# Soil control over the distribution of Mediterranean oak forests in the Montsec mountains (notheastern Spain)[1]

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**Abstract**

Models of plant species distribution and response to global change rely mostly on climatic variables alone, whereas soil variables are usually not taken into account. Evergreen and marcescent oaks are therefore considered to share environmental niches in the Mediterranean region despite their functional differences. We studied the distribution of forests dominated by either *Quercus ilex* (QI plots) or *Q. faginea*/*Q. subpyrenaica* (QF plots) in 46 plots at an altitude between 570 m and 980 m on a north-facing slope in northeastern Spain. We used binomial logistic regression and classification tree analysis to explain the distribution of the two types of forest. Soils of the sample plots were mostly Lithic Xerorthents developed from limestone. Surface mineral horizons of QI forests had higher organic carbon (C), nitrogen (N), and NaOH-extractable phosphorus concentrations, while organic layers had smaller values of the C/N and C/P ratios. Soils of QF forests accumulated higher amounts of C despite the lower concentration in their surface mineral horizons. The distribution of QF and QI forests was significantly explained by the variability in soil available water-holding capacity and rock fragment content, QF forests appearing on soils with over 22 mm of available water-holding capacity and less than 26% rock fragments. The presence of *Acer monspessulanum*, a secondary tree species, was related to soils with few rock fragments and high pH. Soil variability produces different patterns of water availability under homogenous macroclimatic conditions that are differently suited to the two types of

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forest. Information about whole soil profiles is required in the assessment of present vegetation distribution and future response to climate change.

**Keywords**: available water-holding capacity, land evaluation, *Quercus faginea*, *Quercus ilex*, rock fragments, soil rootable depth

## 1. Introduction

Soil science and terrestrial ecology are rarely integrated (Binkley, 2006), and the analysis of the distribution and performance of plant species is frequently based on climatic variables only (Coudun et al., 2006; Bertrand et al., 2012). Models of the effect of climate change, past or future, on vegetation distribution also avoid studying soils in many cases (e.g., Sánchez de Dios et al., 2009; Felicísimo, 2011; López-Tirado and Hidalgo, 2016).

Most of the studies that actually include soil information concentrate on the effect of surface-soil, mostly chemical, characteristics (e.g., Kooijman et al., 2005; Maltez-Mouro et al., 2005; Laliberté et al., 2014), but soil type and whole-profile features such as rootable depth, available water-holding capacity, and soil aeration may have a much more important role in vegetation distribution (McAuliffe, 1994; Romanyà et al., 2005; Sajedi et al. 2012) and performance (Dana and Mota, 2006; Olarieta et al., 2006, 2016; Hamerlynck and McAuliffe, 2008).

The presence of adjacent or mixed forests of marcescent or semi-deciduous (e.g., *Q. faginea* Lam., *Q. subpyrenaica* Villar) and evergreen (e.g., *Quercus ilex* L.) oak species in the Mediterranean region has been the subject of much research in plant ecology. Among these oak species, *Q. ilex* appears to be the one best adapted to drought according to studies comparing their production, biomass allocation, and growth response to increasing moisture deficits (Montserrat-Martí et al., 2009; Mediavilla and Escudero, 2010). Macroclimatic studies have reported the vulnerability of *Q. faginea* to drought (Urbieta et al., 2011; Granda et al., 2013; Urli et al., 2013), while the influence of human disturbance in restricting the distribution of *Q. faginea* has also been stressed (Kouba et al., 2011). But these comparative studies avoid  the study of soils in the field by relying either on geology as a surrogate (e.g., Thuiller et al., 2003; Kouba et al., 2011; Ruiz-Labourdette et al., 2012), on broad soil maps (e.g., Urbieta et al., 2011), or on a few soil surface descriptors obtained in forest inventories (e.g., Olthoff et al., 2016).

Reviews describing the habitats of marcescent (Pérez-Ramos and Marañón, 2009) and evergreen oaks (Rodà et al., 2009) in Spain show very few studies on the soils supporting forests of each individual species. Stands dominated by *Q. ilex* have been described in a semiarid area on very shallow calcareous soils with over 30% sand (Rodríguez-Ochoa et al., 2014). *Q. ilex* has also been reported on soils with pH of 4.5-8.5 and *Q. faginea* in soils with a pH of 5.8-6.8 (Núñez et al., 2003). In another study, forests dominated by *Q. faginea* were described on soils with a pH range of 5.8-8.2, a water holding-capacity over 68 mm, and a rock fragment content of 3-81% (López and Sánchez, 2008). *Acer monspessulanum* L. is one of the secondary tree species that frequently appears in *Q. faginea* forests (Pérez-Ramos and Marañón, 2009). It is one of the *Acer* species most resistant to dry conditions (Tissier et al., 2004), but otherwise there is also very little information about its environmental requirements.

Studies about the performance of these species show that growth and productivity of adult trees of *Q. ilex* improve with increased soil water availability during the warm season (Rodà et al., 1999), soil rootable depth (Bichard, 1982; Curt and Marsteau, 1997), phosphorus, potassium, and magnesium availability (Bichard, 1982; Pascual et al., 2012), and lower levels of pH, calcium carbonate, and active lime in the soil (Curt and Marsteau, 1997; Pascual et al., 2012). Seedling survival of *Q. ilex* also increases with soil phosphorus and potassium availability (Valdecantos et al., 2006; Gómez-Aparicio et al., 2008). In plantations on deep soils, growth of *Q. faginea* increased with increasing concentrations of potassium and lower concentrations of gypsum (Olarieta et al., 2009).

Forests dominated by *Q. ilex* subsp. *ballota* (Desf.) Samp. in Bol. (= *Q. rotundifolia* Lam.) and forests dominated by marcescent oaks (*Q. faginea* and/or *Q. subpyrenaica*) frequently appear side by side in the southern Pyrenees, occupying areas which are homogeneous from a topo-climatic point of view, and therefore suggesting that soil characteristics control the distribution of both types of forest. Following on the argument that *Q. ilex* is better adapted to drought than *Quercus faginea/Q. subpyrenaica* (hereafter we will refer to *Q. faginea* implying any of these two species), the objective of this paper is to test the hypothesis that the presence of forests dominated by either *Q. ilex* or *Q. faginea* is significantly influenced by soil conditions, and particularly by the available water-holding capacity of soils (AWHC).

## 2. Materials and methods

### *2.1. Location and field work*

The study area is located in the Montsec mountains (northeast Spain) on a north-facing slope covering over 1000 ha at an altitude between 570 m and 980 m (41º 58’ latitude, 0º 46’ longitude) (Figure 1). Mean annual temperature is 10.5-13.2 ºC, mean annual rainfall 520-680 mm, and mean annual evapotranspiration (Turc method) 605-850 mm.

We studied 46 plots with a size of 200 $m^2$ each in areas which were either dominated by *Quercus ilex* (QI plots; n=23) or by *Quercus faginea* and/or *Quercus subpyrenaica* (QF plots; n=23). Locations with a concave or convex shape along or across the contour were rejected as well as those that deviated clearly from the north aspect (outside the northwest-to-northeast range). In each plot, the number of trees with a diameter at breast height (dbh) greater than 5 cm were counted, and their height and dbh measured. The degree of the slope was measured with a clinometer and aspect with a compass. A soil pit was described in each plot to a depth of 100 cm or to underlying rock or strongly-cemented horizon following the SINEDARES criteria (CBDSA, 1983), rock fragment content was visually estimated for each horizon, soil rootable depth was estimated following Fitzpatrick (1996), and horizons and soils were classified according to Soil Taxonomy (SSS, 1999). Ten readings of penetration resistance were obtained in each soil horizon with an Eijkelkamp hand penetrometer (model IB) with a 0.25 $cm^2$ surface-area cone and a compression spring of 220 N, and the mean value per horizon calculated. Samples of the mineral horizons were collected from the soil pit, and samples of the organic soil horizons were obtained from five 20x20 cm quadrats randomly placed within each plot. In 30 plots (15 QI plots and 15 QF plots) the Oi horizon was separately sampled (Oi samples) from the rest of the organic horizon (Oe samples), while in the remaining 16 plots (8 QI plots and 8 QF plots) we obtained a single sample of the whole organic horizon per plot.

*2.2. Laboratory analyses*

Field samples of organic horizons were oven-dried at 60ºC and the dry weight obtained after separation of rock fragments by a 2 mm sieve. Samples were then grounded to pass a 1 mm sieve. Organic carbon concentration (C) was estimated as 50% of loss on ignition at 550 ºC. After wet-ashing in a nitric-perchloric acid solution, samples were analysed for potassium (K), calcium (Ca), and magnesium (Mg) by atomic absorption spectrophotometry, phosphorus (P) by colorimetry using the phospho-molybdo-vanadate method, and total nitrogen (N) by the Kjeldahl method. We used the Van Soest (1963) procedure in eight samples of Oi horizons (4 from QI stands and 4 from QF stands) to determine the concentration of lignin (acid detergent lignin), hemicellulose (as the difference between neutral detergent fibre and acid detergent fibre), and cellulose (as the difference between acid detergent fibre and acid detergent lignin).

Samples of the mineral soil horizons were dried at 60ºC and sieved to 2 mm, and analysed for pH (1:2.5 in water), organic carbon (Walkley-Black procedure considering a recovery factor of 1.58 (De Voos et al., 2007)), total nitrogen (Kjeldahl method), Olsen phosphorus, exchangeable potassium (determined by atomic absorption spectrophotometry after extraction with 1N $NH_4OAc$ at pH 7), calcium carbonate equivalent (volumetric calcimeter method), active lime (using the volumetric calcimeter method to determine the $CO_2$ produced by treating with HCl (50%) the extract obtained from the reaction of the sample with ammonium oxalate 0.2N), and texture (pipette method). Plant-available water-holding capacity of soils (AWHC) was estimated from rootable depth and coarse-fragment content and texture of horizons within the rootable depth (NEH, 1997). The organic carbon to total N (C/N) ratio was estimated from these analyses.

Phosphorus fractions were determined following the Olsen and Sommers (1982) fractionation method in a total of 15 samples, 9 corresponding to surface mineral horizons of QI plots and 6 to QF plots covering the range of calcium carbonate contents. This method included four sequential extractions with 0.1 M NaOH + 1 M NaCl (NaOH-P), 0.27 M Na citrate + 0.11 M NaHCO3 (CB-P), 0.27 M Na citrate + 0.11 NaHCO3 + 2% Na dithionite (CBD-P), and 1 M HCl (HCl-P). After each extraction, the suspension was centrifuged and the supernatant analysed for inorganic P (Pi) by the molybdate-ascorbic method (Murphy and Riley, 1962) and for total P by nitric-hydrochloric acid digestion. Organic P (Po) in each step was determined by subtracting inorganic P from total P. Total phosphorus in the original samples of mineral horizons was determined separately from this fractionation scheme and following the acid digestion procedure.

The total organic carbon content of soils was estimated by adding the contents of the organic and mineral horizons. The contents of the organic horizons were estimated from the dry weights and the organic carbon concentrations, and those of mineral horizons from their thickness, bulk density, and organic carbon concentration taking into account the proportion of rock fragments. Bulk density was estimated following Adams (1973, cited by De Vos et al., 2005).

### *2.3 Data analysis*

Statistical analyses were performed in R (R Development Core Team, 2009). Soil variables determined in the laboratory and in the field, except for rootable depth and AWHC, were introduced as thickness-weighted means of the values for the mineral horizons in the upper 30 cm of soil. Aspect was included after linearization with the function: Linear_aspect

= 180 - |aspect – 180|. As a result, values near 0 correspond with northerly aspects whereas values close to 180 correspond with southerly aspects. Other site variables included as explanatory variables were altitude and degree of slope.

Comparisons between the two types of plots (QI and QF) in terms of individual continuous variables were performed with the Kruskal-Wallis test. Differences between the two types of forests in terms of soil taxa were analysed with Fisher's exact test. We used logistic regressions to define the soil and/or site variables explaining the type of stand (QI or QF) in three sets of data: the whole set of plots (n=46), a set with plots supporting only *Q. ilex* or only *Q. faginea* ("pure stands") (n=21), and the set of plots in which fractionation of P was performed (n=15). Models which showed *P* values higher than 0.05 or which included explanatory variables with individual *P* values higher than 0.05 were rejected. Classification trees were used with the "rpart" package (Therneau et al., 2015) to define the threshold values for the variables explaining the type of stand. Similar analyses were performed to explain the presence or absence of *Acer monspessulanum*.

## 3. Results and discussion

### *3.1. Stand and plot characteristics*

The study plots had slopes ranging from 8% to 35% that did not vary significantly between QI and QF stands (p>0.15). Stands had a mean total density of 3238 trees $ha^{-1}$ and a mean basal area of 17.2 $m^2$ $ha^{-1}$, with similar values for QI plots (3202 trees $ha^{-1}$ and 17.1 $m^2$ $ha^{-1}$) and QF plots (3274 trees $ha^{-1}$, and 17.3 $m^2$ $ha^{-1}$). There was a limited degree of mixture of species in the two types of stands. 'Pure' QI stands, with no presence of *Q. faginea* at all, were 39% of all QI stands, and 'pure' QF stands, with no *Q. ilex* trees, were 52% of all QF stands. Nevertheless, *Q. faginea* trees represented at most 10% of all trees in the QI stands in which they appeared, whereas *Q. ilex* always accounted for less than 15% of the total density of trees in QF stands.

*Acer monspessulanum* (AM hereafter) appeared as a secondary tree species with densities of less than 400 trees $ha^{-1}$ in most cases. It appeared in 75% of the QF plots (with a mean density of 378 trees $ha^{-1}$ in those plots in which it did appear), but only in 26% of the QI plots (with a mean density of 192 trees $ha^{-1}$), and in 20% of the pure QI stands (with a density of 75 trees $ha^{-1}$).

### *3.2 Soils*

Soils were mostly (80% of the plots) classified as well drained, non-saline Lithic Xerorthents, and were developed from limestone, or in a few cases from local colluvium or from sandy limestone. Despite the highly calcareous parent material, significant processes of decarbonation have occurred in some of these soils, as 58% of the mineral surface horizons had $CaCO_3$ concentrations smaller than 100 mg $g^{-1}$. There were no differences between the soils of QI and QF plots in terms of their classification at the higher levels of Soil Taxonomy, but differences were significant (P=0.002) at the subgroup level, as QI soils were always classified in lithic subgroups whereas only 78% of QF soils were classified in these subgroups (the rest were classified in Entic, Pachic, Typic, or Vermic subgroups). Significant differences appeared at the particle-size family level (P<0.001), as 78% of QI soils and only 4% of QF soils were classified in skeletal or fragmental particle-size families, and 35% of QF soils but no QI soils were classified in clayey or fine families. Furthermore, soils in QF stands were deeper than those in QI stands (mean rootable depths of 36 cm and 17 cm, respectively; P<0.001) and had higher values of AWHC (51 mm vs. 15 mm; P<0.001) (Figure 2).

There were no significant differences in the dry weight of the organic horizons between the QI (mean value of 3.3 kg $m^{-2}$) and QF (2.8 kg $m^{-2}$) plots, nor in the organic carbon content of these horizons (1.4 kg $m^{-2}$ vs. 1.1 kg $m^{-2}$, respectively). But they differed significantly in various aspects. While Oi horizons of QI stands had significantly higher pH, organic carbon, and total nitrogen and phosphorus concentrations, Oi horizons of QF stands had significantly higher values of C/N and C/P ratios (Figure 3). These differences also appeared in Oe horizons, except for pH and C concentration. Differences in relation to the organic carbon concentration and C/N and C/P ratios should be taken with caution as the use of the same LOI to TOC conversion factor may not be appropriate when comparing two types of forest. The C/N and C/P ratios showed a significant positive correlation both in the Oi (r=0.51; P<0.005; n=30) and Oe (r=0.80; P<0.001; n=30) horizons.

There were no significant differences in the concentrations of cellulose, hemicellulose and lignin between the samples of Oi horizons from QI and QF stands (252 mg $g^{-1}$ vs. 141 mg $g^{-1}$; 175 mg $g^{-1}$ vs. 137 mg $g^{-1}$; and 189 mg $g^{-1}$ vs. 281 mg $g^{-1}$, respectively). Cellulose and hemicellulose behaved similarly, as their concentrations were positively correlated between them and with pH and N and P concentration, and negatively correlated with the C/P ratio in the Oi horizon (Table 1). On the other hand, lignin concentration was negatively correlated with both cellulose and hemicellulose concentrations and with pH and phosphorus concentration in the Oi horizon, while it was positively correlated with the C/P ratio in the Oi horizon and with active lime content in the surface mineral soil horizon (Table 1).

Values of the lignin/N ratio in Oi horizons mostly varied between 16 and 28, except in two QF plots where they were as high as 64 and 147, and there were no significant differences between the two types of forest (mean values of 19 for QI and 65 for QF). The lignin/P ratio in these horizons varied between 400 and 496, except for the above-mentioned two plots in which it reached values of 2254 and 1610, respectively. Differences between QI and QF forests were significant in this case (mean values of 413 and 1207, respectively; $P=0.02$). The lignin/N and lignin/P ratios showed a significant positive correlation ($r=0.72$; $P<0.05$; $n=8$).

Surface mineral horizons of QI stands had significantly higher concentrations of total nitrogen, exchangeable potassium, and rock fragments, whereas those of QF stands had significantly higher pH values (Figure 2).

Organic carbon concentration in the surface mineral soil horizon was significantly higher in QI stands (Figure 2), and for all plots, C concentration in the surface mineral horizon was negatively correlated with soil depth ($r = -0.56$; $P<0.001$; $n=46$). Total organic carbon content in soils was significantly bigger ($P<0.005$) in QF stands (14.2-23.1 kg $m^{-2}$) than in QI stands (4.9-12.3 kg $m^{-2}$). Mineral horizons stored 47-97% of all organic carbon in the soil, and only in 21% of the cases this proportion was smaller than 80%, but there were no significant differences between the QF and the QI forests ($P=0.08$).

The concentration of total P in the surface mineral horizon was significantly higher ($P=0.03$) in QI (345 mg $kg^{-1}$) than in QF stands (218 mg $kg^{-1}$), but there were no significant differences in the concentrations of the various P fractions in this horizon, except for a higher concentration of NaOH-P ($P=0.04$) in QI (mean value of 40 mg $kg^{-1}$) than in QF stands (24 mg $kg^{-1}$).

*3.3 Forest distribution*

The best logistic model explaining the presence of the two types of forest (QF plots vs. QI plots) included the content of rock fragments and soil rootable depth as explanatory variables, with increasing probability of dominance by QF as rock fragment content decreases and rootable depth increases (Table 2 and Figure 4). Soil available water-holding capacity (AWHC) was the variable that best explained individually the distribution of the two types of stands, with QF stands developing on soils with higher AWHC (Table 2 and Figure 4).

The classification tree analysis for the whole set of plots produced a model, with an internal prediction error of 9%, in which AWHC and rock fragments in the mineral surface horizon were the defining variables, and QF stands were coupled with soils with values of AWHC over 22 mm and a proportion of rock fragments smaller than 26% (Figure 5).

Applying the logistic regression analysis to only those plots in which the stands are pure QF or pure QI (i.e., with no presence of *Q. ilex* in the QF stands and no presence of *Q. faginea*/*Q. subpyrenaica* in the QI stands), the rock fragment fraction was the only significant explanatory variable, and the model showed and increasing probability of QF stands as this fraction decreased (Table 2).

Using the logistic model analysis for those plots in which soil P fractionation was performed we obtained  a model in which soil rootable depth was the best predictor of the forest types (Table 2) and the introduction of the various P fractions did not improve the performance of the model.

### *3.4 Presence of Acer monspessulanum*

Stands where *Acer monspessulanum* (AM) was present had significantly higher AWHC and pH values in the surface mineral horizon, whereas they had smaller rock fragment, coarse silt, organic carbon, and total nitrogen concentrations than stands where this species was absent (Table 3).

The logistic models for the presence of AM (Table 4) showed that this species had a higher probability of occurrence in soils with a smaller content of rock fragments and with a higher pH value of the surface mineral horizon. The classification tree analysis showed that the presence of AM had a probability of 80% in soils with less than 28% rock fragments in the mineral surface horizon.

## 4. Discussion

### *4.1 Forest distribution*

Our results stress the importance of soils as determinants of plant species distribution, in accordance with previous literature (McAuliffe, 1994; Romanyà et al., 2005; Andreetta et al., 2016). The models obtained indicate that the available water-holding capacity of soils is the major factor explaining the distribution of the two types of forests studied, dominated by either *Quercus ilex* or *Q. faginea*/*Q. subpyrenaica* (Table 2; Figures 4 and 5). These results are congruent with the higher resistance of *Q. ilex* to climatic drought, which confers this species with a certain advantage under increasingly drier conditions (Montserrat-Martí et al., 2009). The preference of *Q. faginea* for soils with bigger AWHC is consistent with the higher water demand of its canopy in comparison to that of *Q. ilex* (Mediavilla and Escudero, 2010). While the growth of *Q. ilex* improves on deeper soils (Bichard, 1982; Curt and Marsteau, 1997; Rodà et al., 1999), this does not mean that the species will necessarily become dominant, as Martre et al. (2002) have shown for other species in the Sonoran Desert (USA).

Models 1 and 2 (Table 2) provide similar information, because AWHC was estimated from rootable depth, and rock fragment content and texture within this depth. Nevertheless, the rock fragment content in the surface mineral horizon appears to have a specific effect on the distribution of these forests beyond its influence on soil AWHC, as it is the only variable explaining the distribution of 'pure stands' (Table 2). This may reflect different requirements of these two species in relation to soil bulk density and/or total and aeration porosity, as these variables are modified by the rock fragment content of soils (Torri et al., 1994; van Wessemael et al., 1996; Baetens et al., 2009). But stony soils also show a different pattern of water availability throughout the year in comparison to stone-free soils (van Wessemael et al., 1996). At field capacity, e.g. at the end of the winter, water content in the soil increases as rock fragment content decreases, and therefore *Q. faginea*, occupying soils with few stones, may take advantage of spring showers as it produces most of its shoot growth and leaf development in the spring (Montserrat-Martí et al., 2009). On the other hand, when small summer showers fall on a dry soil, soil water potential increases in stony soils compared to stone-free soils, as water is concentrated in a smaller amount of fine earth (van Wessemael et al., 1996). *Q. ilex* can therefore produce significant growth in the summer (Montserrat-Martí et al., 2009) using the improved availability of water in stony soils after those showers. Furthermore, rock fragments may release water during dry periods, and could reduce plant water stress during moderate droughts (Tetegan et al., 2015). These ecohydrological patterns conform to the model of hierarchical response to resource pulses proposed by Schwinning and Sala (2004).

Soil pH did not reach a significant level in explaining the distribution of these forests, but QI forests had lower pH values in the mineral surface horizon than those supporting QF forests (Figure 2). We described QF forests developing on soils with up to 596 mg $g^{-1}$ calcium carbonate, and therefore we suggest that the definition of *Q. faginea* as intolerant to soils with calcium carbonate (Núñez et al., 2003) may refer to *Q. faginea* subsp. *broteroi* and not to *Q. faginea* subsp. *faginea* (Pérez-Ramos and Marañón, 2009).

The logistic models show that the presence of *Acer monspessulanum* (Table 4) follows a similar pattern to the dominance of *Q. faginea*, which is congruent with the forest inventory data, which showed that AM appeared in 75% of the QF plots but only in 26% of the QI plots. Nevertheless, AM has a stricter requirement for a higher soil pH (Table 4).

*Q. ilex* and *Q. faginea* are frequently considered to share environmental conditions (Sánchez de Dios et al., 2009; Montserrat-Martí et al., 2009), but this is only true as far as climatic conditions are concerned. Our results show that forests dominated by either of these two species occupy soils with different characteristics. They also show that lithological data cannot be used as a substitute of soil data, as our plots were mostly located on soils developed from limestone but still soil variability was enough to explain to a considerable extent the distribution of the two types of forest. The use of soil maps, particularly those at broad scales, to infer soil conditions at the plot scale cannot be used as a substitute of the field study of soils either. In these cases, there is a complete mismatch between the scale at which the information on vegetation is collected (usually at the plot scale) and that on soils (e.g., 1:1,000,000). The variability within the soil taxonomic units used in these maps is too high to properly assess soil characteristics at the plot scale, and, in any case, these characteristics should not be reduced to those of the soil surface horizon.

The area occupied by forests of *Q. faginea* decreased significantly during the second half of the 20th century in the southern Pyrenees and this process has been linked to the expansion of agriculture (Kouba et al., 2011). Our results may help explain this change in land-use, as the soils occupied by *Q. faginea*, with relatively high AWHC and few rock fragments, are also those preferred by farmers for agriculture (Wulf et al., 2010).

### *4.2. Organic carbon stocks in soils*

The difference in total organic carbon content in the soils of the two types of forest studied is related to the deeper soils and smaller rock fragment content in QF stands, because C concentration was higher in mineral soil horizons of QI forests and C content in organic horizons did not vary significantly between forest types. Furthermore, the negative correlation between C concentration in the surface mineral horizon and soil rootable depth indicates that relying on the analysis of soil surface samples may lead to conclusions about soil carbon stocks that are contrary to actual values for the entire soil profile. De Vos et al. (2015) and Willaarts et al. (2016) have also stressed the importance of considering the whole soil depth to estimate C stocks in soils.

### *4.3 Soil organic horizons*

We will discuss the characteristics of the Oi horizons of our plots in comparison to data from leaf litter of the same species, but such comparisons should be taken with care as they obviously refer to two proximate but different components. No comparative values are available for QF forests, but the lignin and cellulose concentrations of Oi horizons in QI forests were within the range reported for undecomposed leaf litter of this species (Gessner, 2005). N and P concentrations in these horizons were also similar to those obtained by Rapp et al. (1999) and Serrasolses et al. (1999), but less than half the concentration of P obtained by Santa Regina (2001) (0.7 mg $g^{-1}$) and by Sardans and Peñuelas (2007) (0.87-1.06 mg $g^{-1}$) in leaf litter of QI.

N concentration increased from Oi to Oe horizons in QI plots but decreased sharply from the latter to the surface mineral horizons, while C/N ratio decreased continuously from Oi to Oe and to mineral horizons, particularly in the first step. These changes in the values of N concentration and C/N ratio among the organic and surface mineral horizons follow the general pattern described by Serrasolses et al. (1999) for other QI forests.

Organic soil horizons in QI plots belong, therefore, to the intermediate class of rate and completeness of decay (Parton et al., 2007; Prescott, 2010), and no immobilization of N or P may be expected as the lignin/N and lignin/P values were smaller than the critical values proposed by Osono and Takeda (2004). On the other hand, Oi horizons of QF forests belong to the low N group (5.8-8.0 mg $g^{-1}$) defined by Parton et al. (2007), and their lignin/N ratio indicates that they will undergo slow or incomplete decay according to Prescott’s model (2010). The critical values proposed by Osono and Takeda (2004) were exceeded in three QF plots for the lignin/N ratio and in two plots for the lignin/P ratio.

The characteristics of the Oi horizons, therefore, show significant differences between the two types of forest that point to a higher rate but a lower limit value of decomposition (Berg, 2000) in QI organic horizons. The higher N concentration in these horizons may reflect increased N concentration in leaves as a result of the higher intensity of water stress in QI plots (Laureano et al., 2013), which develop on soils with lower AWHC than QF forests.

*4.4 P fractions*

None of the phosphorus fractions provided any significant input to explain forest distribution (Table 2), but the results suggest a different pattern of P cycling in QI forests compared to QF forests. The high  water-use efficiency of *Q. ilex* requires, among other factors, good P availability (Sardans and Peñuelas, 2007). This improved availability may result from the lower values of the lignin/P ratio on Oi soil horizons of forests of this species (see previous section), and higher values of NaOH-P, which which is known to contribute to plant-available P from both its organic and inorganic fractions (Gressel and McColl, 1997; Rosling et al., 2016).

## 5. Conclusions

The distribution of evergreen and marcescent oak forests is influenced by the variability in the available water-holding capacity and rock fragment content of soils, which produces different ecohydrological patterns of water availability. Field study of whole soil profiles is therefore required to understand present plant distribution and future response to environmental change.

Soil variables related to organic matter or nutrients do not provide any significant explanation of forest distribution. But we hypothesize that these variables show the response of the two types of forest to their particular environmental conditions in terms of higher phosphorus availability in evergreen forests to allow for drier conditions.

Simple and cheap soil measurements or estimates, such as AWHC and rock fragment content, usually ignored in plant species distribution models, may provide more valuable information than more expensive and time-consuming chemical variables.


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Table 1.- Correlation among the characteristics of the Oi horizons, including samples from both QF and QI stands (n=8).

| | hemicellulose | cellulose | lignin |
|---|---|---|---|
| Hemicellulose | - | 0.91<br>0.002 | - 0.84<br>0.009 |
| Cellulose | - | - | - 0.95<br>< 0.001 |
| pH | 0.86<br>0.006 | 0.91<br>0.002 | - 0.94<br>< 0.001 |
| N | 0.72<br>0.04 | 0.75<br>0.03 | ns |
| P | 0.86<br>0.006 | 0.97<br>< 0.001 | - 0.91<br>0.002 |
| C/P | - 0.88<br>0.004 | - 0.99<br>< 0.001 | 0.96<br>< 0.001 |
| active lime* | ns | ns | 0.81<br>0.03 |

*: concentration in the surface mineral horizon

Table 2.- Logistic models showing the probability of the forest being dominated by *Quercus faginea*/*Q. subpyrenaica* for the three sets of plots: all the study plots, only those with "pure stands", and only those with analyses of P fractions (AWHC: available water-holding capacity (mm); rock fr.: proportion (%) of rock fragments in the surface mineral horizon; root. depth: soil rootable depth (cm)).

| Plots | | Variables | Parameter estimate | Pr>\|z\| | n | AIC | Residual deviance | Null deviance |
|---|---|---|---|---|---|---|---|---|
| All plots | Model 1 | Intercept<br>AWHC | -4.17<br>0.16 | <0.005<br><0.005 | 46 | 35 | 31 | 64 |
| | Model 2 | Intercept<br>rock fr.<br>root. depth | 0.46<br>-0.10<br>0.12 | 0.74<br>0.001<br>0.03 | | 31 | 25 | |
| Pure stands | | Intercept<br>rock fr. | 4.18<br>-0.12 | 0.01<br>0.01 | 21 | 17 | 13 | 29 |
| P fractions | | Intercept<br>root. depth | -3.66<br>0.11 | 0.04<br>0.04 | 15 | 15 | 11 | 20 |

Table 3.- Mean values and standard errors of some characteristics of the soil and soil surface mineral horizon in plots where *Acer monspessulanum* is present and in those where it is absent (AWHC: soil available water-holding capacity; root. depth: soil rootable depth; rock fr.: proportion of rock fragments in the surface mineral horizon).

| | AWHC (mm) (P=0.003) | root.depth (cm) (*P*=0.04) | pH (*P*=0.01) | rock fr. (% vol.) (*P*<0.0001) | C ($mg.g^{-1}$) (*P*=0.01) | N ($mg.g^{-1}$) (*P*=0.01) | coarse silt ($mg.g^{-1}$) (*P*=0.01) |
|---|---|---|---|---|---|---|---|
| Present (n=24) | 45 (31) | 32 (20) | 7.9 (0.2) | 20 (17) | 58 (26) | 2.2 (0.8) | 108 (44) |
| Absent (n=22) | 21 (20) | 21 (12) | 7.6 (0.5) | 49 (22) | 81 (30) | 2.9 (0.8) | 146 (55) |

Table 4.- Logistic models for the presence of *Acer monspessulanum* (rock fr.: percentage in volume of rock fragments in the soil surface mineral horizon; pH: pH of the soil surface mineral horizon) (n= 46).

<table>
<tr><th>Variables</th><th>Parameter estimate</th><th>Pr>|z|</th><th>AIC</th><th>Residual deviance</th><th>Null deviance</th></tr>
<tr><td>Intercept<br>rock fr.</td><td>2.37<br>- 0.07</td><td><0.001<br><0.001</td><td>48.41</td><td>44</td><td rowspan="2">64</td></tr>
<tr><td>Intercept<br>rock fr.<br>pH</td><td>-17.00<br>- 0.07<br>2.50</td><td>0.08<br><0.001<br>0.04</td><td>43.84</td><td>38</td></tr>
</table>

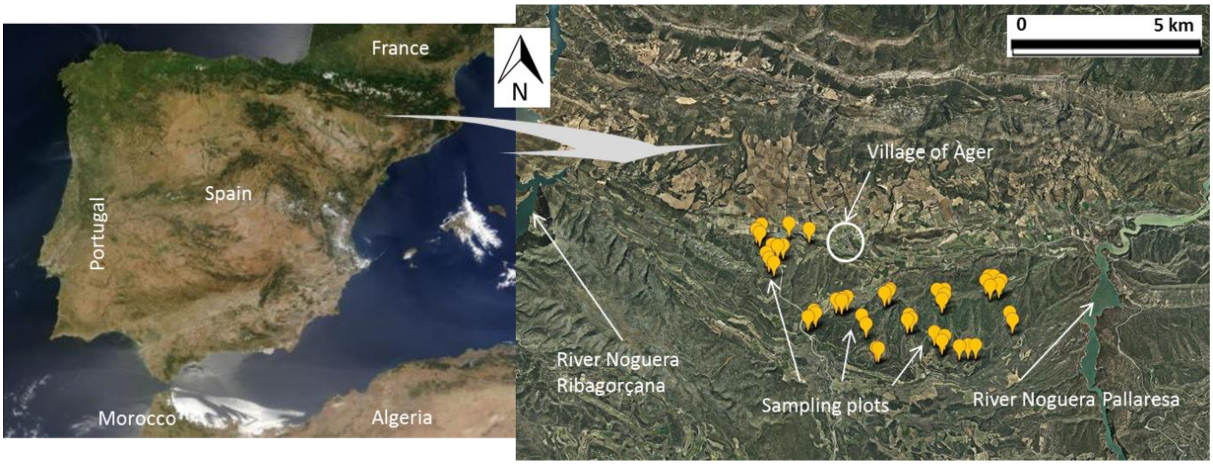


Figure 1.- Location of the study area and sampling plots

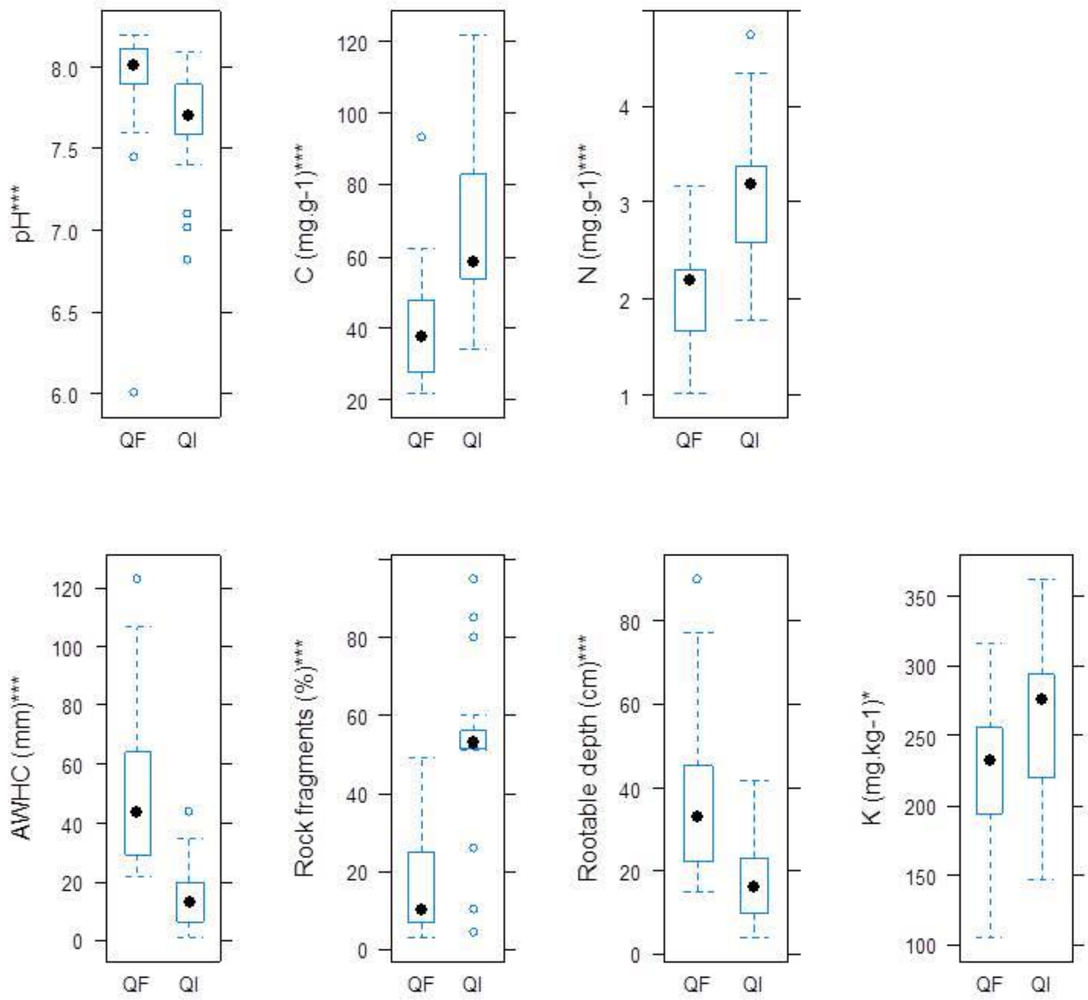


Figure 2.- Rootable depth and available water holding capacity (AWHC) of soils, and some characteristics of the surface mineral horizons of the stands dominated by either *Quercus faginea*/*Q. subpyrenaica* (QF) or *Q. ilex* (QI) (n=23 for both QF and QI; *: P<0.05; ***: P<0.001).

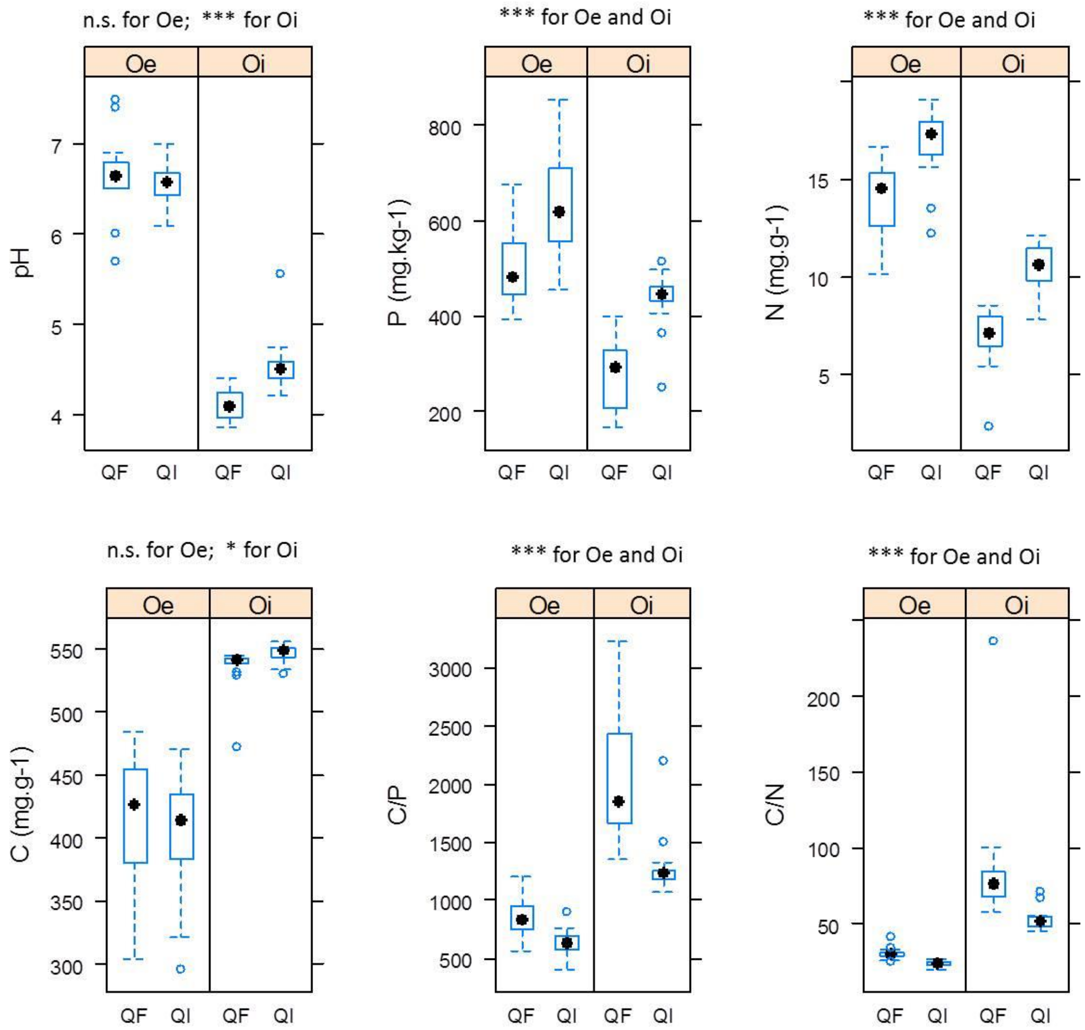


Figure 3.- Some characteristics of the organic horizons of the stands dominated by either *Quercus faginea*/*Q. subpyrenaica* (QF) or *Q. ilex* (QI) (n=8 for both Oi and Oe horizons; n.s.: not significant; *: P<0.05; ***: P<0.001)

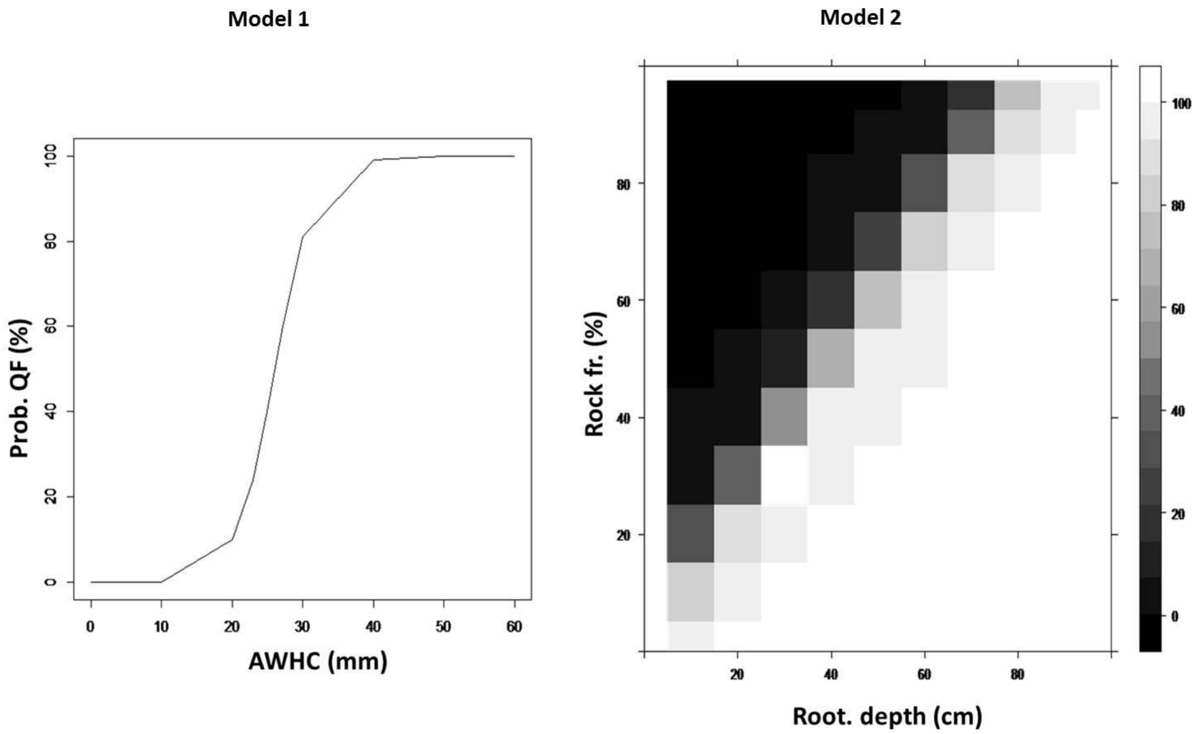


Figure 4.- Logistic models showing the probability of the forest being dominated by *Quercus faginea*/*Q. subpyrenaica* ("Prob. QF"), as opposed to being dominated by *Q. ilex*, as a function of soil available water-holding capacity ("AWHC") (Model 1), and as a function of soil rootable depth ("Root. depth") and proportion of rock fragments in the surface mineral horizon ("Rock fr.") (Model 2). The scale on the right shows the probability of QF forest in Model 2. For details, see Table 2.

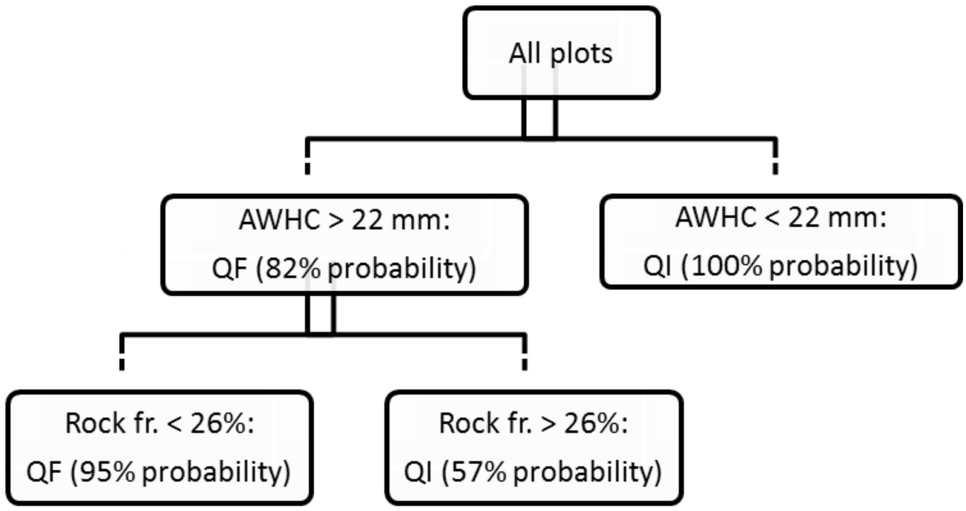


Figure 5- Classification tree for forest types (QF: *Quercus faginea*/*Q. subpyrenaica*-dominated; QI: *Q. ilex*-dominated) (AWHC: soil available water-holding capacity; Rock fr.: proportion of rock fragments in the mineral soil surface horizon).