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Soil control over the distribution of Mediterranean oak forests in the Montsec mountains (northeastern Spain)

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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 $<26\%$ 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 forest. Information about whole soil profiles is required in the assessment of present vegetation distribution and future response to climate change.

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

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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 (41° 58′ latitude, 0° 46′ longitude) (Fig. 1). Mean annual temperature is 10.5–13.2 °C, 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) >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 20 × 20 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 60 °C 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 °C. 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 60 °C 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 Vos et al., 2007)), total nitrogen (Kjeldahl method), Olsen phosphorus, exchangeable potassium (determined by atomic absorption spectrophotometry after extraction with 1 N 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 0.2 N), 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