



# Agricultural matrix affects differently the alpha and beta structural and functional diversity of soil microbial communities in a fragmented Mediterranean holm oak forest



Dulce Flores-Rentería<sup>a, \*</sup>, Ana Rincón<sup>b</sup>, Fernando Valladares<sup>a, c</sup>, Jorge Curiel Yuste<sup>a</sup>

<sup>a</sup> Department of Biogeography and Global Change, Museo Nacional de Ciencias Naturales (MNCN), Spanish Scientific Council (CSIC), Serrano 115bis, 28006 Madrid, Spain

<sup>b</sup> Department of Plant Protection, Instituto de Ciencias Agrarias (ICA), Spanish Scientific Council (CSIC), Serrano 115bis, 28006 Madrid, Spain

<sup>c</sup> Departamento de Biología y Geología, Universidad Rey Juan Carlos, C/Tulipán s/n, 28933 Móstoles, Madrid, Spain

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## ABSTRACT

Given the increase in habitat fragmentation in the Mediterranean forests, understanding its impacts over the ecology of soil microbial communities, responsible for many ecosystem functions, and their capacity to metabolize different substrates from soil organic matter, is of utmost importance. We evaluated how the influence of the agricultural matrix, as one of the main consequences of forest fragmentation, may affect both the composition and the functioning of soil microbial communities in Mediterranean holm oak forests. We determined structural and functional alpha and beta-diversity of microbial communities, as well as microbial assemblages and metabolic profiles, by using a commonly used fingerprinting technique (Denaturing Gel Gradient Electrophoresis) and a community level physiological profiles (CLPP) technique (EcoPlate). Key drivers of soil microbial structure and metabolism were evaluated by using structural equation models (SEM) and multivariate ordination (envfit) approaches. Our results pointed out that forest fragmentation affects microbial community structure and functioning through a complex cascade of causal-effect interactions with the plant–soil system, which ultimately affects the nutrient cycling and functioning of forest soils. We also found a strong scale-dependency effect of forest fragmentation over the ecology of microbial communities: fragmentation increases the local (alpha) diversity, but affected negatively microbial diversity at the landscape scale (beta diversity). This homogenization of the microbial communities and their metabolism at landscape scale resulting from habitat fragmentation may have unknown potential consequences on the capacity of these communities, and hence these ecosystems, to respond to the climate change. Finally, we found a consistent relation between the structure and functional diversity of bacterial community, which further showed the important role that the assemblage of microbial communities might have over their functioning.

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## 1. Introduction

In the Mediterranean basin, forest fragmentation, resource overexploitation, and poor management are the main drivers of forest degradation (FAO, 2011), which is likely to be magnified by the increasing intensity of summer drought induced by climate change (Valladares et al., 2014a). Little research has been conducted to understand the effects of forest fragmentation on ecosystem functioning (Turner, 2005), despite the fact that it has important

implications for forest conservation and management strategies (Saunders et al., 1991), particularly taking into account its strong impact on the plant–soil–microbial system (Flores-Rentería et al., 2015). Within this framework, microbes are critical for driving ecosystem nutrient cycling, providing plants with the necessary nutrients to grow. Moreover, bacteria and fungi are responsible for about 90% of all organic matter decomposition (McGuire and Treseder, 2010; Ushio et al., 2013), and at least 50% of all CO<sub>2</sub> globally emitted from soils (Bond-Lamberty et al., 2004). However, very few studies have been designed to understand how forest fragmentation may affect the functioning of these microbial communities (Flores-Rentería et al., 2015).

\* Corresponding author. Tel.: +34 917452500x980801; fax: +34 915640800.  
E-mail address: [yaahid@gmail.com](mailto:yaahid@gmail.com) (D. Flores-Rentería).

Disturbance is generally detrimental to soil biodiversity, especially in agro-ecosystems (Walker, 2012). However, depending on the disturbance regime, changes in spatial environmental heterogeneity associated with fragmentation have been linked to either increases or decreases in soil biodiversity (Rantalainen et al., 2005; Flores-Rentería et al., 2015). For example, studies on forest fragmentation effects on microbial community structure have shown modest changes (Malmivaara-Lämsä et al., 2008; Flores-Rentería et al., 2015) or no changes (Rantalainen et al., 2005) in species composition. On the contrary, forest fragmentation can affect the functioning of microbial communities, as previously showed in other studies (Malmivaara-Lämsä et al., 2008; Riutta et al., 2012; Flores-Rentería et al., 2015). Furthermore, while it is often hypothesized that diversity is important for the maintenance of soil processes, and that reductions in the richness of soil microbial communities will disrupt the functional capability of soils (Giller et al., 1997; Wagg et al., 2014), we are just beginning to address this question, and the results presented so far draw contradictory conclusions (Griffiths et al., 2000; O'Donnell et al., 2001; Bell et al., 2005; Langenheder et al., 2010; Levine et al., 2011; Curiel Yuste et al., 2014; Tardy et al., 2014; Mendes et al., 2015). More knowledge about microbial diversity and its function is therefore required for current and future predictions of ecosystem functioning in a changing world; much more empirical work is needed to define the functional consequences, at the ecosystem scale, of changes in microbial composition and their responses to disturbances and global change.

Diversity measurement is particularly challenging for microbial communities (Magurran, 2004; Lozupone and Knight, 2008; Haegeman et al., 2013). Commonly, microbial diversity has been characterized as the diversity within a given community (alpha-diversity) generally using the total number of operational taxonomic units (OTU's richness), their relative abundances (Shannon diversity), or indices that combine these two dimensions (evenness). Studies have generally used microbial alpha-diversity to explore the relationships between structure and functioning of microbial communities (e.g. Curiel Yuste et al., 2011), whereas beta-diversity, which analyses the biological diversity among communities along environmental gradients (Anderson et al., 2006; Lozupone and Knight, 2008; Maaß et al., 2014), has been probably less studied for these communities. However, patterns of microbial community structure and diversity at the landscape scale and in perturbation gradients may also add info on co-occurrence – examining which organisms sometimes or never occur together –, that may help us understanding which conditions prefer or not (Fuhrman, 2009; Rincón et al., 2014). Several ecological processes potentially contribute to changes in co-occurrence patterns at the landscape scale, including competition, habitat filtering, historical effects and neutral processes (Horner-Devine et al., 2007; Maaß et al., 2014).

In this study, we used a molecular fingerprinting technique, Denaturing Gradient Gel Electrophoresis (DGGE), to characterize the structure of microbial communities (bacteria and fungi) coupled with the community level physiological profiles (CLPP), using Biolog™ EcoPlates, as indicator of microbial functioning, in order to evaluate the influence of the agricultural matrix, as one of the main consequences of forest fragmentation, on soil microbial ecology (i.e. structure and functioning) in fragmented Mediterranean holm oak forests. More precisely, we evaluated if the impact of forest fragmentation on the capacity of soil microbial communities to metabolize different substrates (metabolic profile) could be explained through its effects on microbial structure (assemblage, alpha and beta diversity) and/or changes in microhabitat characteristics. Based on previous studies, we here hypothesized that the agricultural matrix will exert strong direct (via changes in nutrient

availability) and indirect (via its influence over tree growth) effects over the microbial community structure, as well as over its capacity to metabolize different substrates (Fig. 1). Secondly, we hypothesized that the metabolic activity of soil microbial communities will be largely influenced by the structure of these communities (Fig. 1). Specifically, our objectives were: (1) to analyze the response of structural and functional diversity of soil microbial communities to the agricultural matrix influence; (2) to understand which biotic and abiotic factors associated with fragmentation (i.e. matrix influence) affect this diversity; and (3) to analyze causal relations between microbial community structure and its capacity to metabolize different substrates.

## 2. Material and methods

### 2.1. Study area

The study area is located near Quintanar de la Orden (39°30'–39°35'N, 02°47'–02°59'W; 870 a.s.l.), in Toledo, south-eastern Spain. This area has a Mesomediterranean climate characterized by 434 mm of mean annual precipitation and 14 °C of mean annual temperature, respectively (Ninyerola et al., 2005), with a pronounced summer drought, usually lasting from July to September. The landscape, a former predominant holm oak Mediterranean forest, is currently highly fragmented and surrounded by active croplands of cereals and legumes, with scattered grape crops that complete the mosaic. The original forests are in a variety of patch sizes, covering only 28% of their original area (Díaz and Alonso, 2003). The dominant tree is the holm oak (*Quercus ilex* L. ssp. *ballota* (Desf.) Samp; Fagaceae), with the understory mainly composed by shrubs of *Kermes oak* (*Quercus coccifera* L.) and scattered *Genista*, *Asparagus*, and *Rhamnus* species (for a full description of the study area see: Santos and Tellería, 1998; Díaz and Alonso, 2003).

### 2.2. Experimental design and sampling

A total of three large (>10 ha) and five small (<0.5 ha; with at least three trees) forest fragments within an area of 1000 ha,

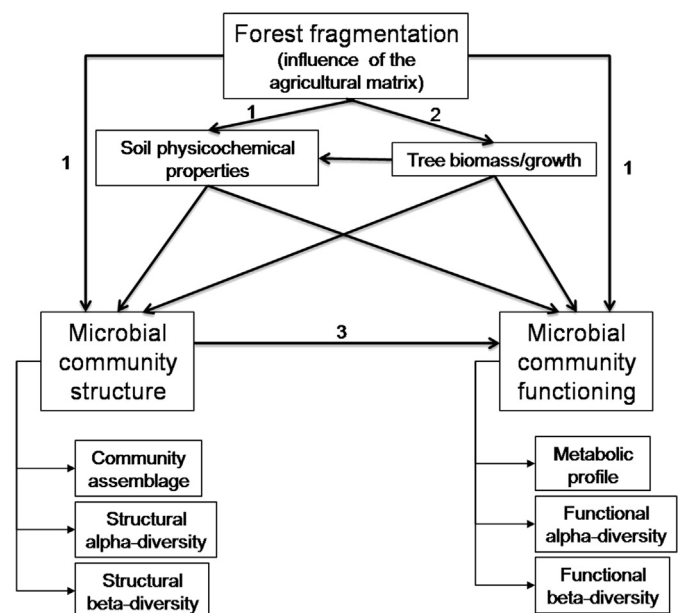


Fig. 1. Hypothesized direct (1) and indirect (2) effects of forest fragmentation over soil microbial communities and functioning and between this last (3).

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