal area at the neighborhood level (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). Different letters indicate differences among stand types (p<0.05) in total density and basal area without differentiating *Pinus* species

**Table 1** Spatial distribution of trees regardless of species (all trees: *P. sylvestris*+*P. pinaster*), and for each *Pinus* species separately, in each type of stand, calculated by Hopkins’ coefficient of aggregation

	<i>P. sylvestris</i> monospecific stand	Mixed stand	<i>P. pinaster</i> monospecific stand
All trees	Random (piD=iiD)	Random (piD=iiD)	Random (piD=iiD)
<i>Pinus sylvestris</i>	Random (piD=iiD)	Regular (piD<iiD)	–
<i>Pinus pinaster</i>	–	Regular (piD<iiD)	Random (piD=iiD)

(684 ± 49 ind. ha<sup>-1</sup>) to PP (776 ± 137 ind. ha<sup>-1</sup>), whereas at the neighborhood level (Fig. 2b) density seemed to be higher in MM (869 ± 128 ind. ha<sup>-1</sup>) with respect to the monospecific stands (PS: 567 ± 97 ind. ha<sup>-1</sup>; PP: 728 ± 107 ind. ha<sup>-1</sup>).

In contrast, significant differences in the total basal area were found among stands at both spatial scales (Fig. 2c, d, ‘Appendix 2’). At the stand level (Fig. 2c), the total basal area increased from PS (48.04 ± 3.19 m<sup>2</sup> ha<sup>-1</sup>) to PP (62.19 ± 5.19 m<sup>2</sup> ha<sup>-1</sup>), being intermediate in MM (55.24 ± 4.94 m<sup>2</sup> ha<sup>-1</sup>). At the neighborhood level (Fig. 2d), the total basal area increased from PS (39.15 ± 4.93 m<sup>2</sup> ha<sup>-1</sup>) to MM (66.21 ± 8.00 m<sup>2</sup> ha<sup>-1</sup>) and no difference was found between MM and PP (63.31 ± 6.79 m<sup>2</sup> ha<sup>-1</sup>).

### Tree spatial distribution pattern

The spatial distribution of trees regardless of species was random in the three stand types (Table 1). However, the spatial distribution of *P. sylvestris* and *P. pinaster* considered separately was random in monospecific stands and regular in mixed stands (Table 1).

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 (Fig. 3a, 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 (Fig. 3b, d).

### Understorey richness

Thirty understorey 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 understorey richness showed an increasing trend bounded below the maximum attainable response as the percentage of basal area of *P. sylvestris* increased (HOF-model III; Fig. 4).

(1954) with p<0.05; piD: distance from a random point (the center of the quadrat for understorey sampling) to the nearest tree, and iiD: distance from that tree to its nearest neighbor

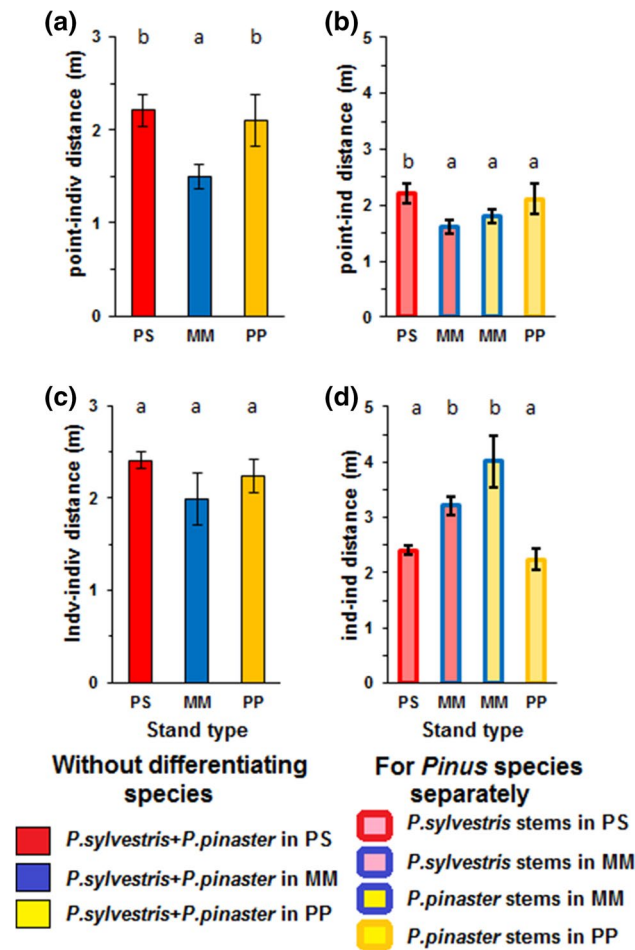


Fig. 3 Comparing stands for each distance (piD: the distance from a random point to the nearest tree; iiD: the distance from that tree to its nearest neighbor): a, c without differentiating species (*P. sylvestris* + *P. pinaster* as a whole), and b, d for each species separately (*P. sylvestris* or *P. pinaster*)

**Understory richness maintenance in the mixtures 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 (Fig. 5). The SEM clearly showed that soil fertility (SBstock) affected positively the basal area of *P. sylvestris* (G-PS) and the cover of hemicryptophytes (Hemi), whereas soil moisture (WHC) affected negatively the basal area of *P. pinaster* (G-PP) 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 and hemicryptophytes affected positively the understory richness (S). The overall goodness of the model fit increased when including hemicryptophytes.

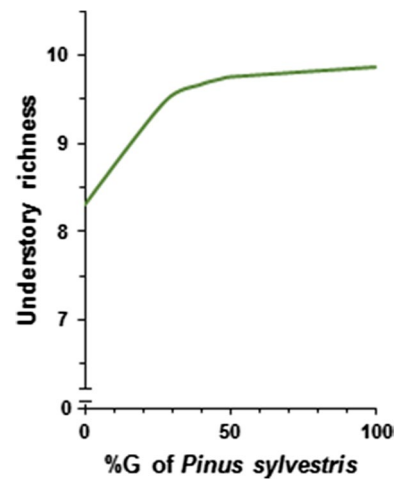


Fig. 4 HOF-derived response curve of understory richness relative to the percentage (%) of basal area (G) of *P. sylvestris*

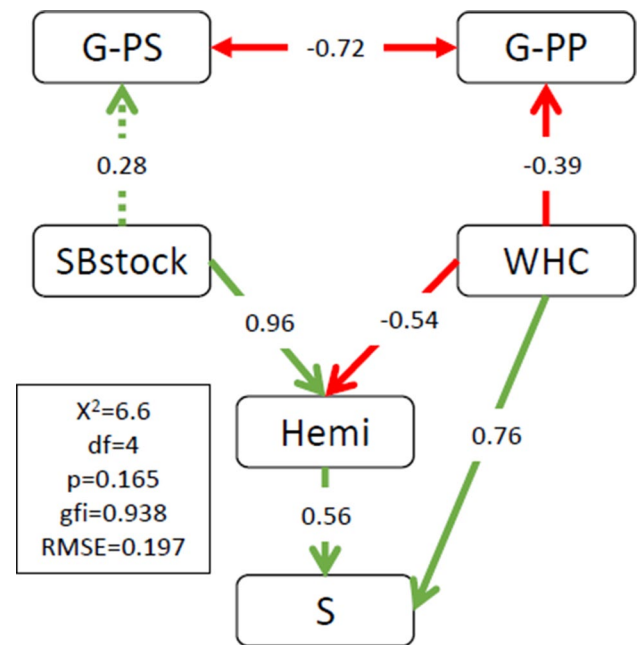


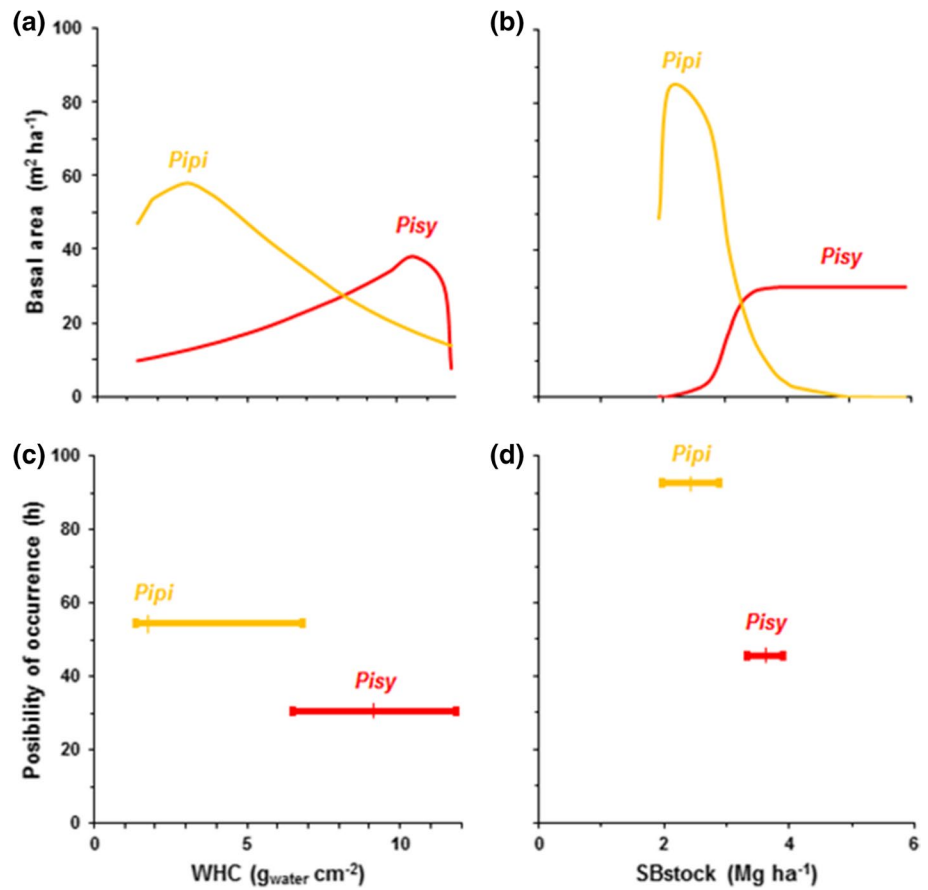
Fig. 5 Conceptual model of the effects of soil moisture (WHC: water holding capacity) and fertility (SBstock: stock of sum of bases) on the basal area of the overstory species (G-PS: basal area of *P. sylvestris*, G-PP: basal area of *P. pinaster*) and the understory species richness (S) through the hemicryptophytes cover (Hemi). Continuous and dashed lines represent the significance 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 (Fig. 6a, b). *P.*



**Fig. 6** 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 ( $\mu$ ) and niche width ( $2t$ ) for both *Pinus* species relative to **c** soil moisture (WHC) and **d** fertility (SBstock) gradients



**Table 2** Location of optimum ( $\mu$ ), 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	$h$	$\mu$	$2t$
WHC	<i>P. sylvestris</i>	V	30.56	9.12	5.35
	<i>P. pinaster</i>	V	54.21	1.75	5.45
SBstock	<i>P. sylvestris</i>	V	45.06	3.61	0.57
	<i>P. pinaster</i>	V	92.63	2.42	0.90

*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-model V) with the maximum skewed at the lowest WHC and SBstock values.

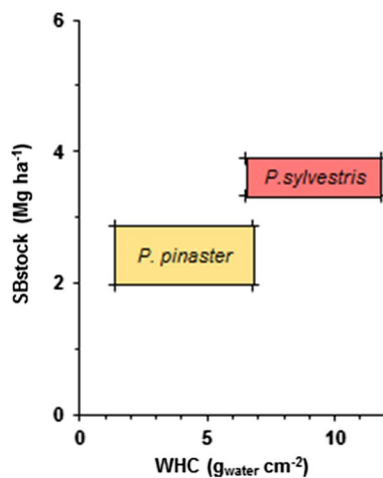
In fact, the location of the optimum of overstory species along WHC and SBstock gradients (Fig. 6c, d, Table 2) showed how *P. pinaster* had the greatest probability of occurrence ( $h > 50$  and  $h > 90$  for WHC and SBstock, respectively) in soils with low WHC ( $\mu < 2$  g<sub>water</sub> cm<sup>-2</sup>) and SBstock ( $\mu < 3$  Mg ha<sup>-1</sup>), whereas *P. sylvestris* had the greatest probability of occurrence ( $h > 30$  and  $h > 40$  for WHC and SBstock, respectively) in soils with higher WHC ( $\mu > 5$  g<sub>water</sub> cm<sup>-2</sup>) and SBstock ( $\mu > 3$  Mg ha<sup>-1</sup>). Both *Pinus*

species showed broader niches widths for WHC than for SBstock (Fig. 6c, d, Table 2), and low degree of overlap between them (Fig. 7).

## Discussion

### The heterogeneity in the mixture of both *Pinus* species promotes higher overstory yield at a smaller spatial scale (Hypothesis 1)

The heterogeneous distribution of *Pinus* species in the mixtures yields differences among patches within the stand. In particular, a ‘patch mixture’ is observed at the stand level, i.e., *P. sylvestris* trees surrounded by *P. pinaster* trees or vice versa, whereas within the stand, at the neighborhood level, an ‘intensive tree-wise mixture’ where both species are closely interlocked was observed. The intimate mixture at a smaller 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 because of the different spatial mixing patterns (patch mixture vs. intimate mixture) since plant interactions at the neighborhood scale



**Fig. 7** Bidimensional niche for both overstory species (*P. sylvestris* and *P. pinaster*) including simultaneously the  $2t$  tolerance intervals to soil moisture (WHC) and fertility (SBstock) shown in Fig. 6c, d

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).

Consequently, some evidence of overyielding in the total basal area and density in our mixed stands were found when the overstory was studied at the neighborhood scale, although it was not statistically significant. 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. 2017b), suggesting that tree species richness fosters forest productivity (Fichtner et al. 2018). The biodiversity loss has also been linked to the productivity loss (Vilà et al. 2007). However, tree mixture not always increases productivity as shown in experiments that have been designed to specifically test this because it depends on the size of the blocks relative to the distance over which the species interactions occur (e.g., Forrester and Smith 2012).

Here, we propose the greatest efficiency in the use of space for growth (higher density and basal area) where *P. sylvestris* and *P. pinaster* cohabit as the cause of the higher yield in these admixtures as previously reported by Riofrío et al. (2017b). 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 is random in monospecific stands but 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). Pretzsch and Schütze (2009) have also 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 et al. 2020).

### More efficiency in the use of space thanks to the belowground niche complementarity (Hypothesis 2)

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 use 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 device 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 2003). Here, we found that the basal area of *P. sylvestris* is positively related to soil moisture and fertility, whereas the basal area of *P. pinaster* is negatively related to both soil variables (Fig. 6a, b). Moreover, the bidimensional niche model for both *Pinus* species (Fig. 7) showed a low degree of overlap between them, suggesting resource-use complementarity for soil water and fertility when mixed.

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. 2016) as in mixtures, the efficiency in the use of resources increase (Binkley et al. 2004) since no species are competitively superior (Tilman et al. 1997). 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. 1997). 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 (Hypothesis 3)

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 (Fig. 4). The high understory richness found in monospecific *P. sylvestris* stands seems reasonable since they have the lowest total basal area at both spatial scales, and it is expected to find the higher understory richness the lower basal area due to the higher light availability (Dorman et al. 2020). 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 Dorman et al. (2020), and like 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 were the only Raunkiaer'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 were the only Raunkiaer's life-form whose inclusion in the structural equation model improved the goodness of model fit.

A previous study carried out in the same experimental device 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. 2020). 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. 2020).

### 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 *P. sylvestris* and

*P. pinaster* allows achieving a higher overstory yield 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 both *Pinus* species, 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 *Pinus* species 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.

### Conclusion

Our results highlight the fundamental role of scale in determining the observed relationship between species richness and ecosystem functioning in forests. Evidence of a small-scale overyielding was found in mixed stands related to the greater density and basal area, as distances between trees were reduced in admixtures in relation to monospecific stands thanks to the more intimate mixture of both *Pinus* species at the neighborhood level. This more efficient use of the space by the species of the overstory when mixed is in turn related to the niche complementarity with respect to the use of soil resources (water and fertility) of both *Pinus* species. The higher overstory yield in mixed stands has no negative effect on the understory richness.

### Appendix 1: Data analyses of overstory and soil properties

#### Basal area of *Pinus sylvestris* (G-PS)

$$G\text{-PS} = \sum g_{\text{PSi}} / S_i$$

$g_{\text{PSi}}$ : section of *Pinus sylvestris* stem ( $\text{m}^2$ )  
 $S_i$ : surface (ha)

#### Section of *Pinus sylvestris* stem ( $g_{\text{PSi}}$ )

$$g_{\text{PSi}} = \pi/4 \, dn_{\text{PSi}}^2$$

$dn_{\text{PSi}}$ : normal diameter of every *Pinus sylvestris* stem > 7.5 cm at the breast height (m)

## Basal area of *Pinus pinaster* (G-PP)

$$G-PP = \sum g_{PPi} / Si$$

$g_{PPi}$ : section of *Pinus pinaster* stem ( $m^2$ )  
 $Si$ : surface (ha)

## Section of *Pinus pinaster* stem ( $g_{PPi}$ )

$$g_{PPi} = \pi/4 \cdot dn_{PPi}^2$$

$dn_{PPi}$ : normal diameter of every *Pinus pinaster* stem > 7.5 cm at the breast height (m)

## Total basal area (G-T)

$$G-T = G-PS + G-PP$$

G-PS: basal area of *Pinus sylvestris*  
 G-PP: basal area of *Pinus pinaster*

## Water holding capacity

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

$$WHC_{Hi} = UW_{Hi} \cdot bD_{Hi} \cdot \%EF_{Hi} \cdot T_{Hi}$$

$UW_{Hi}$ : 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 (0–50 cm; WHC)

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

## Sum of bases stock

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

$$SBstock_{Hi} = SB_{Hi} \cdot bD_{Hi} \cdot \%EF_{Hi} \cdot T_{Hi}$$

$SB_{Hi}$ : 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

**Table 3** Results of the LMMs to analyze differences between stand types in basal area ( $G$ ;  $m^2 \text{ ha}^{-1}$ ) and density ( $N$ ; trees  $m^{-2}$ ) at the two different spatial scales; the global results of the models ( $F$ ,  $p$ ) and the pairwise comparisons between stand types (MM=mixed stands; PS=monospecific stands of *Pinus sylvestris*, and PP=monospecific stands of *P. pinaster*) are shown

	Stand level		Neighborhood level	
	$N$	$G$	$N$	$G$
AIC	223.34	119.13	228.26	142.65
$F$	0.26	14.62	1.83	7.00
$p$	0.77	0.00	0.21	0.01
MM-PS	0.65	0.02	0.08	0.01
MM-PP	0.82	0.02	0.39	0.72

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

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

## Appendix 2

See Table 3.

**Acknowledgements** We would like to thank Luis Alfonso Ramos Calvo for his invaluable help with soil sampling, Carmen Blanco and Juan Carlos Arranz for their advice in the laboratory analyses, José Riofrío and Cristóbal Ordoñez for their assistance in the characterization and location of plots in the field, and the Regional Forest Service of Castilla and León to facilitate the triplet's installation and monitoring. We also thank Josu G. Alday for his assistance with structural equations modeling and Juan Manuel Diez Clivillé (deceased) for his assistance with English.

**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.

**Funding** This research was funded by a predoctoral grant to DLM (BES-2015-072852) and the Project FORMIXING (AGL2014-51964-C2-1-R) from the Ministry of Economy and Competitiveness of the Spanish Government.

**Availability of data and materials** Available upon reasonable request.

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

## References

- Aizpiru I, Aseginolaza C, Uribe-Echebarría PM et al (2007) Claves ilustradas de la Flora del País Vasco y Territorios Limítrofes, 2a. Gobierno Vasco, Departamento de Medio Ambiente y de Ordenación del Territorio, Vitoria
- Akaike H (1973) Information theory as an extension of the maximum likelihood principle. In: Brillinger D, Gani J, Hartigan J (eds) Second international symposium on information theory. Akademiai Kiado, Budapest, pp 267–281
- Alday G, Martínez-Ruiz C, Marrs RH, Bravo F (2010) Influence of harvesting intensity on the floristic composition of natural Mediterranean maritime pine forests. *Acta Oecol* 36:349–356. <https://doi.org/10.1016/j.actao.2010.03.001>
- Alday JG, Zaldívar P, Torroba-Balmori P et al (2016) Natural forest expansion on reclaimed coal mines in Northern Spain: the role of native shrubs as suitable microsites. *Environ Sci Pollut Res* 23:13606–13616. <https://doi.org/10.1007/s11356-015-5681-2>
- Alía R, Martín S (2003) EUFORGEN technical guidelines for genetic conservation and use for Maritime pine (*Pinus pinaster*). In: International Plant Genetic Resources Institute, Rome, p 6
- Andivia E, Ruiz-Benito P, Díaz-Martínez P et al (2020) Inter-specific tolerance to recurrent droughts of pine species revealed in saplings rather than adult trees. *For Ecol Manag* 458:117848. <https://doi.org/10.1016/j.foreco.2019.117848>
- Antos JA (2009) Understorey plants in temperate forests. In: Owens JN, Lunday HG (eds) Forests and forest plants. University of Victoria, Victoria
- Assmann E (1970) The principles of forest yield study. Studies in the organic production, structure, increment and yield of forest stands. Pergamon-Elsevier, Oxford
- Balvanera P, Pfisterer AB, Buchmann N et al (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol Lett* 9:1146–1156. <https://doi.org/10.1111/j.1461-0248.2006.00963.x>
- Barbier S, Gosselin F, Balandier P (2008) Influence of tree species on understorey vegetation diversity and mechanisms involved—a critical review for temperate and boreal forests. *For Ecol Manag* 254:1–15. <https://doi.org/10.1016/j.foreco.2007.09.038>
- Binkley D, Stape JL, Ryan MG (2004) Thinking about efficiency of resource use in forests. *For Ecol Manag* 193:5–16. <https://doi.org/10.1016/j.foreco.2004.01.019>
- Bogino S, Bravo F (2014) Carbon stable isotope-climate association in tree rings of *Pinus pinaster* and *Pinus sylvestris* in Mediterranean environments. *Bosque* 35:175–184. <https://doi.org/10.4067/S0717-92002014000200005>
- Brassard BW, Chen HYH, Cavard X et al (2013) Tree species diversity increases fine root productivity through increased soil volume filling. *J Ecol* 101:210–219. <https://doi.org/10.1111/1365-2745.12023>
- Bravo-Oviedo A, Montero G (2008) Descripción de los caracteres culturales de las principales especies forestales. In: Serrada R, Montero G, Reque JA (eds) Compendio de Selvidultura Aplicada en España. INIA-Ministerio de Educación y Ciencia, Madrid, pp 1036–1114
- Bravo-Oviedo A, Pretzsch H, Ammer C et al (2014) European mixed forests: definition and research perspectives. *For Syst* 23:518–533. <https://doi.org/10.5424/fs/2014233-06256>
- Byth K, Ripley BD (1980) On sampling spatial patterns by distance methods. *Biometrics* 36:279–284
- Cardinale BJ, Wright JP, Cadotte MW et al (2007) Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proc Natl Acad Sci USA* 104:18123–18128. <https://doi.org/10.1073/pnas.0709069104>
- Cattaneo N, Schneider R, Bravo F, Bravo-Oviedo A (2020) Interspecific competition of tree congeners induces changes in crown architecture in Mediterranean pine mixtures. *For Ecol Manag*. <https://doi.org/10.1016/j.foreco.2020.118471>
- Chesson P (2000) Mechanisms of maintenance of species diversity. *Annu Rev Ecol Syst* 31:343–366
- Chisholm RA, Muller-Landau HC, Abdul Rahman K et al (2013) Scale-dependent relationships between tree species richness and ecosystem function in forests. *J Ecol* 101:1214–1224. <https://doi.org/10.1111/1365-2745.12132>
- Colwell RK (2009) Biodiversity: concepts, patterns and measurement. In: Simon AL (ed) The Princeton guide to ecology. Princeton University Press, Princeton, pp 257–263
- Del Río M, Pretzsch H, Alberdi I et al (2015) Characterization of the structure, dynamics, and productivity of mixed-species stands: review and perspectives. *Eur J For Res*. <https://doi.org/10.1007/s10342-015-0927-6>
- Dorman CF, Bagnara M, Boch S et al (2020) Plant species richness increases with light availability, but not variability, in temperate forests understorey. *BMC Ecol* 20:43. <https://doi.org/10.1186/s12898-020-00311-9>
- Ettema CH, Wardle DA (2002) Spatial soil ecology. *Trends Ecol Evol* 17:177–183. [https://doi.org/10.1016/S0169-5347\(02\)02496-5](https://doi.org/10.1016/S0169-5347(02)02496-5)
- Felton A, Lindbladh M, Brunet J, Fritz Ö (2010) Replacing coniferous monocultures with mixed-species production stands: an assessment of the potential benefits for forest biodiversity in northern Europe. *For Ecol Manag* 260:939–947. <https://doi.org/10.1016/j.foreco.2010.06.011>
- Fichtner A, Härdtle W, Bruehlheide H et al (2018) Neighbourhood interactions drive overyielding in mixed-species tree communities. *Nat Commun*. <https://doi.org/10.1038/s41467-018-03529-w>
- Forrester DI (2014) The spatial and temporal dynamics of species interactions in mixed-species forests: from pattern to process. *For Ecol Manag* 312:282–292. <https://doi.org/10.1016/j.foreco.2013.10.003>
- Forrester DI, Albrecht AT (2014) Light absorption and light-use efficiency in mixtures of *Abies alba* and *Picea abies* along a productivity gradient. *For Ecol Manag* 328:94–102. <https://doi.org/10.1016/j.foreco.2014.05.026>
- Forrester DI, Smith RGB (2012) Faster growth of *Eucalyptus grandis* and *Eucalyptus pilularis* in mixed-species stands than monocultures. *For Ecol Manag* 286:81–86. <https://doi.org/10.1016/j.foreco.2012.08.037>
- Forrester DI, Bauhus J, Khanna PK (2004) Growth dynamics in a mixed-species plantation of *Eucalyptus globulus* and *Acacia mearnsii*. *For Ecol Manag* 193:81–95. <https://doi.org/10.1016/j.foreco.2004.01.024>
- Forrester DI, Bauhus J, Cowie AL (2005) On the success and failure of mixed-species tree plantations: lessons learned from a model system of *Eucalyptus globulus* and *Acacia mearnsii*. *For Ecol Manag* 209:147–155. <https://doi.org/10.1016/j.foreco.2005.01.012>
- Forrester DI, Bauhus J, Cowie AL (2006) Carbon allocation in a mixed-species plantation of *Eucalyptus globulus* and *Acacia mearnsii*. *For Ecol Manag* 233:275–284. <https://doi.org/10.1016/j.foreco.2006.05.018>
- Forrester DI, Theiveyanathan S, Collopy JJ, Marcar NE (2010) Enhanced water use efficiency in a mixed *Eucalyptus globulus* and *Acacia mearnsii* plantation. *For Ecol Manag* 259:1761–1770. <https://doi.org/10.1016/j.foreco.2009.07.036>
- Forrester DI, Ammer C, Annighöfer PJ, Barbeito I, Bielak K, Bravo-Oviedo A, Coll L, Río MD, Drössler L, Heym M, Hurt V, Löf M, Ouden JD, Pach M, Pereira MG, Plaga B, Ponette Q, Skrzyszewski J, Sterba H, Svoboda M, Zlatanov T, Pretzsch H (2018) Effects of crown architecture and stand structure on light absorption in mixed and monospecific *Fagus sylvatica* and

- Pinus sylvestris* forests along a productivity and climate gradient through Europe. *J Ecol* 106:746–760
- Gamfeldt L, Snäll T, Bagchi R et al (2013) Higher levels of multiple ecosystem services are found in forests with more tree species. *Nat Commun* 4:1340. <https://doi.org/10.1038/ncomms2328>
- Gaudio N, Balandier P, Perret S, Ginisty C (2011) Growth of understorey Scots pine (*Pinus sylvestris* L.) saplings in response to light in mixed temperate forest. *Forestry* 84:187–195. <https://doi.org/10.1093/forestry/cpr005>
- Grace JB (2006) Structural equation modeling and natural systems. Cambridge University Press, Cambridge
- Grossman JJ, Cavender-Bares J, Hobbie SE et al (2017) Species richness and traits predict overyielding in stem growth in an early-successional tree diversity experiment. *Ecology* 98:2601–2614. <https://doi.org/10.1002/ecy.1958>
- Hector A, Hooper R (2002) Ecology. Darwin and the first ecological experiment. *Science* 295:639–640. <https://doi.org/10.1126/science.1064815>
- Hooper DU, Dukes JS (2004) Overyielding among plant functional groups in a long-term experiment. *Ecol Lett* 7:95–105. <https://doi.org/10.1046/j.1461-0248.2003.00555.x>
- Hopkins B (1954) A new method of determining the type of distribution of plant individuals. *Ann Bot* 18:213–227
- Huisman J, Olff H, Fresco LFM (1993) A hierarchical set of models for species response analysis. *J Veg Sci* 4:37–46. <https://doi.org/10.2307/3235732>
- IGME (2015) Mapa Geológico de la Península Ibérica, Baleares y Canarias a escala 1M. IGME, Madrid
- Jactel H, Nicoll BC, Branco M et al (2009) The influences of forest stand management on biotic and abiotic risks of damage. *Ann For Sci* 66:1–18. <https://doi.org/10.1051/forest/2009054>
- Jactel H, Gritti ES, Drössler L et al (2018) Positive biodiversity–productivity relationships in forests: climate matters. *Biol Lett* 14:12–15. <https://doi.org/10.1098/rsbl.2017.0747>
- Jansen F, Oksanen J (2013) How to model species responses along ecological gradients—Huisman-Olff-Fresco models revisited. *J Veg Sci* 24:1108–1117. <https://doi.org/10.1111/jvs.12050>
- Johnson JB, Omland KS (2004) Model selection in ecology and evolution. *Trends Ecol Evol* 19:101–108. <https://doi.org/10.1016/j.tree.2003.10.013>
- Kelty MJ (2006) The role of species mixtures in plantation forestry. *For Ecol Manag* 233:195–204. <https://doi.org/10.1016/j.foreco.2006.05.011>
- Knoke T, Ammer C, Stimm B, Mosandl R (2008) Admixing broad-leaved to coniferous tree species: a review on yield, ecological stability and economics. *Eur J For Res* 127:89–101. <https://doi.org/10.1007/s10342-007-0186-2>
- Köppen W (1936) Das geographische System der Klimate. In: Handbuch der Klimatologie. Verlag von Gebrüder Borntraeger, Berlin, pp 7–30
- Lanz A, Alberdi I, Barbati A et al (2010) A sample of COST action E43 reference definitions. In: Tomppo E, Gschwantner T, Lawrence TM, McRoberts RE (eds) National forest inventories. Pathways for common reporting. Springer, Berlin
- Lawesson JE, Oksanen J (2002) Niche characteristics of Danish woody species as derived from coenoclines. *J Veg Sci* 13:279–290
- Liu Y, Lei P, Xiang W et al (2017) Accumulation of soil organic C and N in planted forests fostered by tree species mixture. *Biogeosciences* 14:3937–3945. <https://doi.org/10.5194/bg-14-3937-2017>
- López-Marcos D, Martínez-Ruiz C, Turrión M-B et al (2018) Soil carbon stocks and exchangeable cations in monospecific and mixed pine forests. *Eur J For Res* 137:831–847. <https://doi.org/10.1007/s10342-018-1143-y>
- López-Marcos D, Turrión MB, Bravo F, Martínez-Ruiz C (2019) Understorey response to overstorey and soil gradients in mixed vs monospecific Mediterranean pine forests. *Eur J For Res* 138:939–955. <https://doi.org/10.1007/s10342-019-01215-0>
- López-Marcos D, Turrión M, Bravo F, Martínez-Ruiz C (2020) Can mixed pine forests conserve understorey richness by improving the establishment of understorey species typical of native oak forests? *Ann For Sci* 77:15. <https://doi.org/10.1007/s13595-020-0919-7>
- López-Marcos D, Turrión MB, Bravo F, Martínez-Ruiz C (2021) Characterization of mixed and monospecific stands of Scots pine and Maritime pine. Soil profile, physiography, climate, overstorey and understorey data. *Ann For Sci*. <https://doi.org/10.1007/s13595-021-01042-7>
- Loreau M, Hector A (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature* 412:72–76. <https://doi.org/10.1038/35083573>
- Luo W, Liang J, Cazzolla Gatti R et al (2019) Parameterization of biodiversity–productivity relationship and its scale dependency using georeferenced tree-level data. *J Ecol* 107:1106–1119. <https://doi.org/10.1111/1365-2745.13129>
- Madrigal-González J, Ruiz-Benito P, Ratcliffe S et al (2016) Complementarity effects on tree growth are contingent on tree size and climatic conditions across Europe. *Sci Rep* 6:1–11. <https://doi.org/10.1038/srep32233>
- Michalet R, Chen SY, An LZ et al (2015) Communities: are they groups of hidden interactions? *J Veg Sci* 26:207–218. <https://doi.org/10.1111/jvs.12226>
- Nafría-García DA, Garrido-del-Pozo N, Álvarez-Arias MV et al (2013) Atlas agroclimático de Castilla y León. Instituto Tecnológico Agrario, Junta de Castilla y León-Agencia Estatal de Meteorología. <http://atlas.itacyl.es>
- Ngo Bieng MA, Perot T, de Coligny F, Goreaud F (2013) Spatial pattern of trees influences species productivity in a mature oak-pine mixed forest. *Eur J For Res* 132:841–850. <https://doi.org/10.1007/s10342-013-0716-z>
- Nguyen H, Herbohn J, Firn J, Lamb D (2012) Biodiversity–productivity relationships in small-scale mixed-species plantations using native species in Leyte province, Philippines. *For Ecol Manag* 274:81–90. <https://doi.org/10.1016/j.foreco.2012.02.022>
- Nilsson MC, Wardle DA (2005) Understorey vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. *Front Ecol Environ* 3:421–428. [https://doi.org/10.1890/1540-9295\(2005\)003\[0421:UVAAFE\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2005)003[0421:UVAAFE]2.0.CO;2)
- MAPA (1994) Tomo III. In: Métodos oficiales de Análisis. Ministerio de Agricultura, Pesca y Alimentación, Madrid
- Pinheiro J, Bates D (2000) Mixed-effects models in S and S-Plus. Springer, New York
- Pinheiro J, Bates D, DebRoy S, et al (2018) Package ‘nlme’. nlme: linear and nonlinear mixed effects models. R Package Version 3.1-137
- Poorter L, Lianes E, Moreno-de las Heras M, Zavala MA (2012) Architecture of Iberian canopy tree species in relation to wood density, shade tolerance and climate. *Plant Ecol* 213:707–722. <https://doi.org/10.1007/s11258-012-0032-6>
- Pretzsch H, Schütze G (2009) Transgressive overyielding in mixed compared with pure stands of Norway spruce and European beech in Central Europe: evidence on stand level and explanation on individual tree level. *Eur J For Res* 128:183–204. <https://doi.org/10.1007/s10342-008-0215-9>
- Pretzsch H, Dieler J, Seifert T, Rötzer T (2012) Climate effects on productivity and resource-use efficiency of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* L.) in stands with different spatial mixing patterns. *Trees Struct Funct* 26:1343–1360. <https://doi.org/10.1007/s00468-012-0710-y>
- Pretzsch H, Schütze G, Uhl E (2013) Resistance of European tree species to drought stress in mixed pure forests: evidence of stress release by inter-specific facilitation. *Plant Biol* 15(3):483–495

- Pretzsch H, del Río M, Schütze G et al (2016) Mixing of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) enhances structural heterogeneity, and the effect increases with water availability. *For Ecol Manag* 373:149–166. <https://doi.org/10.1016/j.foreco.2016.04.043>
- Pukkala T (1989) Methods to describe the competition process in a tree stand. *Scand J For Res* 4:187–202
- R Development Core Team (2016) R: a language and environment for statistical computing. <https://www.r-project.org/>
- Raunkiaer C (1934) The life forms of plants and their bearing on geography. Oxford University Press, Oxford
- Reineke LH (1933) Perfecting a stand-density index for even-aged forests. *J Agric Res* 46:627–638
- Reyer C, Lasch P, Mohren GMJ, Sterck FJ (2010) Inter-specific competition in mixed forests of Douglas-fir (*Pseudotsuga menziesii*) and common beech (*Fagus sylvatica*) under climate change—a model-based analysis. *Ann For Sci* 67:805–805. <https://doi.org/10.1051/forest/2010041>
- Richards A (2005) Testing ecological theory using the information-theoretic approach: examples and cautionary results. *Ecology* 86:2805–2814. <https://doi.org/10.1890/05-0074>
- Riofrío J, del Río M, Pretzsch H, Bravo F (2017a) Changes in structural heterogeneity and stand productivity by mixing Scots pine and Maritime pine. *For Ecol Manag* 405:219–228. <https://doi.org/10.1016/j.foreco.2017.09.036>
- Riofrío J, del Río M, Bravo F (2017b) Mixing effects on growth efficiency in mixed pine forests. *Forestry* 90:381–392. <https://doi.org/10.1093/forestry/cpw056>
- Riofrío J, del Río M, Maguire D, Bravo F (2019) Species mixing effects on height–diameter and basal area increment models for Scots pine and Maritime pine. *Forests* 10:249. <https://doi.org/10.3390/f10030249>
- Rodríguez-Calcerrada J, Nanos N, del Rey MC et al (2011) Small-scale variation of vegetation in a mixed forest understorey is partly controlled by the effect of overstorey composition on litter accumulation. *J For Res* 16:473–483. <https://doi.org/10.1007/s10310-010-0237-2>
- Rosseel Y (2012) lavaan: an R package for structural equation modeling. *J Stat Softw* 48:1–36
- Saetre P, Brandtberg PO, Lundkvist H, Bengtsson J (1999) Soil organisms and carbon, nitrogen and phosphorus mineralisation in Norway spruce and mixed Norway spruce—Birch stands. *Biol Fertil Soils* 28:382–388. <https://doi.org/10.1007/s003740050508>
- Sánchez-Gómez D, Valladares F, Zavala MA (2006) Functional traits and plasticity in response to light in seedlings of four Iberian forest tree species. *Tree Physiol* 26:1425–1433. <https://doi.org/10.1093/treephys/26.11.1425>
- Schollenberger CJ, Simon RH (1945) Determination of exchange capacity and exchangeable bases in soil—ammonium acetate method. *Soil Sci* 9:13–24
- Seidel D, Leuschner C, Scherber C et al (2013) The relationship between tree species richness, canopy space exploration and productivity in a temperate broad-leaf mixed forest. *For Ecol Manag* 310:366–374. <https://doi.org/10.1016/j.foreco.2013.08.058>
- Serrada R, Montero G, Reque JA (2008) Compendio de silvicultura aplicada en España. Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria-INIA, Madrid
- Smith DM, Larson BC, Kelty MJ, Ashton PNS (1997) The practice of silviculture. Wiley, New York
- Soil-Survey-Staff (2014) Keys to soil taxonomy, 12th edn. USDA-Natural Resources Conservation Service, Washington, DC
- Szwagrzyk J (1992) Small-scale spatial patterns of trees in a mixed *Pinus sylvestris*–*Fagus sylvatica* forest. *For Ecol Manag* 51:301–315
- Thurm EA, Pretzsch H (2016) Improved productivity and modified tree morphology of mixed versus pure stands of European beech (*Fagus sylvatica*) and Douglas-fir (*Pseudotsuga menziesii*) with increasing precipitation and age. *Ann For Sci* 73:1047–1061. <https://doi.org/10.1007/s13595-016-0588-8>
- Tilman D, Tilman D, Lehman CL et al (1997) Plant diversity and ecosystem productivity: theoretical considerations. *Proc Nat Acad Sci USA* 94:1857–1861. <https://doi.org/10.1073/pnas.94.5.1857>
- Van de Peer T, Verheyen K, Ponette Q et al (2018) Overyielding in young tree plantations is driven by local complementarity and selection effects related to shade tolerance. *J Ecol* 106:1096–1105. <https://doi.org/10.1111/1365-2745.12839>
- Vandermeer J (1989) The ecology of intercropping. Cambridge University Press, Cambridge
- Vila M, Vayreda J, Comas L et al (2007) Species richness and wood production: a positive association in Mediterranean forests. *Ecol Lett* 10:241–250. <https://doi.org/10.1111/j.1461-0248.2007.01016.x>
- Vilà M, Carrillo-Gavilán A, Vayreda J et al (2013) Disentangling biodiversity and climatic determinants of wood production. *PLoS ONE* 8(2):e53530. <https://doi.org/10.1371/journal.pone.0053530>

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.