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Secondary succession and parent material drive soil bacterial community composition in terraced abandoned olive groves from a Mediterranean hyper-humid mountainous area

Jaume Company ^{a,b,*}, Nicolas Valiente^c, Josep Fortesa ^{a,b}, Julián García-Comendador ^{a,b}, Manuel Esteban Lucas-Borja^d, Raúl Ortega^e, Isabel Miralles^e, Joan Estrany ^{a,b}

^a Mediterranean Ecogeomorphological and Hydrological Connectivity Research Team, Department of Geography, University of the Balearic Islands, Carretera de Valldemossa km 7.5, 07122 Palma, Balearic Islands, Spain

^d Department of Agroforestry Technology and Science and Genetics, School of Advanced Agricultural and Forestry Engineering, University of Castilla La Mancha, Campus Universitario, 02071 Albacete, Spain

^e Department of Agronomy and Center for Research in Intensive Mediterranean Agrosystems and Agri-food Biotechnology (CIAIMBITAL), University of Almeria, E-04120 Almería, Spain

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ABSTRACT

Mediterranean humid mountains are ecological hotspots with high water availability that may accelerate their recovery after farmland abandonment, a widespread phenomenon in marginal areas of the European Mediterranean Region. This land use change led to secondary succession processes triggering changes in soil properties and soil microorganisms. This is the first study in assessing the environmental influence of both ecological succession and parent material over soil properties and soil bacterial communities in these habitats. To examine the effects of secondary succession and elucidate the role of parent material in soil bacterial communities, six soil plots were sampled from the combination of abandoned and rainfed olive groves, terraced or non-terraced, and over four parent materials in Lluc Valley, a Mediterranean hyper-humid mountainous area on the island of Mallorca, Spain. Soil bacterial diversity and taxonomic composition at phylum and family level in each field were analyzed by rRNA 16 S amplicon sequencing. In addition, a series of soil physicochemical and microbiological properties, together with enzyme activities were assessed. Results showed that secondary succession and parent material significantly affected soil physicochemical and microbiological properties, soil enzyme activities and soil bacterial communities' diversity and taxonomic composition. Secondary succession following farmland abandonment triggered higher total organic carbon (TOC), microbial biomass carbon (Cmic), basal soil respiration (REB), alkaline phosphatase activity (Php) and dehydrogenase activity (DHA), thus enhancing soil quality. In contrast, parent material significantly shaped pH, specific surface area (SSA), TOC, Cmic, REB and soil enzyme activities, playing a key role in land use effects modulation. According to the distance-based redundancy analysis (db-RDA), SSA, TOC, REB, C_{mic}, urease activity (Ur) and Php were the soil properties that contributed to significant changes in bacterial communities' composition at the family level. This study evidenced that farmland abandonment led to improve soil quality in Mediterranean humid mountains, with positive feedbacks provided by parent material.

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^b Institute of Agro-Environmental and Water Economy Research –INAGEA, University of the Balearic Islands, Carretera de Valldemossa km 7.5, 07122 Palma, Balearic Islands, Spain

^c Centre for Biogeochemistry in the Anthropocene, Department of Biosciences, Section for Aquatic Biology and Toxicology, University of Oslo, PO Box 1066 Blindern, 0316 Oslo, Norway

^{*} Corresponding author at: Mediterranean Ecogeomorphological and Hydrological Connectivity Research Team, Department of Geography, University of the Balearic Islands, Carretera de Valldemossa km 7.5, 07122 Palma, Balearic Islands, Spain.

E-mail address: jaume.company@uib.cat (J. Company).

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1. Introduction

Soil microorganisms play a key role in ecosystem functioning, carrying out crucial biogeochemical processes and providing essential ecosystem services like soil fertility, water and air purification or climate change mitigation (Bardgett et al., 2008; Bodelier, 2011; Sofo et al., 2019). Among soil microorganisms, bacteria represent the most abundant and diverse group (Gans et al., 2005; Roesch et al., 2007). Soil bacterial communities are dynamic components of terrestrial ecosystems, presenting spatiotemporal variations (Koranda et al., 2013; O'Brien et al., 2016; Sauvadet et al., 2016). In this way, the structure, activity and gene expression patterns of soil bacterial communities are considered good indicators of soil quality and ecosystem stability (Hermans et al., 2017; Vázquez et al., 2020). Hence, soil bacterial communities enable the monitoring and assessment of anthropogenic perturbation effects and detect changes in nutrient and energy cycles in terrestrial ecosystems.

Soil enzymatic activities are considered one of the best proxies of soil health and related processes (Dick et al., 1997), and are useful to understand how soil bacterial communities were adapted to soil driven factors such as parent material or land use, since these soil enzymatic activities are directly or indirectly linked to soil organic matter or soil status (Doran and Parkin, 1994; Fernández-Romero et al., 2014).

Assessing the links between soil bacterial communities' composition and other soil parameters can reveal the bacteria-environment interactions, and explain how these communities respond to parent material and secondary succession processes. Several studies have reported that the geologic parent material controls a variety of soil properties; i. e., pH (Alfaro et al., 2017; Deng et al., 2015), soil texture (Angst et al., 2018; Sheng et al., 2015), SSA (Angst et al., 2018; Ersahin et al., 2006), soil nutrient composition (Deng et al., 2015; Sheng et al., 2015) and soil organic carbon (Angst et al., 2018; Deng et al., 2015); which exert a long-term influence on both soil bacterial communities and soil fertility/productivity. However, soil bacterial communities are especially sensitive to farmland abandonment, as this process triggers modifications in soil properties and plant communities that affect soil bacteria. In terms of soil properties, farmland abandonment results in higher values of organic matter (Nadal-Romero et al., 2016; Vázquez et al., 2020), nutrient stocks (Wang et al., 2011; Zhang et al., 2016), soil enzyme activities (Garcia et al., 1997; Xiao et al., 2021) and microbial activity (Kurganova et al., 2019; Marzaioli et al., 2010). With regard to plant-soil interactions, plant attributes such as primary productivity, species composition and diversity can shape bacterial communities through soil properties modification (Cline and Zak, 2015; Delgado-Baquerizo et al., 2018; Liu et al., 2020), since the amount and quality of organic substrates that are supplied to soil bacteria vary between land uses (García-Orenes et al., 2013; Jangid et al., 2011; Sauvadet et al., 2016). Consequently, the establishment of different tree species generates distinct litter amounts and qualities that can alter soil physicochemical properties and the abundance of different bacterial groups (Brunel et al., 2020; Panayiotou et al., 2017).

In the European Mediterranean Region, farmland abandonment increased significantly since the mid-20th century under socio-economic changes (Lizaga et al., 2019; Lucas-Borja et al., 2018). This process mainly occurred in marginal areas, frequently covered by terracing (Hooke, 2006), triggering secondary succession processes and changing the Mediterranean palimpsest habitats through the homogenization of plant communities and the consequent loss of biodiversity (Fernandez et al., 2013). During the last decades, studies on ecological succession caused by land use changes have been mainly focused on the evaluation of plant community patterns and mechanisms (Garnier et al., 2004; Kosmas et al., 2000; Wardle et al., 2004). Nevertheless, less is known about the affection of secondary succession following farmland abandonment on soil bacterial communities because of their higher complexity. As soil bacteria are essential components for ecosystem functionality and have been proved to be good indicators for soil quality

assessment, a significant amount of studies have been conducted worldwide on this topic in recent times (Cline and Zak, 2015; Guo et al., 2018; Kang et al., 2018; Tian et al., 2017; Yang et al., 2020; Zhong et al., 2018). At the same time, the application of high throughput sequencing has improved the understanding of the activity and diversity of soil bacterial communities (Liu et al., 2020; Rodríguez-Berbel et al., 2020; Sofo et al., 2019). However, research focused on the influence of parent material on soil properties and, consequently, on soil bacterial communities has received less attention. In the last years, some studies have been carried out in southern China suggesting the important role of parent material in shaping soil microbial communities. In paddy soils, Bai et al. (2017) found that soil properties linked to parent material significantly affected bacterial community structure and function mainly via the determination of soil pH in soils under uniform rice cultivation management; while Sheng et al. (2015) reported that soil properties such as pH, available Mn and total K, which are largely determined by the nature of the soil parent material, are major factors in determining soil bacterial community structure in the top soil (0-20 cm). In addition, Deng et al. (2015) examined the effect of land use type and parent material on red soil microorganisms, discovering how both give rise to significant effects on soil microbial biomass, activity and diversity, though parent material was a more important driver than land use type. Despite this background and the soils vulnerability to degradation, research on this topic in the European Mediterranean Region is scarce. Therefore this present work wishes to fill this gap by elucidating the role of parent material in soil bacterial communities' composition and diversity.

To our knowledge, this is the first study which assesses the effects of both farmland abandonment and parent material on soil bacterial communities in the European Mediterranean region. Our aim is to shed light on how secondary succession processes and parent material affect soil quality in terraced abandoned olive groves in a mountainous hyperhumid Mediterranean location, consistently recognized as ecological hotspot areas (Rundel et al., 2016; van Hall et al., 2017). Soil physicochemical properties, soil microbiological activities and soil bacterial communities' composition were analyzed in three abandoned fields and three rainfed olive groves over different parent materials and terracing. The main objectives were to (i) evaluate soil physicochemical/microbiological properties as well as soil bacterial community composition following secondary succession due to olive groves abandonment, and (ii) to assess the importance of parent material on such features.

2. Material and methods

2.1. Study area

Lluc Valley is located in the axial zone of the Tramuntana Range on the island of Mallorca, Spain (Fig. 1). It is a paradigmatic case of Mediterranean mountainous environment where interactions between natural dynamics and anthropogenic activities have been shaping the landscape for millennia. Agriculture has been the most relevant human activity in the study area. Due to the abrupt relief of the Tramuntana Range, favorable areas for the practice of agriculture were limited. As a result, agricultural terraces were built since the Bronze Age and more intensely between the 18th and 19th centuries, so that nowadays there is an extension of thousands of kilometers of dry-stone walls throughout the Tramuntana Range (i.e., Verger, 2014). Since the 16th century, olive trees became the main crop in the agricultural terraces of the Tramuntana Range. Afterwards, in the mid-20th century, important socioeconomic changes, in conjunction with the high maintenance costs of agricultural terraces and mechanization (Binimelis and Ordinas, 2015), led to the gradual abandonment of olive groves.

The field survey was developed in Menut, a traditional mountainous farm located in Lluc Valley, currently the headquarters of the Balearic Islands Forestry Center (http://www.caib.es/sites/xarxaforestal/ca/inf



Fig. 1. (a) Location of Lluc Valley within Mallorca Island. (b) Location of the Menut farm within Lluc Valley. (c) Sampling plots location in Menut. Sampling plots location with elevation curves (equidistance 10 m) in Menut over (d) lithology distribution and (e) soil type. Sampling plots location over the (f) 1956 and (g) 2019 orthophotographies (http://ideib.caib.es/).

ormacion-19072/). Elevation range varies between 500 and 562 m.a.s.l. The climate is hyper-humid Mediterranean. Mean annual temperature and rainfall are 14.4 °C and 1262 mm yr⁻¹, respectively (1993-2011, data provided by the Spanish Meteorological Agency, AEMET, for Lluc station; 39° 49' 24'' N; 2° 53' 9'' E). Lithology is mainly characterized by micritic limestones from the Lower Jurassic (Lias). To the east, other types of parent material are also found: alternating strata of clays, evaporites, marls, brechoid dolomites and basic rocks from the Upper Triassic (Keuper); folded dolomites, marls and brechoid dolomites from the Upper Triassic (Rhaetian); red silts, detrital limestones and gravels from the Quaternary. Main soil types, present in most of the study area coinciding with the micritic limestones from the Lias, are haplic and lithic leptosols. Through analyzing orthophotographies since the American flight of 1956 (http://ideib.caib.es/), the time of olive groves' abandonment was estimated at ca. 60 years. Currently, only herbaceous crops and some olive groves remain exploited in Menut, whilst most of the farm site is covered by natural vegetation.

2.2. Experimental design and sampling

The evaluation of soil quality indicators between abandoned fields and olive groves was carried out through the selection of six field plots following these criteria: (a) geographic proximity between olive groves with similar areas and elevations, (b) representative presence of abandoned and functioning olive groves with different geologic parent material.

Information about land use, location, lithology, plant species' composition, plant cover and stoniness for every sampled olive grove is detailed in Table 1. In relation to tree species, olive (*Olea europaea* L.) is predominant in terraced olive groves (Olive Terraced Keuper, OTK; Olive Terraced Rhaetian, OTR; Olive Terraced Lias, OTL) and in abandoned terraced fields with Lias lithology (Abandoned Terraced Lias, ATL). Aleppo pine (*Pinus halepensis* M.) and holm oak (*Quercus ilex* L.) are the most common species in abandoned terraced fields with Rhaetian lithology (Abandoned Terraced Rhaetian, ATR) and, together with common hawthorn (*Crataegus monogyna* Jacq.), are the main species in abandoned non-terraced fields with Quaternary lithology (Abandoned Non-Terraced Quaternary, ANTQ). Plant cover, both for shrub and herbaceous species, is greater in abandoned fields than in olive groves.

For each selected olive grove, six plots (5 ×5 m each) were established (Fig. 1) in June 2017. After manual exclusion of litter, samples (one per plot) were collected from the shallowest 15 cm. Each sample was composed of a mixture of six subsamples (200 g each) randomly collected inside the plots. Once in the laboratory, plant remains were removed and the samples were sieved at < 2 mm and stored at 4 °C prior to the analyses.

2.3. Chemical and physical soil analysis

Soil pH and electrical conductivity (EC) were analyzed in an aqueous solution suspension 1:2.5 (w/v) using a pHmeter (Crison BASIC 20 Crison, Barcelona, Spain) for soil pH measurements and a digital conductivity meter (Crison 522, Barcelona, Spain) for EC measurements. TOC was determined by Walkley and Black's method (1934) (rectified by Mingorance et al., 2007). SSA was measured using Mastersizer 2000 (Malvern Instruments, Worcestershire, United Kingdom). REB was measured in a multiple sensor respirometer (Micro-Oxymax, Columbus, OH, USA). Cmic was determined by the fumigation-extraction method (Vance et al., 1987). Ur was measured according to the method of Tabatabai (1994), using urea as substrate. Php and β -glucosidase activity were determined by the use of ρ -nitrophenyl phosphatedisodium and ρ -nitrophenyl- β -D-glucopyranoside, respectively, as substrates. The assay is based on the release and detection of p-nitrophenol (PNP), following Tabatabai (1994). DHA was determined to be the reduction of p-iodonitrotetrazolium chloride (INT) to p-iodonitrotetrazolium formazan, by a modification of the method reported by von Mersi and

Schinner (1991).

2.4. DNA extraction, high-throughput sequencing, and bioinformatics analysis

Microbial DNA was extracted from 0.3 g of soil using the DNeasy PowerSoil Kit (QIAGEN, Hilden, Germany) and quantified using an ND-2000 Nanodrop spectrophotometer (Thermo Fisher Scientific, USA). The V4-V5 regions (400-500 pb) of the bacteria 16 S ribosomal RNA gene were amplified in vitro by PCR using 515FB/8926Rr 16 S rRNA gene primer pair (Walters et al., 2016) and paired-end sequenced on an Illumina MiSeq platform using v3 chemistry (2x300bp), as described in Comeau et al. (2017). Subsequently, sequences were processed and grouped in Amplicon Sequence Variants (ASVs) with Quantitative Insights Into Microbial Ecology version 2 (QIIME2 version 18.8) software (Bolyen et al., 2018) following the protocol initially established in Comeau et al. (2017). Bacterial raw reads were trimmed of primers, quality controlled and contaminant filtered, followed by the creation of ASVs using the Deblur tool of QIIME2. The final taxonomic identification of ASVs was done using the QIIME2 feature-classifier plugin (sklearn method) against the SILVA database (version 132; trimmed to the V4V5 version of the 16 S). To check for no contamination during extraction one blank control was done and checked for no DNA presence with the Nanodrop. Besides PCR negative controls were done (1 for every 96-well plate in each MiSeq run) which were verified to be clean (no bands present) and moreover were sequenced on the MiSeq in order to show no substantial reads coming through on this barcode combination.

All statistical analyses were performed in R version 4.0.3 (R Core Team, 2016). Sample metadata, ASV matrix and taxa information were imported using phyloseq package (McMurdie and Holmes, 2013). Alpha diversity measures were achieved by using Microbiome package (Lahti et al., 2017) on the phyloseq object (i.e. observed ASVs, Chao1 richness index, Shannon diversity index, and Pielou's Eveness index). Bray-Curtis distances were used for calculating beta diversity and non-metric multidimensional scaling (NMDS) by means of phyloseq package. Permutational multivariate analysis of variance (PerMANOVA) was carried out based on the Bray-Curtis dissimilarity matrix by using permutest and adonis functions from vegan package (Oksanen et al., 2013). db-RDA was performed with the capscale function, also from vegan package. NMDS and db-RDA graphs were done using ggplot2 (Wickham, 2011) and ggpubr packages (Kassambara and Kassambara, 2020). Pearson correlations between the bacterial taxa and soil variables were calculated using Hmisc package (Harrel Jr and Harrel Jr, 2019) and displayed using corrplot package (Wei et al., 2017).

3. Results

3.1. Soil physicochemical properties

Beyond the different land uses, parent materials, or terracing, the hyper-humid climate is also a main common driver of soil quality in all the sampled fields. The high rainfall amounts triggered the leaching of soluble salts and their transport into groundwater systems or streams, promoting low EC in the study area (Table 2) and, therefore, the absence of significant differences for this parameter due to land use or parent material (Table 3). Regarding particle size, parent material mineralogy and weathering mainly determined the SSA (p < 0.05; Table 3), which was measured as an indicator of soil texture. In addition, terracing promoted finer soil texture, as the SSA values were higher in terraced fields (Table 2, Table 3). Furthermore, the mineralogy of the underlying parent materials derived in slightly alkaline soils in the ANTQ, ATL and OTL fields and moderately alkaline soils in the ATR, OTR and OTK fields (Table 2). Regardless of the similarity between the sampled parent materials, significant differences for pH values were detected, with highest values in Keuper lithology and lowest in Quaternary lithology

Table 1
Geographical, land use, parent material and vegetation features of the olive grove fields in Menut farm (Lluc Valley, Mallorca Island, Spain)

Field ^a	Latitude	Longitude	Parent material				Plant sp	ecies compos	ition (number of	individu	ials)					Plant cov	er (%)	Stoniness
				P. halepensis ^b	Q. ilex ^c	C. monogyna ^d	O. europaea	P. lentiscus ^f	A. mauritanica ^g	Allium sp.	Cistus sp.	P. lucida ^h	Euphorbia sp.	M. communis ⁱ	Tree species	Shrub species	Herbaceous species	(%)
ANTQ	39° 49' 26.4" N	2° 53' 49.2" E	Red silts, detrital limestones and gravels from the Quaternary	12	3	9	-	8	_	23	33	-	-	16	40	25	< 5	< 5
ATR	39° 49' 33.6" N	2° 54' 3.6" E	Folded dolomites, marls and brechoid dolomites from the Upper Triassic (Rhaetian)	9	3	1	1	53	26	1	-	-	-	_	50	40	< 5	15
ATL	39° 49' 48'' N	2° 53' 20.4" E	Micritic limestones of the Lower Jurassic (Lias)	1	-	-	10	2	87	128	22	-	-	-	20	40	< 5	45
ОТК	39° 49' 37.2" N	2° 53' 56.4" E	Clays, evaporites, marls, brechoid dolomites and basic rocks from the Upper Triassic (Keuper)	_	-	_	1	_	_	4	15	7	3	_	< 5	< 5	< 5	70
OTR	39° 49' 38.9" N	2° 54' 1.5" E	Folded dolomites, marls and brechoid dolomites from the Upper Triassic (Rhaetian)	_	1	-	1	_	-	-	6	-	-	_	15	< 5	50	65
OTL	39° 49' 44.4" N	2° 53' 31.2" E	Micritic limestones of the Lower Jurassic (Lias)	-	-	-	6	13	4	223	9	-	-	2	20	5	10	55

^a Field ANTQ: abandoned non-terraced olive grove with Quaternary parent material; ATR: abandoned terraced olive grove with Rhaetian parent material; ATL: abandoned terraced olive grove with Lias parent material; OTK: rainfed terraced olive grove with Keuper parent material; OTR: rainfed terraced olive grove with Rhaetian parent material; OTL: rainfed terraced olive grove with Lias parent material; OTK: rainfed terraced olive grove with Keuper parent material; OTR: rainfed terraced olive grove with Rhaetian parent material; OTL: rainfed terraced olive grove with Keuper parent material; OTR: rainfed terraced olive grove with Rhaetian parent material; OTL: rainfed terraced olive grove with Keuper parent material; OTR: rainfed terraced olive grove with Rhaetian parent material; OTL: rainfed terraced olive grove with Keuper parent material; OTR: rainfed terraced olive grove with Rhaetian parent material; OTL: rainfed terraced olive grove with Keuper parent material; OTR: rainfed terraced olive grove with Keuper parent material; OTR: rainfed terraced olive grove with Rhaetian parent material; OTL: rainfed terraced olive grove with Keuper parent material; OTR: rainfed terraced olive grove with Keuper parent material; OTR: rainfed terraced olive grove with Rhaetian parent material; OTL: rainfed terraced olive grove with Keuper parent material; OTR: rainfed terraced olive grove with Rhaetian parent material; OTL: rainfed terraced olive grove with Rhaetian parent material; OTL: rainfed terraced olive grove with Rhaetian parent material; OTL: rainfed terraced olive grove with Rhaetian parent material; OTL: rainfed terraced olive grove with Rhaetian parent material; OTL: rainfed terraced olive grove with Rhaetian parent material; OTL: rainfed terraced olive grove with Rhaetian parent material; OTL: rainfed terraced olive grove with Rhaetian parent material; OTL: rainfed terraced olive grove with Rhaetian parent material; OTL: rainfed terraced olive grove with Rhaetian parent material; OTL: rainfed terraced olive grove wi

^b Pinus halepensis Mill.

^c Quercus ilex L.

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^d Crataegus monogyna Jacq.

^e Olea europaea L.

^f Pistacia lentiscus L.

^g Ampelodesmos mauritanica (Poiret) T. Durand et Schinz.

^h Pastinaca lucida L.

ⁱ Myrtus communis L.

Table 2

Physicochemical, microbiological and enzymatic soil parameters.

		e	1							
Field ^a	EC ^b	pH	SSA ^c	TOC ^d	C _{mic} ^e	REB ^f	β-Glu ^g	Php ^h	Ur ⁱ	DHA ^j
ANTQ	0.165 ± 0.038	$\textbf{7.44} \pm \textbf{0.19}$	$\textbf{0.77} \pm \textbf{0.35}$	$\textbf{4.45} \pm \textbf{0.97}$	$\textbf{334.43} \pm \textbf{104.12}$	6.03 ± 1.1	1.76 ± 0.4	$\textbf{2.34} \pm \textbf{0.06}$	$\textbf{0.38} \pm \textbf{0.14}$	$\textbf{3.64} \pm \textbf{1.26}$
ATR	0.160 ± 0.04	$\textbf{8.04} \pm \textbf{0.11}$	0.95 ± 0.37	5.54 ± 1.08	$\textbf{289.73} \pm \textbf{89.4}$	$\textbf{6.48} \pm \textbf{1.38}$	0.56 ± 0.24	2.36 ± 0.17	$\textbf{0.62} \pm \textbf{0.24}$	$\textbf{2.2} \pm \textbf{0.82}$
ATL	0.114 ± 0.013	$\textbf{7.81} \pm \textbf{0.31}$	1.42 ± 0.6	$\textbf{5.42} \pm \textbf{1.1}$	977.81 ± 337.25	5.37 ± 1.41	$\textbf{0.94} \pm \textbf{0.49}$	$\textbf{2.19} \pm \textbf{0.19}$	$\textbf{0.56} \pm \textbf{0.17}$	11.34 ± 0.52
OTK	0.109 ± 0.017	$\textbf{8.49} \pm \textbf{0.31}$	1.26 ± 0.13	1.39 ± 0.26	107.72 ± 74.43	2.22 ± 0.74	1.33 ± 0.31	$\textbf{0.45} \pm \textbf{0.11}$	0.51 ± 0.14	1.61 ± 0.3
OTR	0.152 ± 0.036	8.5 ± 0.13	0.92 ± 0.09	2 ± 1.1	198.22 ± 98.81	2.38 ± 1.28	1.62 ± 0.44	0.79 ± 0.77	1.04 ± 0.2	2.45 ± 0.24
OTL	0.123 ± 0.041	$\textbf{7.84} \pm \textbf{0.19}$	1.12 ± 0.23	$\textbf{4.7} \pm \textbf{1.57}$	459.8 ± 247.06	4.32 ± 1.68	0.66 ± 0.06	2.2 ± 0.32	1.39 ± 0.21	4.51 ± 1.04

^a Field ANTQ: abandoned non-terraced olive grove with Quaternary parent material; ATR: abandoned terraced olive grove with Rhaetian parent material; ATL: abandoned terraced olive grove with Lias parent material; OTK: rainfed terraced olive grove with Keuper parent material; OTR: rainfed terraced olive grove with Rhaetian parent material; OTL: rainfed terraced olive grove with Lias parent material.

^b EC: Electrical conductivity (mS cm⁻¹).

^c SSA: Specific surface area (m² g⁻¹).

^d TOC: Total organic carbon (%).

^e C_{mic}: Microbial biomass carbon (mg C biomass kg soil⁻¹).

^f REB: Basal soil respiration (mg CO₂ kg⁻¹ soil).

^g β -Glu: β -glucosidase activity (umol PNP g⁻¹ dry soil h⁻¹).

 $^{\rm h}\,$ Php: Alkaline phosphatase activity (µmol PNP g $^{-1}$ dry soil h^{-1}).

ⁱ Ur: Urease activity (μ mol N - NH₃⁺ g⁻¹ dry soil h⁻¹).

^j DHA: Dehydrogenase activity (umol INTF g⁻¹ dry soil h⁻¹).

Table 3 F-statistics of the one-way ANOVA (land use, lithology and terraces) and two-way ANOVA (land use: lithology interaction) for the soil parameters.

	ECa	pH	SSA ^b	TOC ^c	C_{mic}^{d}	REB ^e	β -Glu ^f	Php ^g	Ur^{h}	DHA ⁱ
	F	F	F	F	F	F	F	F	F	F
Land use	1.56	17.31 ¹	0.12	21.48^{1}	6.58 ^j	35.87 ¹	0.3	25.6 ¹	20.39 ¹	6.77 ^j
Lithology	0.71	22.55 ¹	4.03 ^j	6.86 ^k	10.86 ¹	4.12 ^j	5.57 ^k	12.25 ¹	5.16^{k}	15.82 ¹
Land use: Lithology	1.05	5.81 ^j	0.89	9.79 ^k	7.62^{k}	8.12 ¹	21.13 ¹	28.05^{1}	7.24 ^j	116.53 ^k
Terraces	0.16	19.41 ¹	4.73 ^j	0.41	0.29	4.15 ^j	10.99 ^k	3.66	7.7 ^k	0.32

^a EC: Electrical conductivity.

^b SSA: Specific surface area.

^c TOC: Total organic carbon.

^d C_{mic}: Microbial biomass carbon.

e REB: Basal soil respiration.

 $^{\rm f}\,$ β-Glu: β-glucosidase activity.

- ^g Php: Alkaline phosphatase activity.

^h Ur: Urease activity.

ⁱ DHA: Dehydrogenase activity.

^j p < 0.05

 $k^{k} p < 0.01$

 $^{1} p < 0.001$

(Table 3). The higher litter biomass on the soil surface of abandoned fields promoted significantly lower pH than in olive groves (Table 2, Table 3). Nevertheless, the land use effects on soil pH were modulated by parent material, considering that an interacting effect was found between both factors (Table 3). In any case, the presence of terraces appeared to play a significant role on soil pH, presenting higher values than the non-terraced field (Table 2, Table 3).

3.2. Soil microbiological properties

Farmland abandonment promoted an increase of the vegetation cover and the supply of greater amounts of plant litter to the soil surface. This higher availability of soil organic matter can enhance the microbial establishment and activity. In this way, abandoned fields presented significantly higher TOC (p < 0.001), C_{mic} (p < 0.05) and REB (p < 0.001) than olive groves, with an increase of 90.37% for TOC, 109.21% for Cmic and 100.67% for REB (Table 2, Table 3). Parent material mineralogy also plays an important role in the organic carbon accumulation capacity of soils, which can derive in microbial biomass and activity variations. According to the ANOVAs, the parent material significantly influenced TOC (p < 0.01), C_{mic} (p < 0.001) and REB (p < 0.05). TOC highest and lowest values were estimated in Lias and Keuper lithology, respectively (Table 2). The highest Cmic was measured

in both the abandoned field (ATL) and the olive grove (OTL) with Lias lithology (Table 2). Concerning REB, it presented the highest values in the Quaternary lithology and the lowest in the Keuper one (Table 2). pvalues for each lithology comparison are listed in Table 4. An interacting effect between land use and parent material was observed in soil microbiological properties, indicating that land use influence on these parameters was modulated by parent material (Table 3). The presence of terraces apparently presents no influence on soil microbiological properties (Table 3).

3.3. Soil enzyme activities

Soil enzyme activities commonly increase following secondary succession after farmland abandonment due to higher plant litter availability, which can enhance Cmic and REB and thus soil organic matter decomposition processes. However, only Php (p < 0.001) and DHA (p < 0.05) were significantly higher in abandoned fields with respect to olive groves, with increases of 99.13% and 100.35%, respectively; whereas β-Glu presented no significant differences between land uses; and Ur (p < 0.001) was lower in abandoned fields than in olive groves, presenting a decrease of 46.94% after farmland abandonment (Table 2, Table 3). Soil physicochemical and microbiological properties were usually correlated with soil enzymatic activity. Thereby, as parent

Lithology	EC	Hq	SSA	TOC	C _{mic}	REB	β-Glu	Php	Ur	DHA	Observed ASVs	Chao1	Shannon	Pielou's Evenness	
Rhaetian -Quaternary	0.147	0.83 ^c	0.163	-0.677	-90.461	-1.595	-0.675 ^a	-0.766	0.446	-1.315	28.75	28.673	0.112	0.009	
Lias -Quaternary	-0.046	0.386^{a}	0.501 ^a	0.611	384.369^{a}	-1.183	-0.965 ^b	-0.143	0.596 ^b	4.288 ^b	ς	-5.261	-0.115	-0.018	
Keuper -Quaternary	0.125	1.046°	0.496	3.061 ^a	-226.712	-3.807 ^b	-0.43	-1.89 ^c	0.127	-2.030	30.233	30.271	0.043	-0.003	
Lias -Rhaetian	-0.193	-0.444 ^c	0.339	1.288	474.83^{c}	0.412	-0.29	0.623	0.15	5.603°	-33.75	-33.934	-0.228 ^b	-0.026^{a}	
Keuper -Rhaetian	-0.022	0.216	0.333	-2.384 ^a	-136.251	-2.211	0.244	-1.124 ^b	-0.319	-0.716	1.483	1.598	-0.069	-0.012	
Keuper - Lias	0.171	0.66 ^c	-0.005	-3.672 ^c	-611.081 ^c	-2.623	0.534	-1.748 ^c	-0.468	-6.318 ^c	35.233	35.532	0.158	0.014	
$a \ n < 0.05$															
b n / 0.01															

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material significantly affected soil pH, SSA, TOC, C_{mic} and REB, it also influenced soil enzyme activities (Table 3). β -Glu (p < 0.01) was highest in Quaternary and lowest in Lias materials, Php (p < 0.001) was highest in Quaternary and Lias lithologies and lowest in Keuper one, Ur (p < 0.01) was highest in Lias and lowest in Quaternary, and DHA (p < 0.001) was highest in Lias and similar among the other parent materials (Table 2). p-values for each parent material comparison are listed in Table 4. An interacting effect between land use and parent material was observed for the soil enzyme activities, so the land use influence on these parameters is strongly modulated by parent material. Eventually, terracing appeared to shape β -Glu (p < 0.01) and Ur (p < 0.01), which were higher in the non-terraced abandoned fields and in the terraced olive groves, respectively (Table 2, Table 3).

3.4. Soil bacterial community composition

Across fields, the more abundant phyla were Proteobacteria (25.77-34.09%). Acidobacteria (16.78–25.21%). Actinohacteria (12.15-14.75%), Planctomycetes (10.75-12.73%) and Bacteroidetes (7.06-13.51%) (Fig. 2). Proteobacteria was the dominant group in all treatments. However, in soils over Lias lithology (OTL, ATL), Acid*obacteria* relative abundances (25.09 \pm 4.96%) were very close to those of Proteobacteria (26.22 \pm 3.27%). Moreover, maximum relative abundances for Bacteroidetes were observed in Rhaetian lithology (12.51 \pm 2.61%). On the one hand, the dominant families in abandoned fields (ATL, ATR, ANTQ), according to the relative abundances, were Chitinophagaceae (7.37 \pm 2.75%), Xanthobacteraceae (5.1 \pm 1.68%), Pyrinomonadaceae $(4.52 \pm 3.31\%),$ Pirellulaceae $(4.05 \pm 1.25\%),$ Gemmataceae (3.77 \pm 0.63%), Burkholderiaceae (3.53 \pm 1.02%) and WD2101 soil group (3.48 \pm 2.23%). On the other hand, the main families in olive groves were *Chitinophagaceae* (9.06 \pm 1.59%), *Burkholderiaceae* (5.81 \pm 2.96%), WD2101 soil group (4.83 \pm 1.22%), Gemmataceae (3.63 \pm 0.61%), Pyrinomonadaceae (3.32 \pm 2.16%), Xanthobacteraceae (3.24 \pm 1.17%) and Pirellulaceae (2.86 \pm 1.09%). For some groups, the influence of parent material was also important. Rhaetian lithology benefited Chitinophagaceae (9.34 \pm 1.59%) and Microscillaceae (3.11 \pm 0.75%), and Lias lithology produced the same effect on WD2101 soil group (5.27 \pm 1.84%), Pyrimonadaceae (6.49 \pm 3.34%) and Gemmatimonadaceae (3.01 \pm 1.08%).

3.5. Soil bacterial alpha diversity

To assess soil bacterial communities' diversity, observed ASVs and three alpha diversity indices were calculated: Chao1 richness index, Shannon diversity index and Pielou's Evenness index. Shannon diversity index and Pielou's Evenness index presented almost the same values in both land uses (Table 5). Nevertheless, observed ASVs (p < 0.05) and Chao1 richness index (p < 0.05) were significantly higher in olive groves compared with abandoned fields (Table 5, Table 6). Regarding parent material, Lias lithology presented the lowest values and Rhaetian the highest for the observed ASVs and the alpha diversity indices calculated (Table 5). From the ANOVAs, parent material apparently significantly influenced the observed ASVs (p < 0.05), Chao1 richness index (p < 0.05) Shannon diversity index (p < 0.001), and Pielou's Evenness index (p < 0.01) (Table 6). Nevertheless, despite the significant differences obtained for the observed ASVs and the Chao1 richness index, Tukey's HSD test did not show significant differences between any of the different parent materials (Table 4). No interacting effect was detected between land use and parent material for observed ASVs and the alpha diversity indices. Presence or absence of terraces did not influence nor observed ASVs, nor the alpha diversity indices (Table 6).

3.6. Soil bacterial beta diversity

PerMANOVA tests based on Bray-Curtis dissimilarity at ASV level indicated that soil bacterial communities composition differed



Fig. 2. Relative abundances (%) of bacteria by field at phylum (a) and family (b) level.

Table 5									
Observed	ASVs	and	estimation	of	alpha	diversity	indices	for	bacterial
communit	ies.								

Field

ATR

ATL

ОТК

OTR

OTL

Observed ASVs Pielou's Evenness Chao1 Shannon ANTO $\textbf{383.17} \pm \textbf{30.29}$ 383.65 ± 30.23 $\textbf{4.78} \pm \textbf{0.07}$ 0.80 ± 0.0151 398.67 ± 15.4 399.28 ± 15.04 4.9 ± 0.05 0.82 ± 0.0095 362.83 ± 21.44 363.16 ± 21.34 $\textbf{4.62} \pm \textbf{0.10}$ 0.78 ± 0.0176 $\textbf{413.4} \pm \textbf{30.85}$ 413.92 ± 30.61 $\textbf{0.8} \pm \textbf{0.0123}$ $\textbf{4.82} \pm \textbf{0.13}$ 425.17 ± 28.84 $\textbf{425.38} \pm \textbf{28.91}$ 4.88 ± 0.07 0.81 ± 0.0103 393.62 ± 47.31 393.5 ± 47.26 $\textbf{4.7} \pm \textbf{0.21}$ 0.79 ± 0.025

^a Field ANTQ: abandoned non-terraced olive grove with Quaternary parent material; ATR: abandoned terraced olive grove with Rhaetian parent material; ATL: abandoned terraced olive grove with Lias parent material; OTK: rainfed terraced olive grove with Keuper parent material; OTR: rainfed terraced olive grove with Rhaetian parent material; OTL: rainfed terraced olive grove with Lias parent material.

Table 6

Results of the one-way ANOVA (lithology, land use, terraces) and two-way ANOVA (land use: lithology interaction) for the observed ASVs and alpha diversity indices at p-value < 0.05.

	Observed ASVs	Chao1	Shannon	Pielou's Evennes
	F	F	F	F
Land use	7.09 ^a	7 ^a	0.47	0.36
Lithology	3.01 ^a	3.06 ^a	7.71 [°]	5.63 ^b
Land use: Lithology	0.03	0.03	1.15	1.44
Terraces	0.92	0.91	0.01	0.24

 $^{\rm a}~p < 0.05$

^b p < 0.01

^c p < 0.001

significantly between parent materials (F = 3.75; p < 0.001) and land use (F = 5.69; p < 0.001). NMDS based on Bray-Curtis dissimilarity showed the patterns of bacterial community composition along different parent materials (Fig. 3a) and land use (Fig. 3b).

db-RDA with Bray-Curtis distances was performed to determine if soil properties had effects on the structure of bacterial communities (p < 0.05; Fig. 4). Likewise, bacterial families were plotted on the db-RDA to relate the significant soil properties correlated with the taxonomic groups. SSA, TOC, REB, Cmic, Ur and Php were the physicochemical and microbiological parameters implied in variations of soil bacterial communities' taxonomic structure. SSA, C_{mic} and Ur were loaded on the positive side of RDA1; while TOC, REB and Php were loaded on the negative side. All the explanatory variables except Ur, which was found at a neutral location, were grouped in the RDA2 positive side. The main associations existed between SSA and Cmic, and between TOC, REB and Php. Pyrinomonadaceae, 67-14 and Gemmatimonadaceae appeared to be positively correlated with Cmic and SSA. Oppositely, *Microscillaceae* showed a negative correlation with these soil properties. Burkholderiaceae, Beijerinckiaceae, Bacillaceae and WD2101 soil group were positively correlated to Ur. The last two families were also positively correlated with SSA. Xanthobacteraceae, Reyranellaceae, Pirellulaceae, Microscillaceae and Nitrosomonadaceae were negatively correlated with Ur. In addition, in terms of soil parameters, TOC, REB and Php were negatively correlated with Ur. In this way, Reyranellaceae, Xanthobacteraceae and Nitrosomonadaceae illustrated a positive correlation with these three variables, while Burkholderiaceae and Beijerinckiaceae negatively correlated.

3.7. Correlation between bacterial diversity and soil properties

The Spearman's correlation coefficients between soil properties and bacterial families with significant correlations (p < 0.05) were calculated (Fig. 5). In terms of soil properties, pH was negatively correlated with TOC, REB, C_{mic} , Php and DHA, as lower pH promoted higher values for these microbiological parameters and soil enzyme activities. In return, TOC and C_{mic} presented a positive correlation between each other and with REB, Php and DHA, since the greater presence of organic carbon favored the microbial establishment and activity. In addition, REB was also positively correlated with Php.

Several correlations were found between soil properties and bacterial families. *Xanthobacteraceae* and *Reyranellaceae* were significantly positively correlated with TOC, REB and Php and negatively correlated with pH. *Nitrosomonadaceae* showed a significant positive correlation with Php and a significant negative correlation with pH. *Pyrinomonadaceae* was significantly positively correlated with C_{mic} and DHA. *Beijerinckiaceae* was significantly positively correlated with pH and negatively correlated with TOC, REB and Php.

Regarding taxonomic groups, Xanthobacteraceae, Pirellulaceae, Reyranellaceae and Nitrosomonadaceae were positively correlated. The first three were negatively correlated with WD2101 soil group and Beijerinckiaceae, while the last was only negatively correlated with Beijerinckiaceae. Pyrinomonadaceae, WD2101 soil group and Gemmatimonadaceae presented a significant positive correlation. Chitinophagaceae and Burkholderiaceae presented only a negative correlation with 67–14 and Xanthobacteraceae, respectively.

4. Discussion

4.1. Soil properties

In this study, farmland abandonment led to higher TOC and higher microbial biomass and activity, although soil enzyme activities did not show a clear trend among land use types (Table 3). Regarding parent material, it significantly shaped pH, SSA, TOC, C_{mic} , REB and soil enzyme activities. Terracing effects on soil properties could be more likely attributed to land use or parent material.

Secondary succession in abandoned fields led to a higher tree cover, mostly compound by Aleppo pines. This generated a greater accumulation of litter on the soil surface that contributed to significant lower soil pH due to the acidifying effect of pine litter (Iovieno et al., 2010; Sariyildiz et al., 2005). In addition to the land use effects on soil pH, the parent material also significantly affected this parameter. Lithology was previously observed as a major driver of soil pH variations in contrasting environments worldwide such as the Lahn-Dill Highlands in central Germany (Breuer et al., 2006), the Ligurian Alps in north-western Italy (Catoni et al., 2016), or temperate forests of Arizona, USA (Heckman et al., 2009). However, soil pH values range was relatively limited because of the presence of carbonates in the underlying lithologies and



Fig. 3. Non-metric multidimensional scaling analysis (NMDS, Bray-Curtis distance) ordination plot of bacterial community composition by (a) parent material (b) and land use.



Fig. 4. Distance-based redundancy analysis (db-RDA) on a Bray-Curtis dissimilarity matrix of the bacterial community composition at the family level. Only significant (p < 0.05) physicochemical and microbiological variables including SSA (specific surface area), TOC (total organic carbon), REB (basal soil respiration), C_{mic} (microbial mass carbon), Ur (urease activity rate) and Php (alkaline-phosphatase activity rate) are shown.



Fig. 5. Spearman's rank correlation coefficients between the physicochemical and microbiological parameters and the taxonomic groups (family level). Circles represent significant correlations at p < 0.05 between variables and colours the value of the Spearman correlation coefficients; blue indicates a positive correlation and red a negative a correlation.

the proximity between the sampled fields. Likewise, terraced fields presented significantly higher soil pH than the non-terraced abandoned field, presumably caused by enhanced accumulations of CaCO₃ by the wall system (Calsamiglia et al., 2017; Lucas-Borja et al., 2018). Nevertheless, the probable influence of land use and parent material should not be discarded. Soil pH is usually considered as a main factor in regulating microbial communities in different magnitudes, especially for bacteria. On reason may be related to confounding effects generated by soil organic carbon and/or clay content. Many previous studies have reported that soil organic carbon is a key factor in regulating microbial biomass at different soil depths (Allison et al., 2010; Chen et al., 2019; Sun et al., 2020). The lack of significant influence of the land use factor on SSA indicated that soil texture mainly derived from parent material characteristics, although significant differences were only observed between Lias and Quaternary lithologies. In any case, both land uses were not developed within each of the different parent materials, making difficult the comparison. It is remarkable that the Quaternary lithology field (ANTQ), which presented the lowest SSA, was abandoned and non-terraced. The same absence of influence by the land use factor on soil texture was observed by Nacke et al. (2011) in south-western Germany and Li and Shao (2006) in the Loess Plateau, China. Accordingly, parent material mineralogy conditioned the weathering process and thereby soil texture under five different parent materials in the Île-de-France region (Barré et al., 2017) and eastern China (Mao et al., 2020); in beech forests developed under distinct parent materials in central Germany (Angst et al., 2018); or under contrasting combinations of forest cover and parent material in the Ligurian Alps (Catoni et al., 2016). In this study, soil texture -assessed through SSA- illustrated an important effect on soil bacterial communities' composition. As a result, an important relation with Cmic (Fig. 4) with a positive feedback on microbial communities' establishment was observed. Likewise, soil texture has been commonly recognized as a main factor in the determination of soil bacterial communities' structure (Lauber et al., 2008; Ma et al., 2021; Ulrich and Becker, 2006). According to the ANOVA, terracing also showed a significant influence on SSA. Nonetheless, these differences could be more likely attributed to the parent material.

Despite natural forests without prior agricultural use were not sampled, basically because there are no primary forests in the island of Mallorca, this land use usually shows -in terms of microbiological parameters and soil enzyme activities- higher soil quality than secondary succession sites following agricultural abandonment (Lucas-Borja et al., 2018; Nadal-Romero et al., 2016). Consequently, the abandoned fields of Menut farm had not yet reached their maximum soil quality. The abandonment of olive groves caused a marked increase of TOC, Cmic and REB. Other studies have previously demonstrated an increase in soil organic carbon, Cmic or REB following farmland abandonment under a typical Mediterranean climate in eastern Spain (García-Orenes et al., 2013) and southern Italy (Marzaioli et al., 2010), or under a continental Mediterranean climate in the southern Pre-Pyrenees (Lizaga et al., 2019) and the western Iberian Peninsula (Vázquez et al., 2020). Both cessation of cultivation and absence of management practices led to higher density vegetation cover following secondary succession processes that generated greater litter accumulation in the soil. This higher availability of C substrate in abandoned fields promoted the increase of TOC, Cmic and REB, which were significantly correlated according to the Spearman's rank correlation coefficients (p < 0.05, Fig. 5). As reported by the ANOVAs, parent material significantly influenced TOC, Cmic and REB. In the same way as land use, the parent material can also regulate the productivity of Mediterranean ecosystems by variations in drought stress and nutrients availability (Kooijman et al., 2005), influencing the organic matter quantity and quality supplied to the soil bacterial communities (Catoni et al., 2016; Mao et al., 2020). In addition, parent material regulates the ability of soils to stabilize organic matter and regulate its inputs (Angst et al., 2018). Several studies have proven the parent material as a major driver of soil organic carbon dynamics and microbial community composition, especially at the local and regional scale (Barré et al., 2017; Carletti et al., 2009; Heckman et al., 2009). As described in the previous paragraph, this is probably because of the influence of the parent materials' mineralogy on soil texture, which is closely related to soil organic carbon stocks (Barré et al., 2017; Heckman et al., 2009; Mao et al., 2020). Although in this study only limestone-derived soils were sampled due to the lithology of the study area, these seem to favor higher soil quality than soils derived from other lithologies, as it had been shown in northern Turkey (Babur, 2019), or in south-western (Chen et al., 2012) and subtropical (Mao et al., 2020) China. In this way, we should expect lower quality in soils developed over different parent materials under the same climate and land uses in Menut. However, it is challenging to check individually the parent material influence on soil quality, as earth-systems are developed in a multi-feedbacking way with other factors such as land use and terracing. Land use showed a more significant effect than parent material on TOC and REB, but parent material presented a greater influence on C_{mic}. Anyway, it is clear that parent material modulates land use impacts on TOC, C_{mic} and REB due to the significant interacting effect between both factors.

In forest soils higher Php, DHA, Ur and β -Glu have been reported than in agricultural soils (Cardelli et al., 2012; Trasar-Cepeda et al., 2008; Wang et al., 2011). Nevertheless, our results showed significantly higher Php and DHA following secondary succession in abandoned fields, while Ur was higher in olive groves, whilst no significant differences existed between both land uses for β -Glu. Php was positively correlated with TOC, REB and C_{mic} and negatively correlated with pH (p < 0.05; Fig. 5). This soil enzyme activity was the most closely associated with the organic matter components in natural forests of south-eastern Spain, showing positive correlations with soil organic carbon, C_{mic} and REB (Zornoza et al., 2007). This is a common trend among different locations and climates, as following farmland abandonment in the Loess Plateau positive correlations of Php with soil organic carbon had been reported (Wang et al., 2011; Xu et al., 2021). Parent material can also be a major driver of the soil enzymatic activity (Liu et al., 2018). The ANOVAs output can interpret that parent material is the main factor determining the enzymatic activity over land use. However, Php significant differences observed between parent materials can be more related with land use influence. In the case of Keuper lithology, the unique lithology type evidencing significant differences with the other types, showed the lowest activity rates and was exclusively located at olive groves (Table 4). Nevertheless, the possible influence of the parent material should not be discarded due to the absence of abandoned fields with Keuper lithology. DHA is positively correlated with TOC and C_{mic} (p < 0.05; Fig. 5). The activity of this enzyme was used as a measure of the total oxidative activity of the soil microflora and therefore of the soil metabolic activity (Bastida et al., 2008). The highest DHA was measured in Lias lithology fields. The significant positive correlation between DHA and Cmic, whose values were also the highest in Lias fields, could imply that this parent material benefited the establishment and metabolic activity of soil bacterial communities. However, it should be taken in mind that the Lias lithology olive grove presented poor agricultural management practices, leading to halfway conditions between both land uses. Ur is involved in nitrogen cycling, catalyzing the release of NH₄⁺ from urea (Caldwell, 2005). Generally, it shows a positive correlation with soil organic carbon, C_{mic} or Php (Li et al., 2020; Xu et al., 2021). Nonetheless, in the present study, no correlation was found between Ur and these parameters, coinciding with the results obtained by Zornoza et al. (2007) in natural forests of south-eastern Spain. As total nitrogen was not assessed in the current study, it is difficult to explain why Ur is lower in abandoned fields than in olive groves. In addition, although significant differences were found between Lias and Quaternary lithologies, it is difficult to discern individually the effect of parent material as the land use influence and terracing is also present. Broadly, β-Glu increased following secondary succession together with soil organic matter (Palese et al., 2013) or soil organic carbon (Yang et al., 2020). However, no significant differences were found between land uses in the present study, which could indicate a fast soil organic carbon turnover rate in farmlands and soil carbon accumulation in forests (Zhang et al., 2019). Otherwise, the parent material presented a significant influence on β -Glu. The highest values for this enzyme activity were measured at the Quaternary lithology field, elucidating the possible effect of parent material and terracing (Table 3). Nonetheless, Quaternary parent material was only present in an abandoned field, so land use could also play an important role in shaping β -Glu.

OTL values for pH, TOC, C_{mic} , REB, Php and DHA were closer to those obtained in the abandoned fields than to the other olive groves' values. This could be because of the practical inexistence of maintenance works due to the difficulty of access to this olive grove, which has resulted in a major presence of plant species. The resulting denser vegetation cover generated more litter that led to greater TOC and higher microbiological activities, typical of abandoned fields. Anyway, Lias lithology illustrated the highest values for C_{mic} and DHA in all the sampled fields together with high values for TOC, REB and Php, suggesting that Lias lithology is a driver of microbial establishment and activity on soils.

4.2. Bacterial diversity, composition and structure

Soil bacterial communities' alpha diversity variations between different land uses have been extensively investigated in the literature. However, there is not a common trend, i. e., Sánchez-Marañón et al. (2017) reported an increase of alpha diversity in natural soils in comparison with managed soils in a Mediterranean calcareous mountain in south-eastern Spain, while Kuramae et al. (2010) found a decrease with

secondary succession in chalk grasslands in the south-eastern Netherlands, whilst Fernández-González et al. (2020) showed no significant differences between natural and agricultural soils in southern Spain. In the present study, observed ASVs and Chao1 richness index were significantly higher in olive groves than in abandoned fields, while Shannon diversity index and Pielou's Evenness index presented no significant differences between land uses (Table 5, Table 6). These results elucidate that land use history effects could be more important than secondary succession influence in terms of alpha diversity of soil bacterial communities (Jangid et al., 2011). In addition, the presence of strong competitors at late stages of secondary succession can lead to a decline in bacterial diversity (Liu et al., 2020). Parent material can also be an important driver in shaping soil bacterial communities' alpha diversity (Adamczyk et al., 2019; Lin et al., 2019; Ma et al., 2021), even being a more important factor than land use due to parent material having a large influence on soil physicochemical properties (Deng et al., 2015). In the current study, the ANOVAs evidenced how parent material significantly affected the observed ASVs and the three alpha diversity indices calculated, producing a more significant effect on soil bacterial communities' alpha diversity than land use (Table 5). Nevertheless, Tukey's HSD tests revealed no significant differences for observed ASVs nor Chao1 richness index between any lithology (Table 4). The parent material influence on the Shannon diversity index and Pielou's Evenness index from the Tukey's HSD tests was only observed between Lias and Rhaetian lithologies. In contrary to the SSA, microbiological properties and enzyme activities, no interaction effect on alpha diversity was found between land use and parent material. As well as alpha diversity, soil bacterial communities' beta diversity can also be shaped by land use (Lauber et al., 2013) and parent material (Adamczyk et al., 2019).

Proteobacteria, Acidobacteria, Actinobacteria, Planctomycetes and Bacteroidetes accounted for > 85% of the total relative abundances in all the sampled fields (Fig. 2). Proteobacteria and Acidobacteria were the most abundant phyla regardless of land use, accounting for approximately 50% of the total relative abundances in all the sampled fields. Proteobacteria had been considered copiotrophic, as many taxonomic groups of this phylum became more abundant when labile substrates were available (Goldfarb et al., 2011), possibly playing a functional role in soil restoration during secondary succession (Zhang et al., 2016). In the present study, relative abundances of Proteobacteria increased in two of the abandoned fields, together with soil quality improvement (Sánchez-Marañón et al., 2017). However, Lias parent material favored Acidobacteria above Proteobacteria, leading the latter to the lowest relative abundances for both land uses among all the sampled fields. Acidobacteria had been regarded both as oligotrophic and as copiotrophic. On the one hand, this phylum showed an opposite trend to Proteobacteria following secondary succession in the Loess Plateau (Zhang et al., 2016) and its relative abundances decreased with soil quality improvement in south-eastern Spain (Sánchez-Marañón et al., 2017). On the other hand, Acidobacteria were more abundant in forest soils than in agricultural soils in north-western South Carolina (Lauber et al., 2008) and its relative abundances increased following farmland abandonment in China's Qinling Mountains (Zhang et al., 2018). In the current study, Acidobacteria relative abundances were similar among land uses, the positive effect of Lias parent material being notorious in this taxonomic group. Actinobacteria had been commonly classified as copiotrophic, being more abundant in higher quality soils (Sánchez-Marañón et al., 2017; Tian et al., 2017) and playing an important role in the soil carbon cycle (Guo et al., 2018). Actinobacteria relative abundances in our study were also higher in abandoned fields, though with small differences. Planctomycetes is believed to possess features from both copiotrophs and oligotrophs (Lauro et al., 2009). This is in line with the results of the present study, as the relative abundances of this phylum among land uses were similar. Bacteroidetes had been commonly classified as copiotrophic (Fierer et al., 2007). However, this group was negatively correlated with dissolved organic carbon in Mediterranean semiarid soils of south-eastern Spain (Bastida et al.,

2016), showing an oligotrophic behavior. In our study, this behavior was also found, as relative abundances were higher in olive groves than in abandoned fields. Regarding parent material influence, Lias lithology decreased the relative abundances of *Proteobacteria* and increased that of *Acidobacteria*. Ma et al. (2021) also observed an important parent material influence on the relative abundances of major phyla in subtropical China. In addition, parent material was a major driver of soil microbial communities composition in northern Italy (Carletti et al., 2009) and in Arizona, USA (Heckman et al., 2009).

At the family level, differences in relative abundances of bacterial taxonomic groups were clearer (Fig. 2). Chitinophagaceae was the most abundant family in both land uses, presenting higher relative abundances in olive groves than in abandoned fields. Other important families in terms of relative abundance, such as Burkholderiaceae and WD2101 soil group, followed the same trend. On the contrary, Xanthobacteraceae, Pyrinomonadaceae or Pirellulaceae were more abundant in abandoned fields. These behaviors were in line with the results from a greenhouse experiment in Germany, where, after organic amendment application, Xanthobacteraceae and Pyrinomonadaceae relative abundances increased while Chitinophagaceae and Burkholderiaceae relative abundances decreased (Obermeier et al., 2020). The most abundant families were differently affected by parent material. Chitinophagaceae and Pirellulaceae relative abundances were higher in Rhaetian lithology, while WD2101 soil group and Pyrinomonadaceae were greater in Lias lithology.

4.3. Correlation between bacterial communities and soil properties

In the present study, beta diversity analyses showed significant changes in soil bacterial communities' structure due to influences from land use and parent material. Soil properties are important environmental buffers for soil bacterial communities' composition (Cline and Zak, 2015; Lauber et al., 2008; Tian et al., 2017; Zhang et al., 2016). According to the Spearman's rank correlation coefficients of the families and soil properties (Fig. 5), five main groups could be distinguished according to its physiological behavior.

In the first group, we found families that presented a copiotrophic behavior, being more abundant in abandoned fields than in olive groves. These were Xanthobacteraceae, Reyranellaceae, Nitrosomonadaceae and Pirellulaceae. The first two presented significant positive correlations with TOC, REB and Php and a negative correlation with pH, while the third only presented a positive correlation with Php and a negative correlation with pH. Negative correlations between pH and the class Alphaproteobacteria, in which the Xanthobacteraceae family is classified, have been previously reported in huge sampling areas in northern New Zealand (29,500 km²; Hermans et al., 2017) and in south-western Germany (202,500 km²; Nacke et al., 2011). However, although significant correlations between soil pH and some families were found in the present study, pH ranges were narrow and, presumably, this soil property was not as important in shaping soil bacterial communities as it would be in wider soil pH ranges. Pirellulaceae, although not significantly positively correlated with any soil property, presented a significant positive correlation with Xanthobacteraceae, Nitrosomonadaceae and Reyranellaceae. In this way, as Pirellulaceae seemed to follow the same behavior as the former, it could be also categorized as a copiotrophic group. In the second group, we found Pyrinomonadaceae, WD2101 soil group and Gemmatimonadaceae. Pyrinomonadaceae is an aerobic chemoorganoheterotrophic group (Wüst et al., 2016) which, as far as soil properties are concerned, was significantly positively correlated with C_{mic} and DHA. As regards significant correlations with other families, Pyrinomonadaceae presented a positive correlation with WD2101 soil group and Gemmatimonadaceae, which were also positively correlated with each other. However, an important difference existed between Pyrinomonadaceae and these families, as the first was more abundant in the abandoned fields with higher resources and the latter in the olive groves. Nevertheless, differences in the relative abundances of

Gemmatimonadaceae among land uses were relatively narrow, as found before and after organic amendment application in a study conducted in Germany (Obermeier et al., 2020). According to the db-RDA, Gemmatimonadaceae was the closest taxonomic group positively correlated with SSA (Fig. 4), with increasing abundances with higher SSA. Returning to the Spearman correlation coefficients (Fig. 5), WD2101 soil group was negatively correlated with Xanthobacteraceae, Reyranellaceae and Pirellulaceae, while Gemmatimonadaceae was only negatively correlated with Pirellulaceae. These correlations indicated that WD2101 soil group possessed a more oligotrophic behavior than Gemmatimonadaceae. In the third group, there were Chitinophagaceae and 67-14 group. These families presented only a significant negative correlation between them. Due to the absence of more correlations it was difficult to establish its physiological behavior. However, observing the relative abundances among land uses, Chitinophagaceae seemed to be more oligotrophic than 67-14 due to its lower abundance in abandoned fields in comparison with olive groves. Chitinophagaceae, together with Burkholderiaceae and Sphingomonadaceae, among others, were recommended as sensitive indicators of soil fatigue in arable soils of south-eastern Poland (Wolińska et al., 2018). The results of the current study coincided with this finding, as the relative abundances of these groups were lower in olive groves in comparison with abandoned fields. In the fourth group, we found Burkholderiaceae, which only presented a negative correlation with Xanthobacteraceae. This fact indicated that Burkholderiaceae followed an oligotrophic behavior, as its relative abundances decreased due to lower resources following the abandonment of olive groves. Finally, Beijerinckiaceae presented a clear oligotrophic behavior, being significantly negatively correlated with the four copiotrophic families, and also with TOC, REB and Php. Moreover, it was positively correlated with pH. The same oligotrophic behavior was reported for this taxonomic group after the conversion of natural subtropical forest to farmland in Brazilian ferrasols (Dörr et al., 2010).

5. Conclusions

The aim of this study was to provide insights into the effects of secondary succession processes and parent material on soil properties and soil bacterial communities in an ecological hotspot environment such as Mediterranean hyper-humid mountains. Secondary succession processes caused by farmland abandonment generated greater litter accumulation in the soil, triggering higher TOC, Cmic and REB in abandoned fields than in rainfed olive groves because of the higher availability of C substrate. Lias parent material fields presented highest Cmic and DHA values. However, further research is needed to clarify the role of each driving factor on soil properties, since the Lias lithology olive grove presented halfway conditions between both land uses due to poor agricultural management. The presence of agricultural terraces promoted higher pH, SSA and Ur values, while lower β-Glu values. Nevertheless, as it was explained in the discussion, terracing effects could not be clearly determined due to the lack of paired comparisons in the study area. Among the bacterial families, copiotrophic and oligotrophic behaviors were observed. Xanthobacteraceae, Pirellulaceae, Nitrosomonadaceae and Reyranellaceae followed a copiotrophic behavior. Otherwise, Chitinophagaceae, Burkholderiaceae, WD2101 soil group and Beijerinckiaceae showed an oligotrophic behavior. This work has made it possible to have a better understanding of the effects of secondary succession and parent material on soil properties and soil bacterial communities in a mountainous Mediterranean hyper-humid environment. However, further research should be carried out in the Mediterranean area to discern the effects of farmland abandonment, parent material and terracing separately.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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