Article

Rapid Assessment of Land Use Legacy Effect on Forest Soils: A Case Study on Microarthropods Used as Indicators in Mediterranean Post-Agricultural Forests

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Abstract: Agriculture is known to strongly influence soil functioning. Nevertheless, its long-term effects remain not well documented in the Mediterranean region, which has a long history of human land use. The “Parc Naturel Régional du Luberon” is a good illustration of these land use changes, as its territory is now covered with forests of differing ages and histories. This study investigates the effect of past land use (agricultural terraces) on microarthropods of current forest soils. In this way, Acari and Collembola of soils from ancient forests, recent forests (developed before 1958), and very recent forests (developed after 1958) were analysed. Different pedoclimatic conditions (Meso-Mediterranean vs. Supra-Mediterranean) and two contrasted seasons (winter and summer) were taken into account in mesofauna responses. A negative effect of past agricultural land use was observed on soil microarthropod abundance in very recent forests only, whatever the pedoclimatic conditions. After at least 60 years of reforestation, this negative effect was no longer observed, indicating a recovery of these communities. Land use legacy effect on oribatid mites in post-agricultural forests depended on the pedoclimatic conditions considered, suggesting that the recovery of microarthropod communities takes more time under more arid conditions. Microarthropods can be considered as good bioindicators of past land use effects depending on pedoclimatic conditions in forest soils.

Keywords: agricultural abandonment; terraces; Collembola; Acari; forest soils; Mediterranean climate

1. Introduction

The impacts of land use and land cover changes on terrestrial ecosystems have been the subject of increasing interest in recent years [1,2]. Numerous studies have indeed shown a significant influence of agricultural activities on biological and physico-chemical properties of soils, threatening soil functioning and associated ecosystem services [3–5]. Recently, some studies have focused on the long-term effect of past land use on current soil functioning [6,7]. Authors highlighted higher pH as well as higher amounts of phosphorus in post-agricultural forest soils [8,9]. Lower biomass and microbial activities have also been observed in soils from past-agricultural forests [10–12]. However, to our knowledge, no study focuses on the effect of land use legacy (LUL) on soil microarthropods despite their strong involvement in organic matter degradation and soil formation. Through their movement, feeding, excretion, and death, mesofauna both physically and chemically modify the plant litter and soil in which they live [13,14]. By influencing microarthropods, past agricultural activities could thus modify the entire soil food chain, causing major changes in soil organic matter degradation and soil formation. Among these organisms,
oribatid mites and collembolans achieve an important part of litter fragmentation. They are known to be sensitive to environmental changes caused by anthropogenic stresses, making them useful indicators of soil quality [15,16]. Although they are considered to be part of the same trophic level and occupy similar niches in organic matter decomposition processes, these two groups could be differentially affected by changes in abiotic conditions [17,18].

The Mediterranean region is known as a biodiversity hotspot where climate conditions have led to the development of specific soils [19,20]. Mediterranean soils are generally calcareous, poor in organic matter, and subjected to leaching and erosion [21,22]. High temperatures associated with low rainfall during summer [23] make water stress the most important environmental constraint for organisms. These constraints, combined with a hilly topography, have resulted in the development of agricultural terraces, allowing cultivation of crops in less accessible landscapes of the Mediterranean region. Terraced structures have thus been found to facilitate the cultivation of slopes due to their potential for increasing soil moisture and nutrient availability by enhancing the water-holding capacity and retention of organic matter content [24]. From 1860 to 1958, terrace cultivation was progressively abandoned due to low crop productivity and the promotion of industrial agriculture [25,26]. Farmers abandoned the least productive and accessible farmlands, resulting in reforestation by pioneer species. The Parc Naturel Régional du Luberon (PNRL), a regional parkland located in the South-Eastern French Mediterranean region, is a good example of these land use changes in the Mediterranean area. In that territory, ancient forests indeed coexist with forests developed after the abandonment of agricultural terraces and for which soil functioning may have been modified by past agricultural activities [25,27].

This study aimed at investigating the LUL effect and, particularly, the past agricultural management (i.e., terraces) effect on soil microarthropods. Moreover, we wanted to test whether these effects differed depending on pedoclimatic conditions and contrasted seasons. We investigated forest soils in the PNRL, where climate, vegetation, and past land use have been previously described in detail [25]. Samplings were performed in the Meso-Mediterranean and Supra-Mediterranean climate zones of the PNRL and for two contrasted seasons (winter vs. post-summer period). Three main questions were addressed here: (i) does LUL impact soil microarthropods according to the pedoclimatic conditions? (ii) does LUL influence the sensitivity of soil microarthropods and their adaptability to seasonal contrasts? (iii) is there a difference in LUL effect depending on the time since farmland abandonment? We expect that modified physico-chemical properties in post-agricultural forests may affect mesofauna communities by decreasing abundance and hampering their response to summer drought. Finally, this study may highlight the potential value of microarthropods as indicators of stress linked to past human activities.

2. Materials and Methods

2.1. Site Description and Soil Sampling

The research was carried out 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 spans throughout 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 previous studies by Abadie et al. [25] and Delcourt et al. [12], 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 bioclimatic zones were considered (Figure 1) corresponding to altitudinal arrangement of vegetation type, specifically Meso-Mediterranean (average temperature: 0–27 °C, annual precipitation: 695 mm) and Supra-Mediterranean (average temperature: −1–25 °C, annual precipitation: 772 mm) levels, respectively [19].
According to Abadie et al. [27], 55% of the territory is covered by forests containing three main dominant species: holm oak (Quercus ilex L.), downy oak (Quercus pubescens Willd), and Aleppo pine (Pinus halepensis Miller). Most of the forests do not receive any specific silvicultural treatments. In this study, only forest patches with Q. pubescens as the dominant species were selected. Based on Abadie et al. [27,28], 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. [29] following Favre et al. [30], 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; and as very recent if they developed after 1958 (Figure 2). Following Abadie et al. [28], we considered that no turnover in land cover occurred between the dates of the two maps, i.e., the “État-Major” map (1860) and the historical aerial photographs (1954).

In addition, the post-agricultural forests selected showed distinct vestiges of terraces, providing evidence of historical agricultural activities. Terraces were most likely used for olive orchards, as olive trees have historically been the primary crop grown on terraces in the French Mediterranean region [31].

For each climate (sub-humid and humid), five pairs of ancient and recent forests and five pairs of ancient and very recent forests were selected based on their geographical proximity. This meant that each post-agricultural forest could be linked to an ancient forest taken as a reference model. Thus, a total of 40 forest patches of a minimum area of two hectares were explored. Soils were sampled in winter (in February) and in late summer (in September after summer drought). We sampled at the end of summer drought,
when temperatures are milder, and before the intense autumn rainfalls, which would cause a boom in the abundance of these organisms and would mask the effects of other environmental factors. On each forest patch, five samples were collected from the top 10 cm of soil (after eliminating leaf material and fine fragments) and pooled to obtain a composite sample. None of the forest plots observed had a soil depth greater than 30 cm above the bedrock. In addition, the number of *Q. pubescens* stems and the recovery percentage of the understory vegetation were determined in a subplot of 10 m².

![Figure 2](image_url)

**Figure 2.** Conceptual scheme of the different historical land uses considered in this study (ancient forests, recent forests, and very recent forests).

2.2. Microarthropods Extraction and Identification

Microarthropods were extracted from fresh soil using the Tullgren funnel method for 10 days [32]. Arthropods collected were stored in 90% ethanol, counted using a binocular microscope, and separated into the four Collembola orders (Entomobryomorpha, Neelipleona, Poduromorpha, and Symphypleona) and in different suborders for Acari (Oribatida, Mesostigmata, and Prostigmata) [33,34]. Additionally, the Prostigmata suborder was separated into different families (i.e., Bdellidae, Eupodidae, Caeculidae, Rhagidiidae, Anystidae, Cunaxidae, and “other Prostigmata”). Collembola and Oribatida were regarded as microbi-detritivorous microarthropods, whereas Acari Mesostigmata and only some families of Prostigmata (i.e., Bdellidae, Eupodidae, Caeculidae, Rhagidiidae, Anystidae, and Cunaxidae) were regarded as predatory microarthropods [35,36].

2.3. Soil Physico-Chemical Properties

After microarthropod extraction, samples were sieved to 2 mm before their physico-chemical properties were determined. For each soil sample, total C (%) and N (%) content (C<sub>tot</sub> and N<sub>tot</sub>, respectively) and their ratio (C/N) were measured using a C/N elementary analyser (Flash EA 1112 Thermo Scientific series, Waltham, MA, USA). Determination of calcium carbonate (CaCO<sub>3</sub>, %) in soil samples was performed using a calcimeter (FOGII Digital Soil Calcimeter) based on volumetric analysis of carbon dioxide CO<sub>2</sub> released during the application of hydrochloric acid solution HCl 6 N. The carbon proportion of CaCO<sub>3</sub> was then calculated using the molar mass of C (Equation (1)). Then, organic carbon (C<sub>org</sub>, %) was calculated as the difference between total C<sub>tot</sub> content and C<sub>CaCO3</sub> content (Equation (2)).
\[
\%C_{CaCO_3} = \frac{12}{100} \times \%CaCO_3
\]

\[
\%C_{org} = \%C_{tot} - \%C_{CaCO_3}
\]

Additionally, the pH of the 80 soil samples from the two sampling campaigns (i.e., 40 × 2, winter and summer) was measured in distilled water with a pH meter (HANNA edge HI 2020-02) after 60 min of magnetic stirring and 60 min equilibration.

2.4. Statistical Analyses

According to previous studies employing a similar sampling design [37,38], 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 land use legacy (ancient forest, recent forest, very recent forest), bioclimatic zone (Meso-Mediterranean vs. Supra-Mediterranean), season (winter vs. summer) and their interactions. LME models were built with R version 3.6.2 (R Core Team 2019), using the nlme package with significance levels indicated as * for \(p < 0.05\), ** for \(p < 0.01\), and *** for \(p < 0.001\). The indicators taken into account were land use legacy, climate and season as fixed factors, and plot geography as a random factor (following R syntax “random = ~1|plot”). 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). The normality and homogeneity of the variances were assessed by conducting Shapiro–Wilk and Levene tests on the residuals obtained from the regression model. Data were transformed to common logarithms (log\(_{10}\)) or square root when necessary to meet the requirements of normality and homogeneity of variance. Finally, we observed relationships linking microarthropod variables to physico-chemical variables by determining the Pearson correlation coefficient.

3. Results

In this study, we focused on a factorial model including all interactions between LUL and climate (i.e., contrasted bioclimatic zones (Meso-Mediterranean vs. Supra-Mediterranean) and seasons (winter vs. summer).

3.1. LUL Effects on Microarthropods Demographic Parameters

LME models showed that the total abundance of microarthropods was affected by LUL independently of the other factors considered: a lower abundance of organisms was observed in soils of very recent forests than in those from ancient forests (−43%) (Figure 3a, Table 1). This trend was similar for both predator and microbi-detritivore groups (−38% and −43%, respectively) (Figure 3b, Table 1). Nevertheless, the effect of LUL depended on the taxon considered: Acari abundance was significantly affected by LUL and followed the same pattern as previously described (−45%), while no effect of LUL was observed on collembolan abundance (Figure 3c, Table 1). Moreover, these trends were observed whatever the bioclimatic zones or season of samplings considered.

Oribatid mites (Oribatida) represented 52% of the total individuals identified (and 68% of the microbi-detritivores). Regarding the abundance of these organisms, LME models showed a significant but climate-dependent influence of LUL. In soils from the Meso-Mediterranean bioclimate, LME models showed a lower oribatid mite abundance in soils of recent forests than in those of ancient forests (−43%) (Figure 3a, Table 1). This trend was similar for both predator and microbi-detritivore groups (−38% and −43%, respectively) (Figure 3b, Table 1). Nevertheless, the effect of LUL depended on the taxon considered: Acari abundance was significantly affected by LUL and followed the same pattern as previously described (−45%), while no effect of LUL was observed on collembolan abundance (Figure 3c, Table 1). Moreover, these trends were observed whatever the bioclimatic zones or season of samplings considered.

Oribatid mites (Oribatida) represented 52% of the total individuals identified (and 68% of the microbi-detritivores). Regarding the abundance of these organisms, LME models showed a significant but climate-dependent influence of LUL. In soils from the Meso-Mediterranean bioclimate, LME models showed a lower oribatid mite abundance in soils of recent forests than in those of ancient forests (−48%). Oribatid abundance in the very recent forests was not significantly different from the ancient or recent forests. In soils from the Supra-Mediterranean zone, LME models showed a lower oribatid mite abundance in soils of very recent forests than in those of ancient forests (−63%) (Figure 4, Table 1). Oribatid abundance in the recent forests was not significantly different from the ancient or very recent forests.
Table 1. Results of full factorial linear mixed-effect model analyses on microarthropod demographic parameters, soil physico-chemical properties, and environmental data depending on land use legacy (LUL), climate (C), and season (S); (* p < 0.05; ** p < 0.01; *** p < 0.001, “ns” for “not significant” and “NA” for “Not Applicable”).

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<th>Climate (C)</th>
<th>Season (S)</th>
<th>LUL × C</th>
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3.2. LUL Effects on Forest Structure and Soil Properties and Links with Microarthropod Indicators

LME models showed that the number of *Q. pubescens* stems and the soil pH were affected by LUL independently of the other factors considered (Table 1). There were fewer *Q. pubescens* stems per ha in very recent forests than in ancient and recent forests (Figure 3a), and the pH of soils from very recent forests was higher than those of soils from ancient forests (Figure 3b). No significant effect of LUL was observed on the understory vegetation. Concerning CaCO$_3$ and organic carbon (C$_{org}$) percentages, LME models showed a significant but bioclimate-dependent influence of LUL (Table 1).

For soils from the Meso-Mediterranean bioclimate, LUL had no effect on soil CaCO$_3$ percentages, while C$_{org}$ percentages were lower in soils from recent forests than in those from ancient forests. For soils from the Supra-Mediterranean bioclimate, CaCO$_3$ percentages were higher in soils from very recent forests than in soils from ancient and recent forests, and C$_{org}$ percentages were lower in soils from very recent forests than in soils from ancient forests.
ancient forests (Figure 6a,b). $C_{\text{org}}$ percentages were intermediate in the recent forests and not significantly different from the ancient or very recent forests. Additionally, LME models also highlighted a significant and season-dependent influence of LUL on $C_{\text{org}}$: no effect of LUL was found in winter, while lower $C_{\text{org}}$ percentages were observed in very recent forest soils than in ancient forest soils in summer (Table 1). In summer, $C_{\text{org}}$ percentages were intermediate in the recent forests and not significantly different from the ancient or very recent forests (Figure 6c).

![Bar chart](image1)

**Figure 5.** Number of *Q. pubescens* stems (a) and soil pH (b) in soils from ancient, recent, and very recent forests. Means ($\pm$ standard error, N = 80) with the same letters are not significantly different (lme models, $p < 0.05$, HSD test, $p < 0.1$, a > b).

Moreover, a positive correlation was observed between total abundance and $C_{\text{org}}$ ($r = 0.44$, $p < 0.01$) and between the abundance of oribatid mites and $C_{\text{org}}$ ($r = 0.42$, $p < 0.001$). Total abundance and oribatid mite abundance were also negatively correlated with pH ($r = -0.37$, $r = -0.47$, $p < 0.01$ and $r = -0.38$, $p < 0.01$, respectively) (Figure S1, Supplementary Material).
percentages were intermediate in the recent forests and not significantly different from the ancient or very recent forests (Figure 6c).

Figure 6. CaCO$_3$ (a) and C$_{org}$ (b) percentages in soils from ancient, recent, and very recent forests in Meso-Mediterranean and Supra-Mediterranean zones. C$_{org}$ percentages (c) in soils from ancient, recent, and very recent forest during either the winter or summer period. Means (±standard error, N = 80) with the same letters are not significantly different (lme models, $p < 0.05$, HSD test, $p < 0.1$, a $>$ b). Lower-case letters compare forest ages in the Meso-Mediterranean zone, and upper-case letters compare forest ages in the Supra-Mediterranean zone for (a,b). Lower-case letters compare forest ages in winter, and upper-case letters compare forest age in summer for (c).

4. Discussion

4.1. Past Agricultural Activities Negatively Affected Microarthropods

This study highlighted a strong negative effect of past agricultural activity on the abundance of soil microarthropods. Acari seemed to be more affected than collembolan, especially predators for which abundance was reduced in very recent forests. This result was observed whatever the bioclimate or season considered, revealing the strong effect of
LUL on this group of microarthropods. The decrease in predator abundance could well decrease the predation pressure and could thus have consequences on the entire soil food chain. Predators indeed play an important role in the regulation of microbi-detritivores including collembolans [39,40]. The lower number of predatory Acari could have promoted the development of collembolan populations and offset the effect of LUL on these organisms. Population recovery after a disturbance can also be linked to the reproductive mode of the different species. For example, Ref. [17] observed that species performing parthenogenesis have a higher capacity of recolonisation than those using sexual reproduction.

However, this negative effect was only observed in soils from very recent forests, where agricultural abandonment occurred less than 60 years ago. These results can be explained by the evolution of agricultural practices from the middle of the 20th century onwards: more intense agricultural practices (e.g., use of agricultural inputs) have indeed been promoted to optimize agricultural production, which thus have modified soil composition and structure in forests subjected to more recent agricultural activities (i.e., very recent forests) [41,42]. Moreover, in line with the previous study of Abadie et al. [28], the smaller number of stems/ha of the dominant tree species Q. pubescens observed in very recent forests indicates a more open environment. Very recent forests thus have a lower vegetation density and, therefore, a smaller amount of plant litter on the soil surface associated with more intense exposure to sunlight, increasing the hydric and thermal stresses to which microarthropods are highly sensitive [39,43–45]. Interestingly, soils from recent forests seemed to present an intermediate state between soils from ancient forests and soils from very recent forests. Depending on the time from when agriculture was abandoned, LUL effects varied for microarthropods, pH, and the number of stems per hectare. LUL effects indeed disappeared when reforestation had been ongoing for more than 60 years (recent forest plots). These results could thus also highlight a form of resilience in soil properties following forest succession and the disappearance of open habitats 60 years after agricultural abandonment, corroborating observations made by previous studies [28,46].

4.2. Pedoclimatic Conditions Influenced Forest Regeneration

Our results also revealed that LUL effects on certain microarthropods and physico-chemical properties varied depending on the bioclimatic zone considered (Supra-Mediterranean vs. Meso-Mediterranean zones). Unlike the other organisms, the effect of past agricultural activity on oribatid mites was dependent on the bioclimate considered. In the Supra-Mediterranean bioclimate, a lower abundance of oribatid mites was observed in soils from very recent forests, while for the Meso-Mediterranean, a lower abundance of oribatid mites was observed in soils from recent forests. Previous studies have shown that the quantity and quality of food resources influence population growth rates of oribatid mites [47–49]. In our study, the observed variation in abundance of oribatid mites seems to be directly linked to organic matter content of the soil. These contrasting results depending on bioclimates can be explained by the fact that plant regeneration is under the influence of pedoclimatic conditions, especially through the control of erosion and leaching processes occurring after the abandonment of agricultural terraces [24,50]. Similar patterns were found by Ackermann et al. [51], who studied the natural vegetation regeneration and erosion intensity after the abandonment of agricultural terraces along a climate gradient from sub-humid to arid conditions. In a previous study, Delcourt et al. [52] also observed a recovery of soil chemical properties in recent forests in the Supra-Mediterranean zone, while in the Meso-Mediterranean zone, the soil chemical signature of post-agricultural forests was different from that of ancient forests. Both studies showed that wetter conditions promoted natural vegetation recovery and, thus, soil stabilisation. Under more arid conditions, afforestation may have taken more time, and erosion processes thus likely occurred for a longer period in post-agricultural forests, explaining the smaller amounts of organic matter.

Oribatid mites represent a particularly important part of the microbi-detritivorous organisms in soils: for example, in our study, they represented more than half of the
total individuals identified (and two-thirds of the microbi-detritivores). A decrease in the abundance of these organisms could particularly affect micro-fragmentation activities, with cascading effects on the soil food web and, thus, on the decomposition of organic matter [53–55]. By controlling vegetation cover, pedoclimatic conditions thus had a major influence on soil stabilisation processes after the abandonment of terraces and, therefore, took an important part in the resilience of soil functioning [52].

4.3. Land Use Legacy and Soil Vulnerability in the Context of Global Change

In our study, it seems that a longer period of recovery of soil properties after the abandonment of agricultural terraces is needed under the Meso-Mediterranean bioclimate than under the Supra-Mediterranean bioclimate since LUL effects are still observable more than 60 years after agricultural abandonment on oribatid mites and on organic matter in soils from the Meso-Mediterranean zone. Moreover, soils from post-agricultural forests may not return to the same state as those from forests that had never been cultivated in the past. Consequently, LUL may affect the resilience capacity of soils, and this factor should be considered to assess soil vulnerability to climate change in the Mediterranean region. Previous studies described the degradation and desertification of abandoned lands as an irreversible process under arid conditions [51,56]. Under a warmest climate change scenario, ecological restoration operations may thus become necessary in post-agricultural forests in order to help plant regeneration and limit soil leaching and erosion. Previous studies have demonstrated the positive effects of terraces in reducing soil erosion [21,57,58] and suggested that active management (maintenance or rehabilitation of terraces) can be applied to facilitate the stabilising of abandoned terraces. The conservation of old agricultural terraces should thus be considered since they are already integral parts of landscapes in many forests of the Mediterranean region.

5. Conclusions

In this study, we highlighted a negative impact of past agricultural activities on soil microarthropods. However, this effect faded when reforestation had been ongoing for at least 60 years after abandonment. The Mediterranean climate, through the control of soil erosion and revegetation processes, modifies the effect of LUL on oribatid mites, as well as on soil organic matter. Our results showed that the resilience of microarthropods seems to take more time under more arid pedoclimatic conditions, which could negatively impact soil organic matter decomposition. In this view, conservation efforts on agricultural terrace remnants in post-agricultural forests could facilitate revegetation processes by limiting soil erosion. Microarthropods have thus proved to be a good indicator of soil functioning, demonstrating in this study that LUL is an important factor to consider when assessing soil vulnerability, especially in a context of climate change.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f14112223/s1, Figure S1: Pearson correlation coefficients between physico-chemical parameters (organic carbon (Corg, %), soil pH) and microarthropod parameters (Total abundance, oribatid mites abundance (individuals 100 g⁻¹ dry soil)) (N = 80).

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