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

Daphne López-Marcos[1,2] · María-Belén Turrión[1,2] · Felipe Bravo[1,3] · Carolina Martínez-Ruiz[1,2]

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 water-stress conditions and improves soil fertility.

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

María-Belén Turrión
bturrion@agro.uva.es

Felipe Bravo
fbravo@pvs.uva.es

Carolina Martínez-Ruiz
caromar@agro.uva.es

1   Sustainable Forest Management Research Institute UVa-INIA, Avda. Madrid 50, 34071 Palencia, Spain

2   Departamento de Ciencias Agroforestales, E.T.S. de Ingenierías Agrarias, Universidad de Valladolid, Campus La Yutera, Avda. Madrid 50, 34071 Palencia, Spain

3   Departamento 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
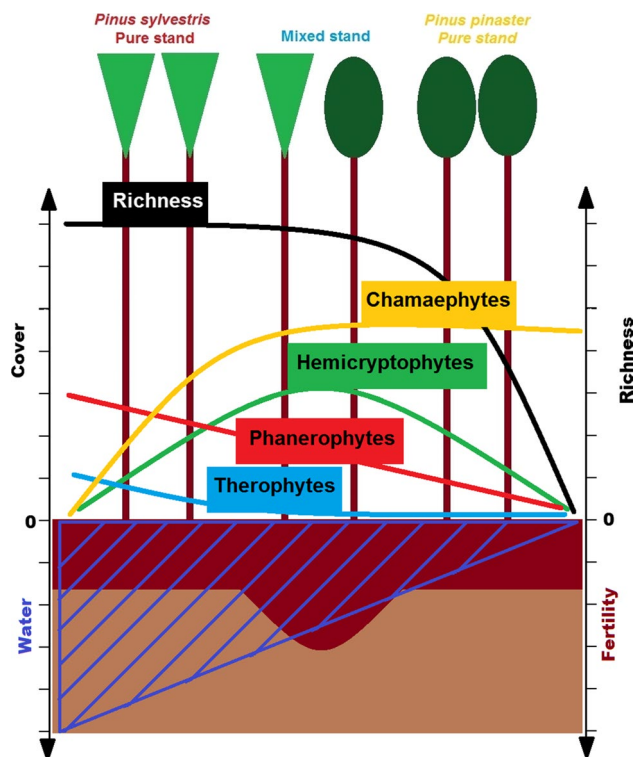
Introduction

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 versus monospecific stands (Riofrío et al. 2017a). 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. 2017a; Condés et al. 2018), structural heterogeneity (Pretzsch et al. 2016; Riofrío et al. 2017a), growth efficiency (Pretzsch et al. 2015; Riofrío et al. 2017b) or modified tree morphology (Thurm and Pretzsch 2016; Dirnberger et al. 2017; Zeller et al. 2017; Cattaneo 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 1992; 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 versus 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 (*P. pinaster* Aiton) in Spain. Both *Pinus* species show similar crown architecture and slight differences in shade tolerance (Riofrío et al. 2017a). 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. 2007). 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 (*P. 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
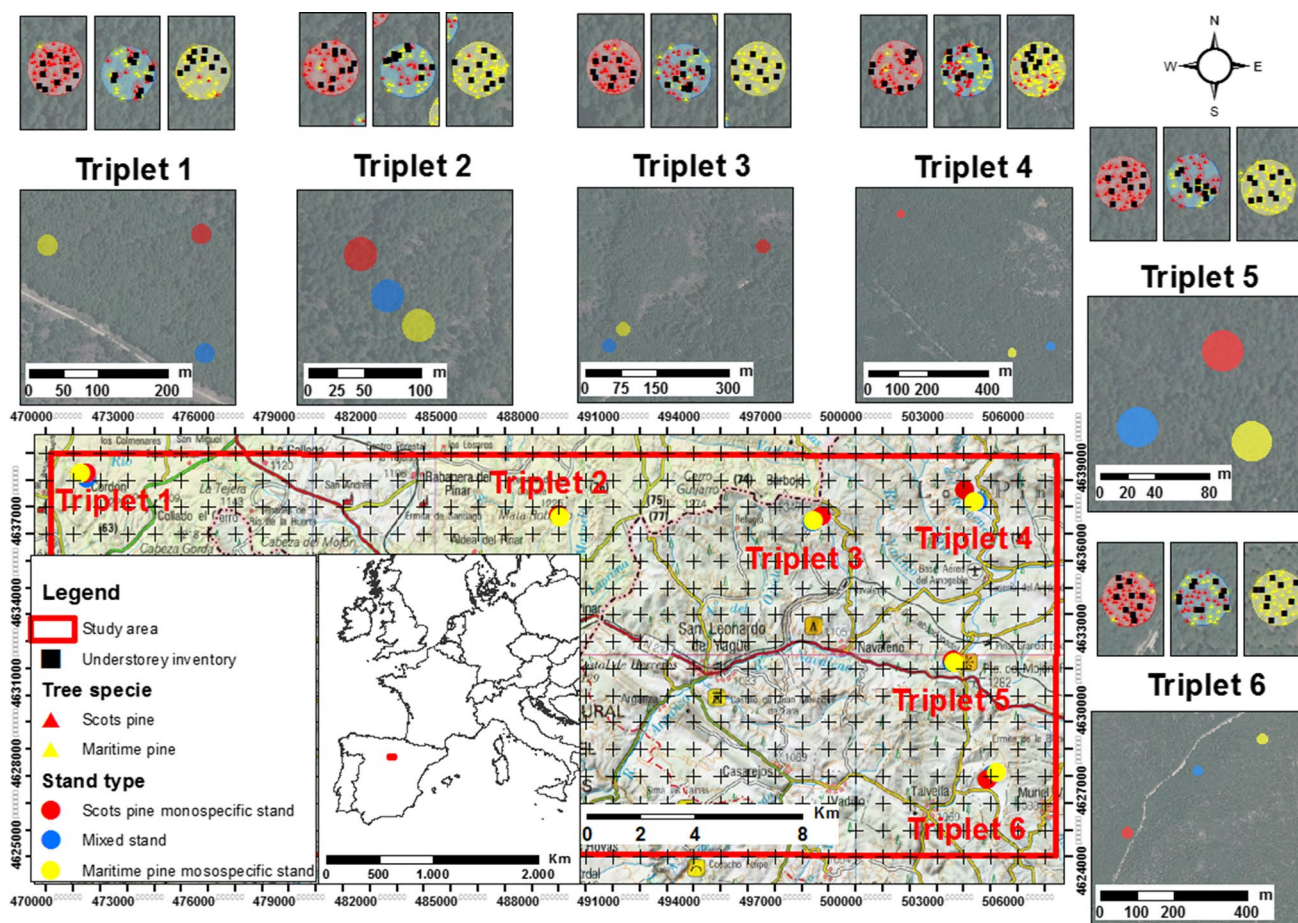
Fig. 1 Location of the triplets in the 'Sierra de la Demanda' in North-Central Spain and location of the plots in each triplet. *Pinus sylvestris* monospecific plots (PS): red circles; *Pinus pinaster* monospecific plots (PP): yellow circles; mixed plots of both *Pinus* species (MM): blue circles. (Color figure online)

vegetation was used. The aims of this study were: (1) to assess the effect of the overstory on the understory life-forms composition; (2) to link differences in the life-forms composition of the understory to soil properties; and (3) 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; 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 (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 characterized 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 *P. sylvestris* (PS) or *P. 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 (Fig. 1). 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 10 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, the basal area from 33.3 to 70.3 m^2/ha 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, b, 2019; Cattaneo 2018; López-Marcos et al. 2018).

Understory and soil sampling

Within each plot, 10 quadrats (1 m × 1 m) 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 life-forms classification (1934) following Aizpiru et al. (2007); see "Appendix 1". Therophytes are annual plants whose shoot and root systems die after seed production and which complete their whole life cycle within 1 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 aboveground 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., *P. sylvestris*, *P. pinaster*, *Q. 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 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 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 1 N 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 2". 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 2").

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 et al. 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 3"), 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 et al. 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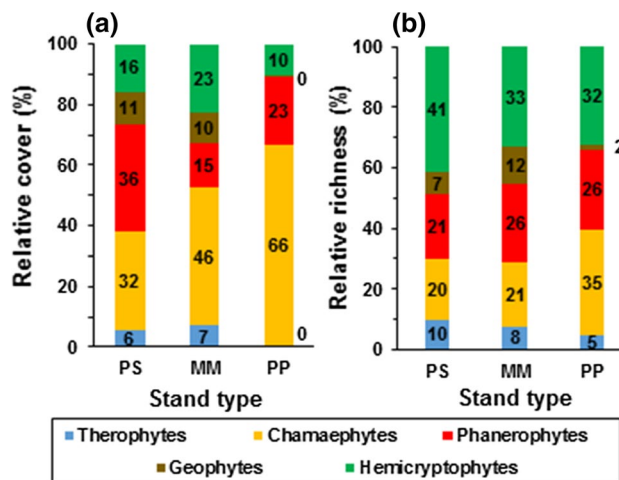 et al. 2018). Soils which have an aquic moisture regime are saturated long enough to cause anaerobic conditions (Soil-Survey-Staff 2014).

Fig. 2 Relative cover (**a**) and species richness (**b**) of different Raunkiær's life-forms in the understory of the three stand types. Abbreviations as in Fig. 1

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: $\chi^2 = 43.7$, $df = 8$, $p < 0.001$, Fig. 2a; richness: $\chi^2 = 16.4$, $df = 8$, $p < 0.04$, Fig. 2b). 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.

Nevertheless, in mixed stands (MM), chamaephytes and hemicryptophytes were the life-forms with the highest relative cover (45.6 ± 14.7 and $22.8 \pm 6.8\%$, respectively) and contributed also to high relative percentages of species richness (21.1 ± 6.7 and $33.0 \pm 6.2\%$, respectively); phanerophytes reached lower relative cover ($14.5 \pm 5.8\%$) but higher or lower relative species richness ($25.7 \pm 8.2\%$) than chamaephytes and hemicryptophytes, respectively; and geophytes and therophytes continue to be the life-forms that less contribute to the total cover and richness.
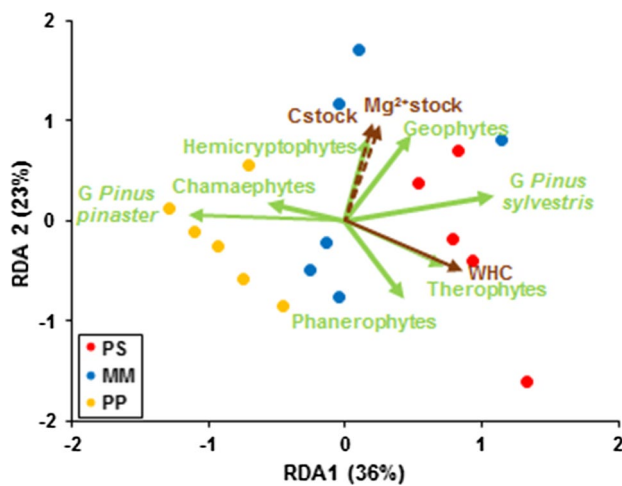
Fig. 3 RDA biplot of plots (dots) and vegetation variables (green lines), i.e., the Raunkiær's life-forms cover, and the basal area (G) of *Pinus sylvestris* and *P. pinaster*; and the significant explanatory soil properties fitted onto the RDA as vectors using the envfit function (brown solid line: $p < 0.05$; 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 Fig. 1. (Color figure online)

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 (Fig. 3). 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 (Fig. 3). 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 toward the negative end of the RDA1 while the basal area of *P. sylvestris* increases toward the positive end. Also the cover of therophytes ($r = 0.59$, $p < 0.01$) and chamaephytes ($r = -0.46$, $p < 0.05$) was 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 Fig. 2a. 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.

Relationship between vegetation composition and soil properties

The vectors of soil properties fitted onto the plot ordination (Fig. 3) showed how WHC ($R^2 = 0.39$; $p = 0.03$), Cstock ($R^2 = 0.32$; $p = 0.07$) and Mg^{2+}stock ($R^2 = 0.31$; $p = 0.08$) were the only significant soil properties from the 'envfit' analysis to explain the plots ordination. In addition, WHC was positively correlated with the plot scores along RDA1 ($r = 0.54$; $p < 0.01$), suggesting a gradient of moisture, along the overstory composition gradient associated with RDA1, which increases toward the *P. sylvestris* plots. On the other hand, Cstock ($r = 0.55$; $p < 0.001$) and Mg^{2+}stock ($r = 0.54$, $p < 0.01$) were positively correlated with the plot scores along RDA2 showing both the same tendency, i.e., increasing toward the positive end. RDA2 represented a gradient of fertility related to the organic matter and exchangeable bases accumulated in the soil profile.

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; Fig. 4a), 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 (Fig. 4c) and Mg^{2+}stock (Fig. 4d) increase, whereas richness showed no response (HOF model I) to Cstock and, thus, it is not shown in Fig. 4b.

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 is not shown in Fig. 4. Therophytes showed HOF model II with increasing trend along RDA1 (Fig. 4a) as WHC increases (Fig. 4c), whereas therophytes showed skewed response curve (HOF model V) for Cstock with a maximum around 75 Mg ha^{-1} (Fig. 4b) and for Mg^{2+}stock with a maximum around 30 kg ha^{-1} (Fig. 4d). Hemicryptophytes showed unimodal response curves along RDA1 (HOF model V; Fig. 4a) and along the WHC gradient (HOF model IV; Fig. 4c) 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 (Fig. 4b), and HOF model III with increasing
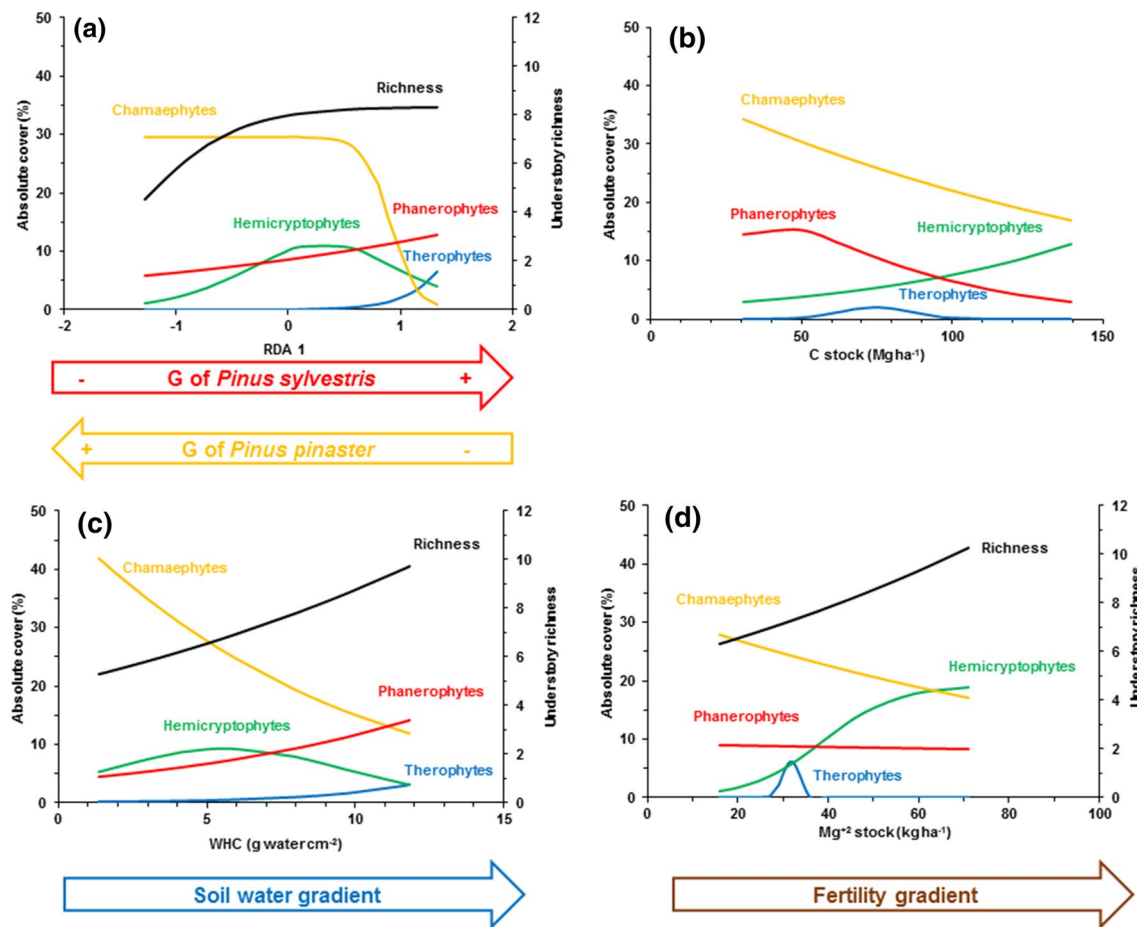
Fig. 4 HOF-derived response curves for the Raunkiær's life-forms cover and total species richness of the understory, relative to RDA1 (**a**), and to significant soil properties, i.e., Cstock (**b**), WHC (**c**) and Mg^{2+}stock (**d**). Abbreviations as in Fig. 3

trend bounded below the maximum attainable response as Mg^{2+}stock increases (Fig. 4d). 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 (Fig. 4c), Cstock (Fig. 4b) and Mg^{2+}stock (Fig. 4d) increase. Finally, phanerophytes showed a cover increasing trend (HOF model II) as G of *P. sylvestris* increases (RDA1 right-end; Fig. 4a), and as WHC increases (Fig. 4c), whereas they showed skewed response curve (HOF model V) for Cstock with a maximum around 50 Mg ha^{-1} (Fig. 4b) and a decreasing trend (HOF model II) as Mg^{2+}stock increases (Fig. 4d).

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* (Fig. 4a) 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 (Fig. 4c) 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 (Guo et al. 2016), and its deficiency can affect forest decline (Hüttl 1993; Zas and Serrada 2003). In the study area, both the greater productivity and overyielding found in mixed stands, compared to monocultures (Riofrío et al. 2017a), 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).

Understory life-forms respond to the overstory composition and soil fertility

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 et al. 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 and 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 in 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 (Fig. 4c). In fact, the cover of chamaephytes is similar in PS and MM (Fig. 4a), 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 (Fig. 4d). Previous studies also showed that many hemicryptophytes were indicative of sites with relatively good soil fertility (Mark et al. 2000; Sigcha et al. 2018).

Implications for forest management

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 *Q. pyrenaica*, which has been granted critically endangered protection status all across Spain (see "Appendix 1"), enjoys higher regeneration when both *Pinus* species cohabit (López-Marcos et al. 2019 under revision). 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 *P. 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.

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.

Appendix 1

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

Life-forms	Species	Protection status				Raunkiaer'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.	SI	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			

Life-forms	Species	Protection status				Raunkiaer's life-forms cover (%)		
		Status	Law	Red book	Region	PS	MM (mean ± SE)	PP
	Pinus sylvestris L.							
	Pinus pinaster Aiton	SI	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			

[1]Orden de 5 de noviembre de 1984 sobre protección de plantas de la flora autóctona amenazada de Cataluña. D.O.G.C. núm. 493, 12 de diciembre de 1984, págs. 3505–3506

[2]Orden de 10 de diciembre de 1984, sobre protección del acebo (*Ilex aquifolium* L.) en el territorio de la Comunidad Autónoma de Galicia. D.O.G. núm. 240, 15 de diciembre de 1984, págs. 4240–4241

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Appendix 2

Data analyses of soil properties.

Water holding capacity

Water holding capacity of each horizon (WHC$_{Hi}$)

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

AW_{Hi}: available 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)

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

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 (0–50 cm; oxCstock)

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

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 (0–50 cm; Cstock)

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

Total nitrogen stock

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

$$Nstock_{Hi} = TN_{Hi} \cdot bD_{Hi} \cdot \%EF_{Hi} \ T_{Hi}$$

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 (0–50 cm; Nstock)

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

Available phosphorus stock

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

$\text{Pavstock}_{Hi} = \text{TN}_{Hi} \cdot \text{bD}_{Hi} \cdot \%\text{EF}_{Hi}$ T_{Hi}	Pav_{Hi}: total nitrogen of each horizon
	bD_{Hi}: bulk density of each horizon
	$\%\text{EF}_{Hi}$: % of earth fraction of each horizon
	T_{Hi}: thickness of each horizon

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

$$\text{Pavstock} = \sum \text{Pavstock}_{Hi}$$

Exchangeable sodium stock

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

$\text{Na}^+\text{stock}_{Hi} = \text{TN}_{Hi} \cdot \text{bD}_{Hi} \cdot \%\text{EF}_{Hi}$ T_{Hi}	Na^+_{Hi}: exchangeable sodium of each horizon
	bD_{Hi}: bulk density of each horizon
	$\%\text{EF}_{Hi}$: % of earth fraction of each horizon
	T_{Hi}: thickness of each horizon

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

$$\text{Na}^+\text{stock} = \sum \text{Na}^+\text{stock}_{Hi}$$

Exchangeable potassium stock

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

$\text{K}^+\text{stock}_{Hi} = \text{TN}_{Hi} \cdot \text{bD}_{Hi} \cdot \%\text{EF}_{Hi}$ T_{Hi}	K^+_{Hi}: exchangeable potassium of each horizon
	bD_{Hi}: bulk density of each horizon
	$\%\text{EF}_{Hi}$: % of earth fraction of each horizon
	T_{Hi}: thickness of each horizon

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

$$\text{K}^+\text{stock} = \sum \text{K}^+\text{stock}_{Hi}$$

Exchangeable calcium stock

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

$\text{Ca}^{2+}\text{stock}_{Hi} = \text{TN}_{Hi} \cdot \text{bD}_{Hi} \cdot \%\text{EF}_{Hi}$ T_{Hi}	Ca^{+2}_{Hi}: exchangeable calcium of each horizon
	bD_{Hi}: bulk density of each horizon
	$\%\text{EF}_{Hi}$: % of earth fraction of each horizon
	T_{Hi}: thickness of each horizon

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

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

Exchangeable magnesium stock

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

$\text{Mg}^{2+}\text{stock}_{Hi} = \text{TN}_{Hi} \cdot \text{bD}_{Hi} \cdot \%\text{EF}_{Hi}$ T_{Hi}	Mg^{2+}_{Hi}: exchangeable magnesium of each horizon
	bD_{Hi}: bulk density of each horizon
	$\%\text{EF}_{Hi}$: % of earth fraction of each horizon
	T_{Hi}: thickness of each horizon

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

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

Appendix 3

Soil properties (mean ± SE), in each stand type, fitted as vectors onto the RDA ordination (Fig. 3). *PS Pinus sylvestris* monospecific plots, *PP Pinus pinaster* monospecific plots, *MM* mixed plots of both *Pinus* species.

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

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