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# Soil legacies determine the resistance of an experimental plant-soil system to drought

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ABSTRACT

This study examines the effects of climate and the degree of forest fragmentation legacies on response of oak to drought. A microcosm approach was set up with holm oak seedlings from three provenances grown in soils coming from two regions of contrasting climate (drier vs. wetter), and three scenarios of forest fragmentation (low, mid, and high agricultural matrix influence). We measured different indicators of the plant-soil system functioning such as ecosystem respiration, net ecosystem exchange, gross primary productivity, stomatal conductance, quantum yield, biomass allocation, and mycorrhization. Legacies of the bioclimatic region and the degree of forest fragmentation on soil properties drove the response to drought of an experimental plant-soil system, masking the effects of seedling provenance. The system was functionally more resistant to drought in soils from forest fragments with more agricultural influence and from the drier region. Our results indicate that the degree of forest fragmentation and bioclimatic legacies on soil properties exerted a much more decisive effect on the response of the plant-soil system to drought than holm-oak seedling provenance.

## 1. Introduction

The functioning of Mediterranean ecosystems is usually constrained by water availability, given that both plant productivity and soil activity are strongly subjected to seasonal and spatial variations of this resource (Rey et al., 2002). The expected reduction in soil water availability due to forecasted temperature increase and rainfall decline for this region (IPCC, 2013) is likely to be associated with profound modifications of carbon and water cycles (Reichstein et al., 2002). In fact, the increased intensity of drought in recent decades has led to a decrease in tree productivity and even to forest decline in some areas of the Mediterranean Basin, which has been related to changes in soil microbial communities and $CO_2$ fluxes (Barba et al., 2013, 2015; Curiel Yuste et al., 2012).

Climate change is not the only threat affecting the ecology and functioning of ecosystems in the Mediterranean Basin. Other factors such as habitat fragmentation can be considered among the most impacting human-related activities that have contributed to the transformation of this area in the past (Alados et al., 2004), although its effects on the ecosystem functioning have been less studied than those related with climate (e.g. drought). The impacts of landscape change (e.g. land-use intensification, forest fragmentation) have been widely analyzed (Fischer and Lindenmayer, 2007; Gossner et al., 2016; Tscharntke et al., 2005). However, most of these studies have focused on the above-ground compartment, while only a few have paid attention to below-ground components in the soil system (Flores-Rentería et al., 2016; Malmivaara-Lämsä et al., 2008; Riutta et al., 2012; Zheng et al., 2005). The effect of forest fragmentation is largely dependent upon the matrix that surrounds the remnant fragments (Fernández et al., 2002); for instance, Flores-Rentería et al. (2015) demonstrated that the agricultural matrix improved local environmental conditions (e.g. at small fragments tightly surrounded by agricultural land) by increasing soil water and nutrient contents, thus buffering the negative drought effects on the soil functioning (e.g. soil respiration and

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enzymatic activity). This increased soil fertility and water availability of fragmented holm oak forests have been further associated with higher organic inputs by trees and enhanced microbial activity (Flores-Rentería et al., 2016), highlighting the important role that fragmentation may have on the functioning of the plant-soil system. In this sense, it has been recently found that past land use largely affects the soil microbial community composition (Jangid et al., 2011), and its enzymatic activity (Fichtner et al., 2014). Similarly, soil respiration and the microbial biomass are influenced by the legacy effects of prior carbon and nitrogen addition (Marschner et al., 2015). Additionally, a long-term fertilization and water addition can result in soil legacies that, in turn, affect the plant resistance to drought (Legay et al., 2017).

Historical precipitation regimes can also lead to legacy effects influencing the response of plants (i.e. local adaptation, Andivia et al., 2012; Gimeno et al., 2009; Gratani et al., 2003) and microbial communities (Curiel Yuste et al., 2014; Evans and Wallenstein, 2012; Evans and Wallenstein, 2014) to drought. However, the simultaneous effect of drought on the response of plants, microorganisms, and their interaction has been poorly explored (Flores-Rentería et al., 2015; Richard et al., 2009).

Moreover, little is known about how the interaction of two important drivers of global change, fragmentation and drought, may affect the responsiveness of Mediterranean forests to global environmental change (plant growth, N and C mineralization rates, etc.). This knowledge is relevant for understanding the resilience of these ecosystems to the global change, because the interaction of different drivers frequently generates non-additive effects that, in turn, can either attenuate or exacerbate the ecosystem responses to individual drivers. For instance, forest fragmentation attenuated the effects of drought on microbial activity in Holm oak forest soils, showing more soil functioning, associated with a higher water retention, in small fragments compared with large fragments (Flores-Rentería et al., 2015). Similarly, forest fragmentation of gypsum soils attenuated the effects of drought on the fertility and microbial activity (Lázaro-Nogal et al., 2012). On the other hand, forest fragmentation may counteract climatic differences among regions and could even override the impacts of increased aridity on acorn crops (Morán-López et al., 2016).

Our general objective was to study the interactive effect of drought and forest fragmentation on the plant-soil system. For this, we used a microcosm approach with different holm oak provenances and soil legacy treatments proxies by soils from forest fragments differentially influenced by the surrounding agricultural matrix, collected in two different climatic regions (Flores-Rentería et al., 2015). As there are evidences of a distinctive functional response of different *Q. ilex* populations to drought (Andivia et al., 2012; Gratani et al., 2003), we first hypothesized that seedling provenance would determine their response to drought (i.e. those seedlings from drier sites would have high resistance to drought). Soil microorganisms are involved in the water stress response of plants (e.g. through nutritional and hormonal feedbacks) (Kreuzwieser and Gessler, 2010; Rincón et al., 2008), so second, we postulated that the presence of soil microorganisms would buffer the effect of drought stress on the plant-soil system (i.e. soils with original microbial propagules would have high resistance to drought). Finally, we hypothesize that the functional response of the plant-soil system and its resistance to drought is determined by soil legacy treatments of climate and the degree of forest fragmentation on soils. According to this, soils from the drier region adapted to drought and those with a higher influence of the agricultural matrix (since are more fertile and with higher water holding capacity), would cope better with drought (Flores-Rentería et al., 2015; Flores-Rentería et al., 2016).

## 2. Material and methods

### 2.1. Soil origin and sampling

We selected large (> 10 ha) and small (< 0.5 ha) forest fragments, resulting from the conversion of a continuous holm-oak (*Quercus ilex* L. ssp. ballota (Desf.) Samp) forest into a patchy agricultural landscape, in two bioclimatic regions of Spain (see Flores-Rentería et al., 2015 for a full description). The northern region (Lerma; 41°58′-42°02′N, 03°45′-03°52′W; 930 m asl) is characterized by 540 mm mean annual precipitation and 10.7 °C mean annual temperature (27.4 °C of maximum and 3.2 °C of minimum monthly temperature), whereas the southern region (Quintanar de la Orden; 39°30′-39°35′N, 02°47′-02°59′W; 870 m asl) is characterized by 342 mm mean annual precipitation and 15.8 °C mean annual temperature (35 °C of maximum and 5.5 °C of minimum monthly temperature); both sites with a pronounced summer drought period, usually lasting from July to September (AEMET, 2017). Accumulated water deficit (drought index estimated as the difference between accumulated precipitation and potential evapotranspiration from April to August 1982–2014) is 60% higher on average in the south (−431.84.2 ± 12.64 mm; −690.92 ± 16.88 mm; north and south, respectively), and water shortage is on average 68% more severe, 0.22 vs 0.07 average P/PET (ratio between precipitation and potential evapotranspiration on a monthly basis from June to August 1982–2014), north and south, respectively (Morán-López et al., 2016). The dominant soils are classified as Cambisols (calcic) (WRB, 2007), with a silty clay texture. In both regions, recent forests are highly fragmented due to the land conversion to cultivation (Flores-Rentería et al., 2015; Flores-Rentería et al., 2016). The large fragments were subdivided into forest interior (> 30 m from the edge) and forest edge. At the end of the dry season and within each region (wet Northern and dry Southern), soil samples were collected from a depth of 0–15 cm and from both under the canopy and open areas, at five small fragments (6 sampling points per fragment) and three large interior fragments (10 sampling points per fragment) and three edges (10 sampling points per fragment). The soil samples were pooled into a single composite sample within each forest fragment (small, large and edges) and region (Northern and Southern), a total of 6 kinds of soils. Soils were sieved (< 2 mm), dried at room temperature. Soil physicochemical characteristics were determined (Table S1; Flores-Rentería et al., 2015).

### 2.2. Seedling provenance

Holm oak 1-yr.-old seedlings of three provenances: Galaico-Leonesa (41°56′N, 06°15′W; 730 m asl; coded as “Gal”), Sistema Iberico (39°88′N, 01°38′W; 1042 m asl; coded as “Sib”) and La Mancha (39°51′N, 02°58′W; 760 m asl; coded as “Lam”) were obtained from the Centro Nacional de Mejora Forestal “El Serranillo” (Guadalajara, Spain). These provenances were selected because they were close to the regions where soils were collected, and were located within a precipitation and temperature gradient, i.e. mean annual values of 756 mm/10 °C for Gal area (supramediterranean), 608 mm/12 °C for Sib (supramediterranean), and 446 mm/14 °C for Lam (mesomediterranean) (Jiménez et al., 1996; Ninyerola et al., 2005; Rivas-Martínez, 1981).

### 2.3. Initial experimental set up

Besides the factor seedling provenance (Gal, Sib, Lam), other three factors were considered: 1) forest fragmentation (named agricultural “matrix influence, MI” from herein) with three treatments: forest interior (Fi), forest edge (Fe) and small fragment (Sf), 2) the bioclimatic region (R) with two treatments: wet and cold northern (N) and dry and warm southern (S) region, and 3) the factor native microorganisms (MO) with two treatments: presence (+) and absence (−). For this last factor, half of the soil in each matrix influence and bioclimatic region treatment was autoclaved. Soils selected for autoclaving were placed in trays to a depth of 1 cm (one treatment per tray), and autoclaved at 121 °C (105 kPa) at two intervals for a total of 60 min.

Each seedling provenance was grown in the respective treatment (full factorial of matrix influence, bioclimatic region and native