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RESEARCH ARTICLE

Microbial functioning in Mediterranean forest soils: Does land use legacy matter?

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Abstract

Land use is known to be one of the major factors driving soil microbial and physico-chemical properties. Understanding its long-term effect remains a major challenge in assessing current soil functioning. Here, soil microbial and physico-chemical properties of recent and very recent forests (forests developed in 1958 vs. after 1958) were compared with those of ancient forests (present in 1860 and 1958) to assess the effect of Land Use Legacy (LUL). LUL effects were further analysed depending on contrasting (i) climate conditions (sub-humid vs. humid Mediterranean climates) and (ii) seasons (winter and summer), to examine whether LUL modified microbial responses to different spatio-temporal climate conditions. Microbial indicators (lignocellulolytic activities, basal respiration, and microbial biomass) and physico-chemical properties (C and N contents, mineralogical analyses, pH and conductivity) were assessed. A strong effect of past agricultural practice (terrace cultivation) was observed in soils from very recent forests: reduced microbial biomass and activities as well as number of *Quercus pubescens* stems together with increased phosphorous content and pH. Interestingly, LUL effect did not affect microbial and physico-chemical responses to seasonal contrasts (winter vs. summer). Microbial response to LUL was not influenced by climate while climate modified LUL effects on some physico-chemical properties (CaCO_3 , C_{org} , and K content). Moreover, soil recovered “pristine” physico-chemical and microbial functional properties after at least 60 years of reforestation.

KEYWORDS

agricultural abandonment, forest soils, land use legacy, Mediterranean climate, soil microbial communities, terraces

1 | INTRODUCTION

Soils provide many ecosystem services such as organic matter turnover, primary production and carbon (C) flux regulation (Berg & McClaugherty, 2008). Soil properties depend on environmental

factors such as climate, plant cover, land use and associated practices, parent rock substratum and their interactions (Bruand & Tessier, 2000; Coûteaux et al., 1995; Delcourt et al., 2019; Traversa et al., 2008). These factors influence soil functioning directly through modification of physico-chemical and microbial properties and

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indirectly through modification of above and belowground inputs (plant chemistry, root exudates and biomass production) (Suseela & Tharayil, 2018). French Mediterranean soils are poor in organic matter, with a hard limestone substrate, and litters contain large quantities of recalcitrant phenolic compounds (Quézel & Médail, 2003). These constraints, together with a rugged topography, led to a type of farming characterised by terraced crops. The “stepped topography” described by Sandor (1998) allowed farmers to cultivate slopes, since terraced crops raise soil moisture and increase nutrient availability by improving water-holding capacity and retention of organic matter content (Stanchi et al., 2012). Nevertheless, terracing is described as an aggressive method that produces physical alterations in soil (Bastida et al., 2007).

From 1860 to 1958, terrace cultivation was progressively abandoned due to low crop productivity and the promotion of industrial agriculture. Farmers abandoned the least productive and least accessible farmland, resulting in reforestation by pioneer species. Thus, forest recovery was observed, with a slight acceleration of the process after 1958 (Abadie et al., 2017). Reforestation has been shown to improve soil properties such as organic matter content, soil structure and infiltration rate, leading to enhanced protection from erosion (Fu et al., 2009; Kosmas et al., 2000). Nevertheless, previous studies have observed lower total nitrogen, C/N ratio and water-holding capacity in soils of post-agricultural forests (Brudvig et al., 2013; Duguay et al., 2007; Falkengren-Grerup et al., 2006); thus, land use legacy (LUL) is sometimes considered as a potential disturbance (Bellemare et al., 2002; Flinn et al., 2005).

Most studies exploring LUL have focused on vegetation communities, while few have investigated to what extent LUL impacts microbial communities and their activities regarding organic matter decomposition in soils (Jangid et al., 2011; Zornoza et al., 2009). Furthermore, interactions between climate, a major driver of soil functioning, and LUL were not considered in the above studies. Climate is a particularly important factor in Mediterranean regions, where summer drought could lead to a reduction in soil microbial activity. These extreme climate conditions and the coexistence of forests of different ages and land-use histories make the Mediterranean area an interesting place to assess how LUL impacts current soil functioning, particularly in anticipation of global climate change. To our knowledge, there has been little exploration of the long-term effect (more than 60 years) of former agricultural terraces under a Mediterranean climate and even less of current soil microbial functioning at such sites.

This study investigated the LUL effect of past agricultural management (i.e., terraces) on soil microbial communities under two different Mediterranean climate conditions (sub-humid vs. humid climates) and in two different seasons (winter vs. post-summer period). We investigated forest soils in the Parc Naturel Régional du Luberon (PNRL), regional parkland located in the eastern French Mediterranean region, where climate, vegetation and past land use were previously described (Abadie et al., 2017). Three main questions were addressed here: (i) Does the LUL effect on the structure of soil microbial communities differ according to climate? (ii) Does LUL influence the sensitivity of microbial communities and their adaptability to

seasonal contrasts? (iii) Is there a difference in LUL effect depending on the date of farmland abandonment and thus the age of forest stands?

2 | MATERIALS AND METHODS

2.1 | Site description and soil sampling

The study was conducted in the Parc Naturel Régional du Luberon (PNRL), located in South-eastern Mediterranean France (Provence Alpes Côte d'Azur region) (Figure 1). This regional parkland straddles Vaucluse and Alpes de Haute-Provence (43°39' N–44°02' N, 4°58' E–5°55' E) and covers 195,413 ha. The study area was chosen for the extensive information on climate and forest stands available from the previous study by Abadie et al. (2017), which identified land use and cover since 1830. Pedoclimatic conditions are typically Mediterranean, characterised by humid winters and intense summer drought, and the soil is mainly calcareous (95%). Two distinct bioclimates were considered (Figure 1, Table 1): sub-humid and humid, corresponding to altitudinal arrangement of vegetation type, that is, Meso-Mediterranean and Supra-Mediterranean levels respectively (Quézel & Médail, 2003).

As described by Abadie et al. (2018), 55% of the area is covered by forests containing three main dominant species: holm oak (*Quercus ilex* L.), downy oak (*Quercus pubescens*) and Aleppo pine (*Pinus halepensis* Miller). Most forests did not receive any specific silvicultural treatment. In the present study, only forest patches with *Q. pubescens* as the dominant species were selected. Based on Abadie et al. (Abadie et al., 2018, 2020), two historical sources were used to assess past land use for each forest patch:

- 1860: The “État-Major” map (EM map; 1858–1861 in the PNRL; 1:40,000), digitised by Salvaudon et al. (2012) following Favre et al. (2013), with a median position error of 26 m after georeferencing and correction;
- 1958: Historical aerial photographs taken between 1953 and 1958, photo-interpreted for each vegetation plot.

Forests were classified as ancient if present in 1860 and 1958; as recent if they developed between 1860 and 1958 (time of abandonment >60 years) and as very recent if they developed after 1958 (time of abandonment >60 years). Following Abadie et al. (2020), we considered that no turnover in land cover occurred between the dates of the two maps, that is, the “État-Major” map (1860) and the historical aerial photographs (1954).

In addition, the recent and very recent forests selected were characterised by visible terrace remnants, attesting to the presence of agriculture in the past. Terraces were most probably used for olive growing, being the main form of terrace cultivation in the French Mediterranean region (de Réparaz, 2000).

For each climate (sub-humid and humid), 5 pairs of adjacent ancient and recent forests and 5 pairs of adjacent ancient and very



FIGURE 1 Location and climate zones (sub-humid and humid climates) of the study site (Parc naturel régional du Luberon, France) and distribution of the different forest patches categories (i.e., ancient, recent and very recent forests). [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/lid.4727)]

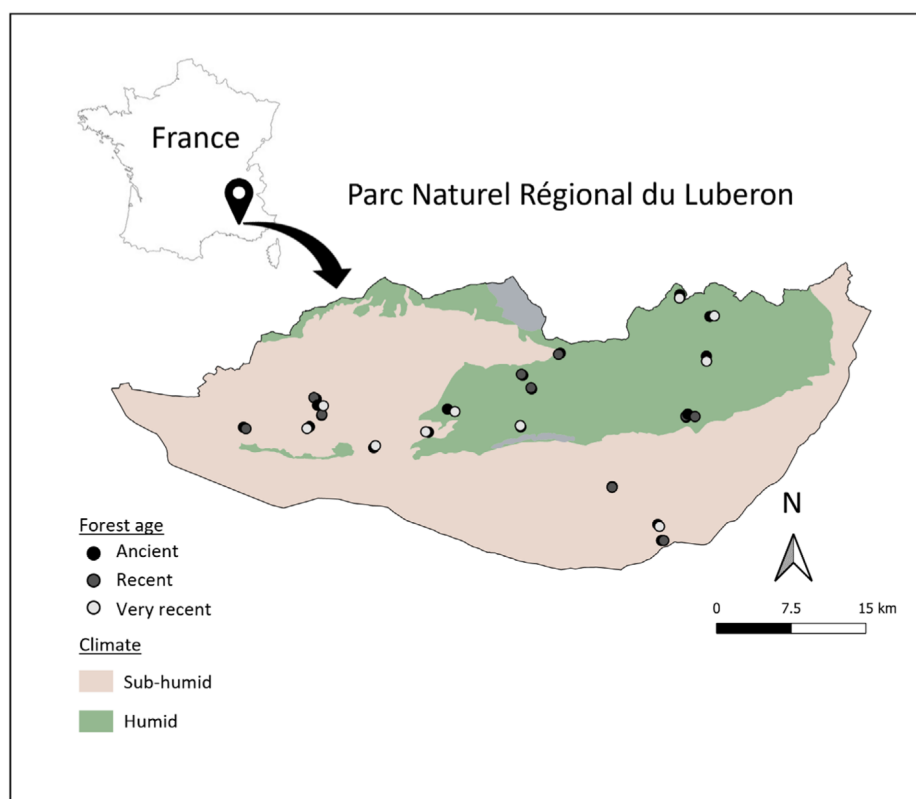


TABLE 1 Bioclimatic variables from Wordclim data (<https://www.worldclim.org>) calculated using temperature and rainfall values for both climates considered (sub-humid and humid).

	Sub-humid	Humid
Annual precipitation (mm)	695	772
Precipitation of driest month (mm)	25	32
Precipitation of wettest month (mm)	86	88
Annual mean temperature (°C)	12	11
Min temperature of coldest month (°C) ^a	0	-1
Max temperature of warmest month (°C) ^b	27	25
Temperature annual range (°C) ^(a-b)	27	26
Isothermality (%)	35	35

Note: Isothermality: (Mean of monthly (max temp – min temp))/ Temperature annual range.

^aMin temperature of coldest month.

^bTemperature of warmest month.

^{a-b}Temperature annual range.

recent forests were selected based on their geographical proximity (Figure 1). This means that each post-agricultural forest could be linked to an ancient forest used as a reference model since they have not been exposed to terraced cultivation. Thus, 40 forest patches with a minimum area of two hectares were explored.

Soils were collected in winter (in February) and in summer (in September after summer drought). On each forest patch, five samples were collected from the top 10 cm of soil and pooled to obtain a composite sample. No forest patch had soil deeper than 30 cm above

bedrock. The sampling campaign lasted 1 week, and samples were stored at 4°C until analysis. Then, samples were sieved to 2 mm before their microbial and physico-chemical properties were determined. During the first sampling, in winter, four cylindrical core samples were collected with PVC cylinders of 98 cm³ (5 cm diameter, and 5 cm height) within each of the sampled plots to determine bulk density.

2.2 | Soil physico-chemical properties

For each soil sample, the total C (%) and N (%) content (respectively C_{tot} and N_{tot}) and their ratio (C/N) were measured using a C/N elementary analyser (Flash EA 1112 Thermo Scientific series). Determination of calcium carbonate ($CaCO_3$, %) in A-horizon samples was performed using a calcimeter (FOGII Digital Soil Calcimeter), based on volumetric analysis of carbon dioxide CO_2 released by the application of 6 M HCl. The carbon proportion of $CaCO_3$ was then calculated using the molar mass of C (Equation 1). Then organic carbon (C_{org} , %) was calculated as the difference between total C_{tot} content and C_{CaCO_3} content (Equation 2).

$$\%C_{CaCO_3} = \frac{12}{100} \times \%CaCO_3, \quad (1)$$

$$\%C_{org} = \%C_{tot} - \%C_{CaCO_3}. \quad (2)$$

pH_{H_2O} and pH_{KCl} of soil samples were determined in distilled water and KCl 2 M respectively, after 40 min equilibration.



Electrical Conductivity (EC, $\mu\text{S}\cdot\text{cm}^{-1}$) was determined in distilled water as described for $\text{pH}_{\text{H}_2\text{O}}$. The pH was measured with pH meter Metrohm 744 and EC with probe DiST 3 (HANNA instruments). Water Holding Capacity (WHC, %) of soils was determined as the amount of water held in the saturated soil sample versus the dry weight (DW) of the sample. Bulk densities ($\text{g}\cdot\text{cm}^{-3}\text{DW}$) were determined by weighing each 90°C-dried core sample (Blake & Hartge, 1986). Mineralogical analysis of soils: phosphorous by Olsen method (P_{Olsen} , $\text{mg}\cdot\text{kg}^{-1}\text{DW}$) and exchangeable cations such as K^+ ($\text{g}\cdot\text{kg}^{-1}\text{DW}$), Mg^{2+} ($\text{g}\cdot\text{kg}^{-1}\text{DW}$), exchangeable Fe (Fe^{3+} and Fe^{2+} , $\text{mg}\cdot\text{kg}^{-1}\text{DW}$) and Ca^{2+} ($\text{g}\cdot\text{kg}^{-1}\text{DW}$) were performed by Laboratoire Développement Méditerranée (Alès, France). Bulk density, EC, and mineralogical analyses were performed on the soils collected during winter.

2.3 | Microbial basal respiration and microbial biomass

For each composite sample and for each sampling time, basal respiration (BR) was measured using 10 g (DW equivalent) of samples standardised at 60% WHC placed in 117 mL glass jars. The glass jars were immediately sealed with hermetic rubber septa and incubated for 4 h at 23°C. After incubation, 1 mL of air was sampled in the headspace with a syringe and injected into a gas chromatograph (Chrompack CHROM 3–CP 9001, Agilent, Santa Clara, CA, USA) to analyse CO_2 production. The gas chromatograph was equipped with a thermal conductivity detector and a packed column (Porapak, Chrompack, Agilent). The flow of the carrier gas, helium, was set to 60 $\text{mL}\cdot\text{h}^{-1}$. Ambient CO_2 concentration was subtracted from sample CO_2 concentrations and resulting values were adjusted to 22°C according to the ideal gas law. BR was expressed as $\mu\text{g CO}_2\cdot\text{C}\cdot\text{h}^{-1}\cdot\text{g}^{-1}\text{DW}$. Substrate-induced respiration (SIR) rates were estimated using a procedure from Anderson and Domsch (1978). For each sample, 10 g DW-equivalent of samples standardised at 60% WHC were placed in 117 mL glass jars and amended with a powder mixture of talc and glucose (1000 $\mu\text{g C}\cdot\text{g}^{-1}\text{DW}$), which was found to maximise the respiration rate in our soils in a preliminary assay (data not shown). 1 mL of air was sampled in the headspace with a syringe and injected into a gas chromatograph to analyse CO_2 production for 2 h 30 min (see above). SIR was converted to Microbial Biomass (MB, $\mu\text{g Cmic}\cdot\text{g}^{-1}\text{DW}$) using the relation established by Beare et al. (1990).

2.4 | Extracellular enzyme activities

Two extracellular enzyme activities involved in lignocellulose transformation were assessed, that is, tyrosinase and cellulase activities. Cellulase activities were determined using Carboxy-MethylCellulose (CMC) 0.1% (w/v) in 8 mL of sodium acetate buffer (50 mM, pH = 5) added to 5 g of soil (DW) incubated for 4 h at 50°C. Glucose content was quantified according to the

Somogyi-Nelson method and absorption was read at 870 nm (Farnet et al., 2010). Tyrosinase activities (phenoloxidase activities) was based on the oxidation of L-DOPA (3,4-dihydroxyphenylalanine) to L-DOPA quinone ($\epsilon^M = 3400 \text{ M}^{-1}\cdot\text{cm}^{-1}$) measured at 475 nm following Saiya-Cork et al. (2002). Briefly, L-DOPA 5 mM in 6 mL of phosphate buffer (50 mM, pH 6.5) was added to 5 g of soil (DW), which was incubated for 3 h at 37°C. Enzyme activities were expressed as μmole of product formed per hour (U) per g of soil dry weight.

2.5 | Statistical analyses

Based on previous studies with similar sampling design (Feng et al., 2019; Santonja et al., 2018), statistical analyses of the data were realised using Linear Mixed-Effect models (LME), followed by Tukey HSD tests for post hoc comparisons ($p < 0.1$), to examine the effect of LUL (ancient forest, recent forest, very recent forest), climate (sub-humid vs. humid), season (winter vs. summer) and their interactions. Pairs were treated as random factors to consider the microclimatic conditions and proved significant in both cases.

LME models were built with R version 3.6.2 (R Core Team 2019), using nlme package with significance levels indicated as * for $p < 0.05$, ** for $p < 0.01$ and *** for $p < 0.001$. The considered indicators were LUL, climate and season as fixed factors, and plot geography as random factor (following R syntax “random = ~1|plot/mesocosm”). The random part of the model allowed us to account for the geographic proximity of each pair of forests (ancient forests vs. recent forests or ancient forests vs. very recent forests) and for repeated measurements at the same place over time (summer and winter). The normality and homogeneity of the variance were determined on the residuals from the regression model using the Shapiro–Wilk and Levene tests, respectively. Data were transformed to common logarithms, \log_{10} , when necessary to meet the requirements of normality and homogeneity of variance.

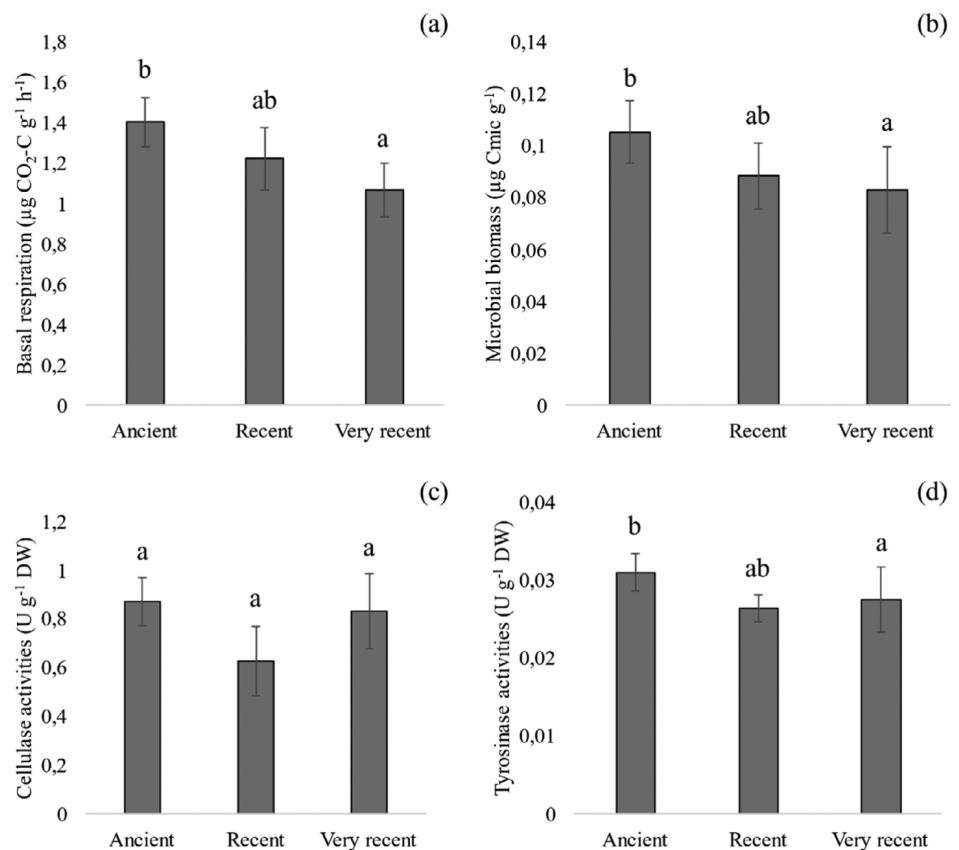
3 | RESULTS

3.1 | Effects of LUL on soil microbial community properties

Interestingly, the LME models showed that BR, MB, and tyrosinase activities were affected by LUL, independent of climate and seasonal contrasts, which are known to be major factors controlling soil microbial properties. Lower values for these microbial markers were observed in soils of very recent forests than in soils from ancient forests (–24%, –21% and –13% respectively) (Figure 2a,b,d, Table 2). In addition, LUL effect on microbial properties depended on the age of forest stands since values observed in recent forests did not differ from the other categories of forests (i.e., ancient and very recent forests). It has to be noted that cellulase activities were not affected by LUL (Figure 2c, Table 2).



FIGURE 2 Land Use Legacy effect on basal respiration (a), microbial biomass, (b) cellulase activities (c) and tyrosinase activities (d) of soil from ancient, recent, and very recent forests. Values are means \pm standard error ($N = 80$). Different letters denote significant differences with $a < b$.



3.2 | Effects of LUL on soil chemical properties

In addition, to better understand how LUL shapes microbial functioning, the soil physico-chemical properties and forest stand characteristics were analysed. LME models showed that, like microbial properties, certain soil chemical and stand properties were also affected by LUL independently of climate and seasonal contrasts: $\text{pH}_{\text{H}_2\text{O}}$ and pH_{KCl} , P_{Olsen} content, exchangeable Fe content as well as the number of *Q. pubescens* stems varied significantly with LUL (Table 2). Higher pH_{KCl} values and P_{Olsen} contents were observed in soils from very recent and recent forests than in those from ancient forests (Table 3). Higher $\text{pH}_{\text{H}_2\text{O}}$ was also observed in soils from very recent forests than in soils from ancient forests, while $\text{pH}_{\text{H}_2\text{O}}$ in soils from recent forests did not differ from those of soils of both other forest categories (Table 3). In addition, a smaller number of *Q. pubescens* stems and lower values of exchangeable Fe in soil were observed in very recent forests than in recent and ancient forests (Table 3).

3.3 | Effects of LUL on soil chemical properties depending on climate

Some soil physico-chemical properties responses to past agricultural activities depended on the climatic context considered. Concerning CaCO_3 , C_{org} percentages and K content, LME models indeed showed a significant and climate-dependent influence of LUL (Table 2). LUL

had no effect on soil CaCO_3 percentages under a sub-humid climate, while under a humid climate, CaCO_3 percentages were significantly higher in soils from very recent forests than in soils from recent and ancient forests (Figure 3a). Concerning C_{org} percentages, the effect differed according to the climate conditions considered: under sub-humid climate, C_{org} percentages were significantly lower in soils from recent forests than in soils from ancient and very recent forests, while under humid climate lower C_{org} percentages were found in soils from very recent forests than in those from ancient forests (Figure 3b). Under sub-humid climate, higher values of K content were observed in soils from very recent forests than in soils from ancient forests, while LUL had no effect on K content under humid climate (Figure 3c).

4 | DISCUSSION

4.1 | LUL controls soil properties independently of other major environmental drivers

LUL strongly affected microbial functioning independently of important environmental factors, such as climate and seasonality. Climate conditions are known to have a strong influence on soil microbial functioning (Berg & McLaugherty, 2008; Dove et al., 2021; Kheir et al., 2020). However, at the scale of this study, its effect (i.e., humid vs. sub-humid Mediterranean climates) appeared to be less significant



TABLE 2 Results of full linear mixed-effect models analyses on microbial communities, physico-chemical properties and environmental data under various conditions of land use legacy (LUL), climate (C) and season (S).

		df	LUL 2	Climate (C) 1	Season (S) 1	LUL × C 2	LUL × S 1	S × C 2	LUL × S × C 2
Microbial communities	Basal respiration ($\mu\text{g CO}_2\text{-C g}^{-1} \text{h}^{-1}$)	χ^2	9.15	8.98	85.65	4.98	0.37	0.00	2.05
		p-Value	*	**	***	ns	ns	ns	ns
	Microbial biomass ($\mu\text{g Cmic g}^{-1}$)	χ^2	7.94	1.14	19.35	0.73	2.00	2.42	0.32
		p-Value	*	ns	***	ns	ns	ns	ns
	Cellulase activities ($\text{U g}^{-1} \text{DW}$)	χ^2	1.99	2.65	22.37	0.30	1.64	8.03	1.15
		p-Value	ns	ns	***	ns	ns	**	ns
	Tyrosinase activities ($\text{U g}^{-1} \text{DW}$)	χ^2	12.95	0.40	40.81	0.54	2.45	1.19	2.26
		p-Value	**	ns	***	ns	ns	ns	ns
Physico-chemical properties	WHC (%)	χ^2	3.96	0.21	0.89	2.40	0.05	4.62	0.30
		p-Value	ns	ns	ns	ns	ns	*	ns
	C_{tot} (%)	χ^2	0.55	0.68	1.98	2.82	0.80	7.04	1.64
		p-Value	ns	ns	ns	ns	ns	**	ns
	N_{tot} (%)	χ^2	0.10	0.82	1.03	4.21	2.05	8.32	3.49
		p-Value	ns	ns	ns	ns	ns	**	ns
	C/N	χ^2	1.27	0.05	1.11	0.20	1.76	0.00	2.79
		p-Value	ns	ns	ns	ns	ns	ns	ns
	CaCO_3 (%)	χ^2	31.44	2.78	0.15	8.27	0.36	0.79	0.54
		p-Value	***	ns	ns	*	ns	ns	ns
	C_{org} (%)	χ^2	4.32	0.83	0.43	10.67	3.06	6.92	1.46
		p-Value	ns	ns	ns	**	ns	**	ns
	pH_{KCl}	χ^2	23.30	3.00	0.01	0.34	2.14	0.41	0.26
		p-Value	***	ns	ns	ns	ns	ns	ns
	$\text{pH}_{\text{H}_2\text{O}}$	χ^2	12.58	11.17	8.01	1.87	5.62	2.21	0.87
		p-Value	**	***	**	ns	ns	ns	ns
	EC ($\mu\text{S cm}^{-1}$)	χ^2	1.70	0.35	33.77	0.85	2.06	0.12	1.49
		p-Value	ns	ns	***	ns	ns	ns	ns
	Mg ($\text{g kg}^{-1} \text{DW}$)	χ^2	3.73	1.18	NA	3.55	NA	NA	NA
		p-Value	ns	***		ns			
Ca ($\text{g kg}^{-1} \text{DW}$)	χ^2	0.05	1.58	NA	1.93	NA	NA	NA	
	p-Value	ns	ns		ns				
Fe ($\text{mg kg}^{-1} \text{DW}$)	χ^2	14.44	24.61	NA	3.24	NA	NA	NA	
	p-Value	***	***		ns				
K ($\text{g kg}^{-1} \text{DW}$)	χ^2	1.77	0.75	NA	7.56	NA	NA	NA	
	p-Value	ns	ns		*				
P_{Olsen} ($\text{mg kg}^{-1} \text{DW}$)	χ^2	12.08	0.17	NA	1.49	NA	NA	NA	
	p-Value	**	ns		ns				
Bulk density ($\text{g cm}^{-3} \text{DW}$)	χ^2	0.45	4.07	NA	4.19	NA	NA	NA	
	p-Value	ns	ns		ns				
Stand properties	Number of <i>Q. pubescens</i> stems /ha	χ^2	12.04	2.17	NA	0.80	NA	NA	NA
		p-Value	***	ns		ns			

Abbreviations: df, degree of freedom; DW, dry weight; NA, not available; ns, non-significant; WHC, water holding capacity.

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

TABLE 3 LUL effect on soil physico-chemical properties from ancient, recent, and very recent forests (LME models).

	N	Ancient	Recent	Very recent	p-value
WHC (%)	80	49.6 ± 1.1	48.9 ± 1.1	46.3 ± 1.7	ns
C _{tot} (%)	80	10.00 ± 0.58	8.86 ± 0.68	10.10 ± 0.86	ns
N _{tot} (%)	80	0.43 ± 0.03	0.40 ± 0.03	0.43 ± 0.03	ns
C/N	80	23.56 ± 0.73	21.96 ± 0.73	23.61 ± 1.03	ns
CaCO ₃ (%)	80	13.5 ± 2.6 ^a	13.8 ± 3.2 ^a	26.7 ± 3.5 ^b	***
C _{org} (%)	80	8.4 ± 0.5	7.2 ± 0.8	7.1 ± 0.6	ns
pH _{KCl}	80	6.92 ± 0.06 ^a	7.14 ± 0.06 ^b	7.22 ± 0.03 ^b	***
pH _{H2O}	80	7.72 ± 0.05 ^a	7.77 ± 0.03 ^{ab}	7.87 ± 0.05 ^b	**
EC (μS cm ⁻¹)	80	115.1 ± 4.7	109.2 ± 5.5	114.7 ± 5.1	ns
Mg (g kg ⁻¹ DW)	40	0.40 ± 0.02	0.35 ± 0.02	0.46 ± 0.09	ns
Ca (g kg ⁻¹ DW)	40	14.9 ± 1.2	14.8 ± 1.3	15.2 ± 1.8	ns
Fe (mg kg ⁻¹ DW)	40	2.0 ± 0.3 ^b	2.1 ± 0.2 ^b	1.0 ± 0.4 ^a	***
K (g kg ⁻¹ DW)	40	0.30 ± 0.03	0.30 ± 0.02	0.29 ± 0.02	ns
P _{Ol_{sen}} (mg kg ⁻¹ DW)	40	23 ± 4 ^a	45 ± 13 ^b	31 ± 7 ^b	**
Bulk density (g cm ⁻³ DW)	40	0.73 ± 0.03	0.76 ± 0.04	0.76 ± 0.06	ns
Number of <i>Q. pubescens</i> stems/ha	40	27 ± 2 ^b	30 ± 3 ^b	15 ± 2 ^a	***

Note: Values are means ± standard error. Different letters denote significant differences with a < b.

Abbreviations: DW, dry weight; EC, electrical conductivity; ns, non-significant; WHC, water holding capacity.

p < 0.01; *p < 0.001.

than the effect of past agricultural activities (i.e., agricultural terraces) on microbial communities. Thus, terrace cultivation appeared here to have a strong long-term negative effect on microbial functioning by reducing microbial biomass, BR and tyrosinase activities in soils of very recent forests. Lower microbial biomass and activities in soil from post-agricultural forests compared to ancient forests may be explained by certain modifications in stand and soil chemical properties induced by LUL. In our study, a lower number of stems/ha of the dominant tree species *Q. pubescens* was observed in very recent forests. Post-agricultural forests are indeed often described as more open environments, and this goes line with the previous study of Abadie et al. (2020) who described the very recent forests studied here as open habitats. Very recent forests thus have a lower canopy density and therefore a lower amount of plant litter on the soil surface associated to more intense exposure to sunlight and temperature variations, increasing hydric and thermal stresses for microbial communities (Pieristè et al., 2020; Zellweger et al., 2020). In these more open forests, soils are also less protected against erosion and leaching than those from habitats with a denser vegetation (Kosmas et al., 2000; Yücesan et al., 2019). Conversely, ancient forests are reported to show greater vegetation cover (de la Peña et al., 2016), inducing a greater accumulation of plant litter that favours microbial biomass and activities.

In ancient forests, higher levels of tyrosinase activities were observed. Previous studies have linked phenol oxidase activities to the degradation of lignin and derived products (de Gonzalo et al., 2016; Romaní et al., 2006; Sinsabaugh, 2010). The higher recalcitrant organic matter content induced by greater plant-litter accumulation in ancient forests indeed heightens the enzyme activities

involved in the transformation of the more recalcitrant fraction. This could also explain why lower pH and higher exchangeable Fe content were observed in soils from the ancient forests. We indeed found soils from ancient forests more acidic than soils from post-agricultural forests, in line with results from previous studies (Brudvig et al., 2013; Falkengren-Grerup et al., 2006) and which was explained by higher phenol quantities. In addition, we found microbial biomass higher in soils from ancient forests. Soil pH is known to influence the abundance and diversity of microorganisms involved in decomposition both directly, by interfering with microbial metabolisms and regulating enzyme activities, and indirectly, by controlling the solubility and thus the availability of nutrients (Frankenberger & Johanson, 1982; Jin & Kirk, 2018; Rousk et al., 2010). Rousk et al. (2009) provided evidence that the relationship between microbial growth and pH depends on the type of microorganisms (i.e., bacteria vs. fungi). Additionally, Brunel et al. (2020) showed that pH variations depend on the type of organic matter inputs (e.g., wood vs. twigs and leaves) and they also observed a negative correlation between pH and microbial biomass in Mediterranean forest litters.

4.2 | Soil properties: Recovery after abandonment of agriculture

Our investigations considered two different time frames of forest recovery after agricultural abandonment. While soil properties from very recent forests (time of abandonment <60 years) strongly differed from ancient forests (age >200 years), those from recent forests (time of abandonment >60 years) were not clearly discriminated from the



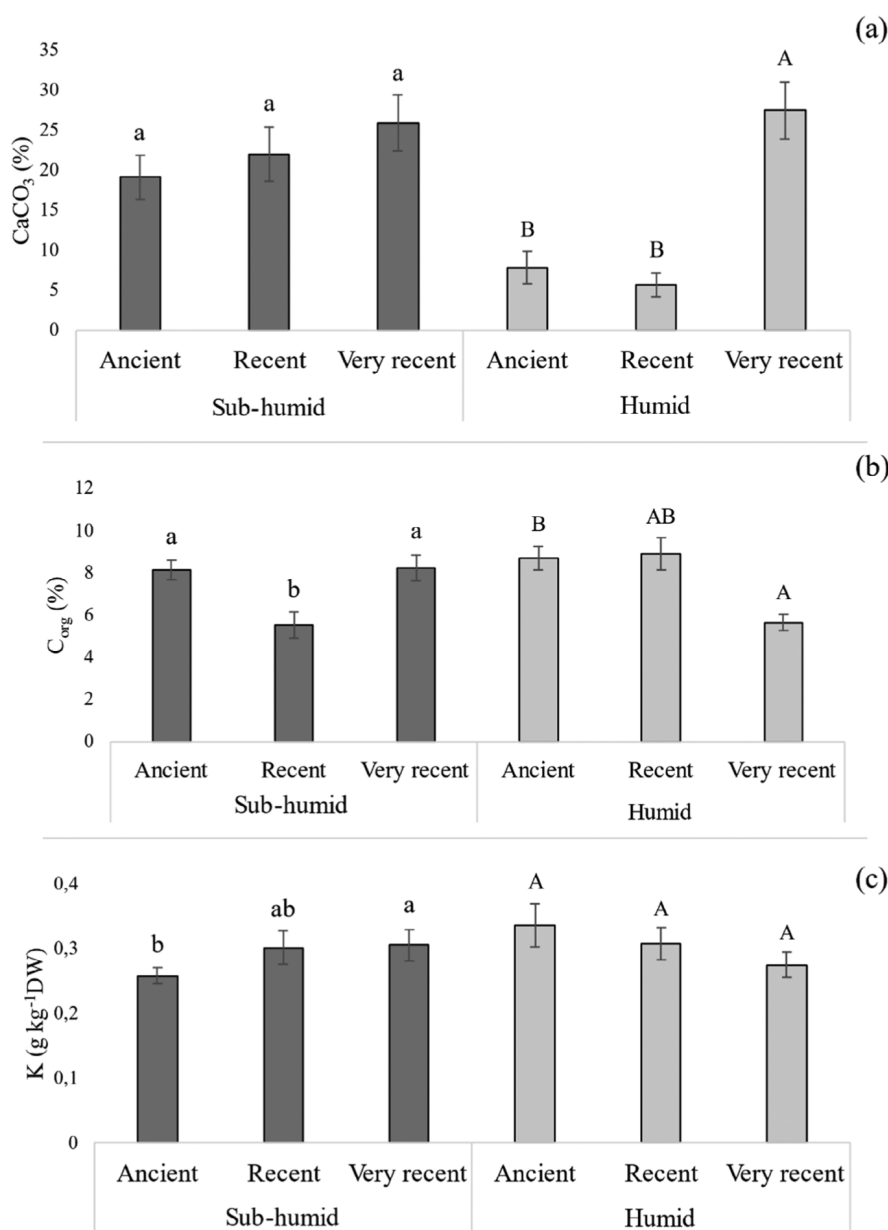


FIGURE 3 Land Use Legacy effect on CaCO₃ percentage (a), Corg percentage (b) and K content (c) of soil from ancient, recent, and very recent forests depending on climate (sub-humid and humid climate). Values are means ± standard error. Different letters denote significant differences with $a < b$.

two other categories. Thus, LUL effects varied depending on the time since when agriculture was abandoned: microbial (i.e., microbial biomass, BR and tyrosinase activities), certain physico-chemical (i.e., pH_{H₂O}, and Fe content) and stand (number of *Q. pubescens* stems) properties appeared to follow similar trends with LUL effects disappearing more than 60 years after reforestation. Nevertheless, pH_{KCl} and P content were higher in both post agricultural forests than in ancient forests, attesting a lasting impact of agricultural terraces on certain soil properties. The legacy of some agricultural practices (i.e., amendment and aboveground plant biomass removal, as mentioned above) thus persists more than 60 years after reforestation, affecting the physico-chemical properties of soils. De Lombaerde et al. (2020) has shown that phosphorus and soil acidity influence seed dispersal and previous studies have shown that past agricultural activities influence the recolonization patterns of some plant species (Baeten & Verheyen, 2017; Valtinat et al., 2008). Past agricultural terraces may

thus have a significant influence on plant species colonisation and persistence in post-agricultural forests more than 60 years after agricultural abandonment. There is no consensus in the literature on how long LUL effects may persist following agricultural abandonment. Some authors reported an “irreversible” effect of LUL on plant diversity (Ackermann et al., 2019; Dupouey et al., 2002; Kosmas et al., 2000), resulting in an effect on soil functioning, while others suggested “a long-term successional process” following forest succession and the disappearance of open habitat (Abadie et al., 2020; Jangid et al., 2011). According to this theory, there may be a progressive return to a non-impacted state of microbial functioning in soils from post-agricultural forests after at least 60 years of reforestation, leading to a resilience in soil functioning. However, previous studies revealed that the extent and duration of LUL effects differ depending on the type of cultivation, land use management and the vegetation type established after abandonment (Macdonald et al., 2012; Wilson et al., 2011).



4.3 | Climate conditions influenced LUL effect on certain soil physico-chemical properties

This work explored the effect of LUL under two Mediterranean climates (sub-humid vs. humid). Annual precipitation is a commonly used rainfall-based index of aridity, which was selected by the IPCC (2007). Annual precipitation of 695 mm under the sub-humid climate versus 772 mm under the humid climate underlined the contrasted climate conditions between the two geographic areas under study. Here, the effect of the interaction between climate and LUL was observed on certain soil physicochemical properties. LUL effect on organic carbon and CaCO₃ percentages as well as K content thus varied differently depending on the climate conditions considered. Under humid climate, higher CaCO₃ percentages and lower percentages of organic carbon were observed in soils from the most recent post-agricultural forests. As mentioned above, these results can be explained by the erosion and leaching that occurred after agricultural abandonment in the absence of a dense vegetation cover (Kosmas et al., 2000). The important contribution of the mineral fraction in soils from a sub-humid climate can explain why no effect of LUL was observed on CaCO₃ percentages in soils from a sub-humid climate. Under this climate, soils are thus less deep and more dependent on the parent rock, leading to poorly developed soils with a lower density and a greater mineral fraction (Comino et al., 2018; Delcourt et al., 2019). Interestingly organic carbon percentages were lower in soils from recent forests under sub-humid climate. This result reflects a longer effect of LUL under this climate, probably due to the more arid conditions resulting in a slower vegetation recovery and therefore to the persistence of soil erosion more than 60 years after agricultural abandonment (Ackermann et al., 2019). Additionally, under sub-humid climate, higher K content was observed in soils from very recent forests than in those from ancient forests. Mineral P and K fertilisation practices were commonly used for crops in Europe in the 1970s and K fertiliser was particularly used in soils with high limestone content that could explain the variations observed in our study in soils from very recent forests under sub-humid climate only (Jouany et al., 1996). Potassium was probably then leached or consumed by plants along the plant recolonization process. By influencing forest recovery, climate conditions thus influenced LUL effect on soils physico-chemical properties. In a context of global change, the more arid climate conditions modelled by the IPCC (2007) thus could modified the response of physico-chemical properties to past land use, which may in turn affect soil microbial communities.

5 | CONCLUSION

This study provides evidence that LUL can affect microbial functioning even years after agriculture abandonment. The influence of LUL on soil microbial and physicochemical properties was linked to the replacement of crop species by Mediterranean plant communities that are more sclerophyllous and rich in secondary recalcitrant metabolites. Under these Mediterranean conditions, at least 60 years of

reforestation are needed for soil to recover the physico-chemical and microbial properties. Interestingly, LUL did not affect microbial responses to seasonal contrasts (winter vs. summer). Microbial responses to LUL were not influenced by climate, whereas climate-modified LUL affected some physicochemical properties (CaCO₃, C_{org}, and K content). Finally, our findings point out LUL as a significant driver of soil functioning that have to be considered when assessing soils' vulnerability in the context of global change.

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CONFLICT OF INTEREST STATEMENT

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.

DATA AVAILABILITY STATEMENT

Data available on request from the authors. The data that support the findings of this study are available from the corresponding author upon reasonable request.

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