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Ecological soil quality affected by land use and management on semi-arid Crete

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Received: 6 February 2015 – Accepted: 24 February 2015 – Published: 3 March 2015

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Published by Copernicus Publications on behalf of the European Geosciences Union.

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Land use and soil management practice can have strong effects on soil quality, defined in terms of soil fertility, carbon sequestration and conservation of biodiversity. In this study, we investigate whether ecological soil quality parameters are adequate to assess soil quality under harsh conditions, and are able to reflect different land uses and intensities of soil management practices.

We selected three sites as main representatives for the dominant types of land use in the region: an intensively cultivated olive orchard (annually tilled), an extensively used olive orchard (not tilled) and a heavily grazed pasture site in the Koiliaris catchment (Crete/Greece). Soil quality was analysed using an ecosystem approach, studying soil biological properties such as soil organism biomass and activity, and taxonomic diversity of soil microarthropods, in connection to abiotic soil parameters, including soil organic matter contents, and soil aggregate stability.

The intensively cultivated olive orchard had a much lower aggregate water stability than the extensive olive orchard and the pasture. Contents of soil organic C and N were higher in the extensively used olive orchard than in the intensively cultivated orchard, with intermediate concentrations in the pasture. This was mainly caused by the highest input of organic matter, combined with the lowest organic matter decomposition rate. Soil organism biomasses in all sites were relatively low compared to values reported from less harsh systems, while microarthropod richness was highest in the pasture compared to both the intensive and extensive olive orchards.

From the present results we conclude that microarthropod taxonomic richness is a very useful indicator for ecological soil quality, because it is not only able to separate harsh sites from other systems, but it is also sensitive enough to show differences between land management practices under harsh conditions. Microbial biomass and especially microarthropod biomass were much lower in our harsh study sites than reported from less affected areas, and have therefore also potential as biological indicators for degradation.

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1 Introduction

Soils provide a wide array of ecosystem services, such as the provision of food, feed and fibre, carbon storage and sequestration, hydrological regulation, and contaminant attenuation (Costanza et al., 1997). Soil quality can be defined as the ability of the soil to provide these services. In large areas in the Mediterranean region, soil quality is adversely affected by overgrazing and overharvesting of natural vegetation, ultimately leading to soil degradation, erosion, and desertification (Milgroom et al., 2007). Such losses in soil quality in semi-arid regions impose a severe and increasing risk for the local populations, because climate predictions indicate decreasing precipitation in the near future for the Mediterranean region (Chartzoulakis and Psarras, 2005).

In order to understand the interrelationships between land use and soil quality, the Critical Zone Observatory (CZO) network was established across the USA and Europe (Anderson et al., 2008). The CZO network is an internationally coordinated interdisciplinary research effort, including chemical, physical, and biological processes that govern soil ecosystem services.

As part of the CZO research effort, the European Commission has provided funding for a large multi-disciplinary research project: Soil Transformations in European Catchments (SoilTrEC) (Bernasconi et al., 2011; Menon et al., 2014). The European CZOs represent different stages in the soil life, including sites along soil formation gradients (Austria, Switzerland, Iceland), along a soil degradation gradient (Greece), along a lithology gradient (Czech Republic), and of agricultural sites differing in soil management (Austria, Iceland) (Banwart et al., 2011; Menon et al., 2014).

The aim of the present study is to investigate soil quality at the Koiliaris CZO sites in Crete (Greece) that are considered to be at risk of potential soil degradation and desertification. Koiliaris CZO is meant to be representative for the soils in the Mediterranean region impacted by a strong climatic gradient, steep upland slopes, and anthropogenic intensification, which make these soils sensitive to degradation. The sites in the Koiliaris CZO (Crete, Greece) include three dominant land use types: an intensively

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cultivated olive orchard, an extensively used olive orchard, and a pasture site. The intensively cultivated olive orchard represents the conventional practice including tillage, litter removal and fertilisation, while at the extensively used orchard these measures are not applied. The pasture site represents a former cropland now used as grazed area for about 70 years.

Loss of soil fertility and soil degradation have mostly been approached from an abiotic perspective, with emphasis on soil structure (Celik, 2005), water erosion (Kosmas et al., 1997), nutrient cycling (Solomon et al., 2000), and organic matter dynamics (Wu and Tiessen, 2002). Here, we look in particular at biological soil quality parameters, in addition to the abiotic parameters. The role of soil organisms has received less attention in assessments of land degradation and desertification, although the importance of biology in soil quality and fertility is more and more acknowledged (Ashford et al., 2013; Brussaard et al., 1997, 2007; Buchan et al., 2013; Cole et al., 2006; De Deyn et al., 2003; Holtkamp et al., 2008; Hunt et al., 1987; Moore, 1994; Oades, 1993; Setälä and Huhta, 1991; Wardle et al., 2004). Up till now, soil quality assessments from an ecological perspective have mostly been carried out in soils that were not prone to severe losses of soil in terms of degradation, erosion and desertification, while focusing on soil quality for sustainable agricultural fertility or for habitat preservation of biodiversity in natural ecosystems (Bending et al., 2004; Birkhofer et al., 2008; Carpenter-Boggs et al., 2000; Doran and Zeiss, 2000; van Leeuwen et al., 2015). In this study we investigate whether ecological soil quality parameters are also adequate to assess soil quality under harsh conditions, and are able to reflect different land uses and intensities of soil management practices.

The present paper investigates soil quality with an emphasis on biological parameters in relation to abiotic properties, i.e. we look at soil structure, soil organic matter, nutrient availability, and soil as a habitat for species-rich communities. These soil properties are all considered to be important aspects of soil quality and are inextricably linked. For example, soil structure affects soil organic matter decomposition and the biological habitat function of the soil, soil organic matter is the most important resource

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an intensively cultivated olive orchard (20 year old trees) where tillage (once a year to facilitate harvesting), litter removal (to be used as fodder for livestock), and fertilisation were applied, at 20 m above sea level (a.s.l.) on alluvium sediments in a floodplain. Site E was an extensively used, 600 year old terrace (no tillage, litter removal or fertilisation) with olive trees on a steep slope at 465 m a.s.l., while site P was formed by a 600 year old terrace, formerly utilised as cropland (until 1940), with permanent grassland and sparse tree/shrub cover at 1065 m a.s.l., currently used as grazed pasture (see Table 1 for site characteristics). Sites E and P were both situated on soils developed on bedded limestone.

2.2 Sampling scheme

Samples were taken in May 2010. In each sampling site, three plots were selected in which all measurements were carried out; the plots were 10–20 m apart. In each plot, mixed soil samples (ca. 1 kg) were taken from the edge of a soil profile pit of about 1 m wide for microbial (bacteria, fungi), microfaunal (protozoa, nematodes) and SOM characterization, and by use of a 5 cm diameter corer for the mesofauna (enchytraeids and microarthropods). All samples were taken from the topsoil (0–10 cm), biologically the most active layer (Ekelund et al., 2001; Miura et al., 2008).

2.3 Soil analyses

Particle size distribution (clay content), soil pH, and calcium content were determined as described in van Leeuwen et al. (2015). Soil structure was experimentally approached by measuring the water stability of aggregates (1–3 mm in diameter), using a standard wet sieving procedure modified after Yoder (1936). Water stable aggregates (WSA) were calculated by the mass of aggregates remaining on the 1 mm sieve after wet sieving and subtracting the mass of sand < 1 mm from this aggregate size fraction (e.g. Kercheva et al., 2011). WSA indicates the suitability of soil for agricultural production.

Total carbon (TOC) and nitrogen (TN) contents, hot-water-extractable carbon (HWC), potentially mineralisable nitrogen (PMN), and C and N mineralisation rates were determined as described in van Leeuwen et al. (2015).

Soil biological measurements included the presence and abundance of the major taxonomic groups of soil organisms: microbes (bacteria, fungi) and soil fauna (protozoa, nematodes and microarthropods). Within these taxonomic groups we defined “trophic groups” based on diet and life-history traits, following the method of Moore et al. (1988). Abundances were transformed into estimates of biomass based on body-size information, and expressed in units of kilograms of carbon per hectare for the 0–10 cm top soil layer. The laboratory techniques used to analyse the biological parameters are described in van Leeuwen et al. (2015).

Regarding the taxonomic species richness in the microarthropods we used three metrics, i.e. the absolute number of taxa present, the Shannon diversity index (H), and the Pielou evenness index (J). For the Shannon diversity index (H) we used the following formula:

$$H = - \sum_{i=1}^N (p_i \cdot \ln(p_i)),$$

in which p_i is the fraction of the total biomass present in species i , i.e. the relative biomass of species i , and N is the total number of taxa present. For the Pielou evenness index (J) we used the formula

$$J = \frac{H}{\ln(N)},$$

in which H represents the Shannon diversity index, and N the total number of taxa present.

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2.4 Statistics

Differences in soil physicochemical and biological properties were tested with an ANOVA for repeated measures (rmANOVA), with the replicates within a site taken as repeated measures from the same object. We tested correlations between soil parameters with Pearson's correlation test. All data were log-transformed to obtain homogeneity of variances. Statistical analyses were carried out using SPSS (20.0.0) and R (2.15.2; R Core Team, 2012).

3 Results

3.1 Soil physicochemical measurements

To quantify soil structure, we measured the water stability of soil aggregates (WSA). The intensively cultivated olive orchard had a significantly lower WSA than the extensively used olive orchard and pasture ($p = 0.005$, Fig. 1a).

Dynamics of soil organic matter and N cycling are biologically mediated soil quality indicators. Total organic carbon (TOC, Fig. 1b) and total nitrogen (TN, Fig. 1c) were both greatest in the extensively used orchard, smallest in the intensively cultivated orchard and intermediate in the pasture ($p = 0.04$ and $p = 0.003$, respectively, Table 2). As a result, TOC and TN were strongly positively correlated with each other (Pearson correlation test, $r = 0.97$, $p < 0.001$). The pool of labile C, measured as HWC, showed the same differences as TOC and TN, and was smallest in the intensively cultivated orchard ($p = 0.045$). No differences in PMN ($p = 0.475$) and the total C : N ratio of the soil (calculated as TOC : TN) were found (Table 2). The C : N ratio of the labile organic matter (calculated as HWC : PMN), however, was larger in the extensively used olive orchard than in the two other sites ($p = 0.042$). C mineralisation rate and especially N mineralisation rate were greatest in the pasture site ($p = 0.048$ and $p = 0.011$, respectively, Table 2).

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To identify the relation of abiotic soil parameters with soil structure formation, we tested the correlations of WSA with TOC, HWC and clay content. WSA was positively correlated with TOC and HWC ($r = 0.89$, $p = 0.001$, and $r = 0.80$, $p = 0.012$, respectively) and clay content ($r = 0.82$, $p = 0.007$).

3.2 Soil biological measurements

Based on presence-absence data of the soil organisms, we constructed soil food web diagrams for the three sites (Fig. 2). These diagrams of the three sites were highly similar and most of the trophic groups were present in all sites. A few trophic groups were missing in some of the sites: Symphyla and fungivore mites were both missing in the intensively cultivated orchards, herbivore collembolans were missing in the extensively used orchards, whereas nematovore mites were only present in the extensively used orchards (Table 3).

Analysis of the soil community as a whole showed the following statistically significant differences between the sites. Total soil biomass was greatest in the intensively cultivated olive orchard, followed by the pasture and smallest in the extensively used olive orchard ($p = 0.024$, Table 3). Bacterial biomass was greatest in the intensively cultivated olive orchard, followed by the pasture and smallest in the extensively used olive orchard ($p = 0.003$, Fig. 1c). Fungal biomass followed the same trend, but here differences were not statistically significant ($p = 0.095$, Fig. 1c). Bacterial activity (measured as labelled thymidine (Thy) and leucine (Leu) incorporation rates) showed the same pattern, and was smallest in the extensively used orchard ($p = 0.026$ and $p = 0.014$, respectively, Table 3). The ratio of fungal to bacterial biomass is indicative for C sequestration and disturbance, where a higher ratio indicates a higher C sequestration and lower disturbance. The ratio did not differ statistically significantly between the sites, although the data indicated a greater ratio in the extensively used orchard compared to the intensively cultivated orchard (Table 3). Soil pH is known to influence microbial activity, but it was not significantly correlated with Thy and Leu ($p = 0.070$ and $p = 0.141$, respectively). To identify the role of microbial biomass in soil structure for-

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the diversity measures, no statistically significant differences were found however, not in the Shannon diversity index nor the Pielou evenness index.

4 Discussion

The aim of the present study was to investigate ecological soil quality in southern European soils that are at risk of potential soil degradation and desertification. In addition, we identified whether the currently used ecological soil quality parameters are adequate to assess soil quality under harsh conditions.

4.1 Soil aggregate formation, soil organic matter, and soil nutrient cycling

Soil aggregate formation is an important index for soil quality. The intensively cultivated olive orchard had a much lower aggregate water stability than the extensively used olive orchard and the pasture. This is consistent with literature, which shows that tillage negatively affects soil aggregate stability (Beare et al., 1994). Soil structure (aggregate stability) was strongly positively correlated to C content and clay content in our study, which is also consistent with literature (Six et al., 2006; Wright et al., 2007). In contrast to our expectation, we found a negative correlation between fungal biomass and aggregate stability. Several studies have shown that fungal biomass and activity enhance aggregate stability (Beare et al., 1997; Bossuyt et al., 2001). Both hyphae and exudates produced by fungi (polysaccharides) are assumed to serve as bonding material (De Gryze et al., 2005). Fungal products, compared to bacterially derived products, are more chemically resistant to decay and preferentially protected from decomposition through interactions with clay and soil aggregates (Simpson et al., 2004). The negative correlation resulted from the extensively used orchard, which had the highest aggregate stability, and the lowest bacterial and fungal biomass and activity. We think that the low water availability limited microbial activity mostly at the extensively used orchard. The limited water availability simultaneously caused physical changes such as swelling

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and shrinking of the clay-rich soils. Physical factors therefore might have been more important than microbial factors in the build-up and stability of soil aggregates in this system.

All parameters related to soil organic matter contents, such as TOC, TN and HWC showed highest values at the extensively used olive orchard, while C and N mineralisation rates were both highest at the pasture. The TOC and TN contents in our study were in the same order of magnitude as contents reported from less harsh environments (Culman et al., 2010; Holtkamp et al., 2011). The lower C and N contents in the intensively cultivated orchard might have been due to leaf litter removal and soil tillage in this site, in combination with the lower clay content. The absence of these activities in the extensively used orchard may have led to an accumulation of plant and olive residues in a relatively undisturbed upper soil horizon, resulting in relatively high amounts of organic C and N. The litter of olive trees is lignin-rich (30.4%), with a high C : N ratio (33.0) and is therefore thought to be difficult to decompose (Canali and Benedetti, 2006; Gallardo and Merino, 1993). This substrate generally favours slow fungal over fast bacterial activity, because fungi are assumed to be better able to degrade lignin-rich substances (Bossuyt et al., 2001). We found indications for a higher fungal to bacterial biomass ratio in the extensively used olive orchard, although differences were not statistically significant. In addition to substrate quality, soil pH is known to affect microbial activity; higher pH is thought to enhance bacterial activity (Bååth and Anderson, 2003) and to decrease the ratio of fungal to bacterial activity (Blagodatskaya and Anderson, 1998). We did indeed find the lowest bacterial activity in the extensively used orchard, which also had the lowest pH (5.4, in comparison with 5.9 at the pasture and 6.9 at the intensively cultivated orchard).

4.2 Soil as habitat for soil organisms

All microbial parameters, i.e. the biomasses of bacteria and fungi and the two indicators for microbial activity, showed statistically significant minimum values at the extensively used olive orchard. The microbial biomass in the extensively used olive orchard was

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with 37 kg C ha^{-1} much lower than reported from less harsh environments (de Ruiter et al., 1993; Holtkamp et al., 2008), while the pasture (72 kg C ha^{-1}), and especially the intensively cultivated olive orchard (111 kg C ha^{-1}), reached values that are closer to values reported in literature. For example, Holtkamp et al. (2008) report 60–100 kg microbial C ha^{-1} for fields in transition from arable field to heathland in the Netherlands, while de Ruiter et al. (1993) report similar biomasses from arable fields in the Netherlands ($90\text{--}100 \text{ kg C ha}^{-1}$) and prairie soil in the USA (150 kg C ha^{-1}), but much higher values for arable fields in USA ($400\text{--}550 \text{ kg C ha}^{-1}$) and Sweden ($900\text{--}1300 \text{ kg C ha}^{-1}$) (all values correspond to 0–10 cm soil depth). Other studies provide higher microbial biomass levels ranging from 300 to $1300 \text{ kg C ha}^{-1}$ based on chloroform fumigation methods (e.g. Culman et al., 2010; Schnürer and Rosswall, 1987; Schröter et al., 2003), but values found using this method are not directly comparable to microscopic counting (Martens, 1995). The intensity of agricultural management at the intensively cultivated olive orchard including tillage and fertilisation, as well as soil pH and leaf litter composition, led to the expectation that we would find a lower fungal to bacterial biomass ratio, as indicator for C sequestration and disturbance, compared with the extensively used orchard and pasture. A lower ratio indicates a lower C sequestration and higher disturbance. We indeed found indications for a lower ratio in the intensively cultivated olive orchard, but the differences were not significant.

4.3 Microarthropod biomass and diversity

Total soil microarthropod biomass and taxonomic richness within the soil microarthropods have been proposed as biological soil quality indicators (Gardi et al., 2009; Parisi et al., 2005), but the suitability of these parameters has not yet been tested on soils under harsh conditions. Total microarthropod biomass in our systems, especially in the intensively cultivated olive orchard, was with $0.06\text{--}0.72 \text{ kg C ha}^{-1}$ lower than biomasses of $0.5\text{--}3.8 \text{ kg C ha}^{-1}$ reported from less harsh arable systems (de Ruiter et al., 1993; Holtkamp et al., 2011). In our sites, microarthropod taxonomic richness strongly in-

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creased along with microarthropod biomass from the intensively cultivated olive orchard, to the extensively used olive orchard, to the pasture. Microarthropod taxa richness was higher in our study than reported from semi-arid croplands in central Spain (Kautz et al., 2006), comparable to the values found by Tsiafouli et al. (2005) in pine forests in Greece, and in the lower range of the values found on farms in Iceland and Austria (van Leeuwen et al., 2015). The higher richness we found in the pasture, compared to the olive orchards, confirms findings in Mediterranean Spain showing the highest richness in Oribatid mite communities in pastures and forests in comparison with cropland (Arroyo and Iturrondobeitia, 2006). This pattern of increasing microarthropod biomass and taxonomic richness could be related to a lower disturbance of the topsoil in the pasture, for which the microarthropods are known to be very sensitive (Wardle, 1995), but could also be related to soil moisture availability. Soil moisture availability in our sites increased with elevation. This was caused by the increasing average precipitation and decreasing average temperature (Table 1), hence decreasing evaporation, leading to a high soil moisture content in the pasture as compared to the olive orchards. Also Tsiafouli et al. (2005) reports an increasing species richness and diversity of soil microarthropods with an increase in water availability in an experimental setup in pine forests in Greece.

We found statistically significant differences in taxa richness, but not in the Shannon diversity index (SDI), nor in Pielou evenness. Kautz et al. (2006) finds comparably low SDI values in croplands in central Spain, despite a lower taxa richness and microarthropod abundance. It appears that taxonomic richness of microarthropods is able to differentiate between land management practices, hence is useful as an indicator of ecological soil quality, whereas the SDI may separate harsh sites from other sites, but is not sensitive enough to detect differences between different land management practices under harsh conditions.

from less affected areas. In this way they may also be suitable as ecological indicators for soil degradation. The ratio of fungal to bacterial biomass, which is frequently proposed as indicator for C sequestration and disturbance, did not show a clear pattern in our study, probably because at our sites many factors may have affected this ratio, such as tillage, pH and leaf litter composition, and might therefore be less suitable as indicator for soil quality under harsh conditions.

Acknowledgements. This research was funded by the EU FP7-ENV-2009 Project SoilTrEC “Soil Transformations in European Catchments” (Contract no. 244118). This research was also supported by the research program KB IV “Innovative scientific research for sustainable green and blue environment” funded by the Netherlands Ministry of Economic Affairs, Agriculture and Innovation, and carried out by Wageningen University and Research Centre.

We thank An Vos, Meint Veninga, Popko Bolhuis and Tamas Salanki for technical assistance. Wim Dimmers, Gerard Jagers and Jeffrey Newton are acknowledged for counting and identifying microarthropods.

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**Table 1.** Characteristics of the Koiliaris Critical Zone Observatory (CZO) at the three different sites (I = intensively cultivated olive orchard, E = extensively used olive orchard, P = pasture).

Site	I	E	P
Land use type	Intensive olive orchard	Extensive olive orchard	Pasture
Tillage	yes	no	no
Fertilization	yes	no	no
Litter removal	yes	no	no
Grazing pressure	Not grazed	Grazed	Heavily grazed
Elevation	20 m	465 m	1065 m
Average rainfall	567 mm	915 mm	1335 mm
Average temp.	19 °C	18 °C	14 °C

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Table 2. Soil physicochemical properties and biologically mediated processes at three different sites in the Koiliaris Critical Zone Observatory (Crete, GR) (I = intensively cultivated olive orchard, E = extensively used olive orchard, P = pasture). Values represent mean and standard deviation (between brackets). The p values represent significance levels from an ANOVA for repeated measures, where the superscript letters denote statistically significant differences between sites, and number of ** denotes statistical significance level (*: $p < 0.05$, **: $p < 0.01$). All measurements were done in the topsoil (0–10 cm).

Site	I	E	P	rmANOVA (p value)
Soil moisture (%)	4.09 (2.21) ^a	9.83 (1.26) ^b	14.47 (0.55) ^c	0.006 **
pH-H ₂ O	6.9 (0.96)	5.4 (0.41)	5.9 (0.11)	0.056
Clay content (%)	5.1 (0.43) ^a	26.6 (10.5) ^b	24.6 (9.2) ^b	0.002**
CaCO ₃ (g kg ⁻¹)	22.2 (18.2)	1.78 (0.59)	1.39 (0.25)	0.086
WSA (%) ¹	38.4 (5.4) ^a	77.0 (7.4) ^b	67.1 (5.4) ^b	0.005**
TOC (kg ha ⁻¹) ²	21 670 (2662) ^a	59 926 (8444) ^c	39 991 (6319) ^b	0.004**
HWC (kg ha ⁻¹) ³	390 (112) ^a	952 (406) ^b	700 (28) ^b	0.045*
Total N (kg ha ⁻¹)	1557 (249) ^a	4246 (363) ^c	2843 (421) ^b	0.003**
PMN (kg ha ⁻¹) ⁴	81.26 (22.97)	66.73 (47.43)	101.8 (20.38)	0.475
TOC : Total N	13.98 (0.54)	14.14 (2.02)	14.07 (0.58)	0.994
HWC : PMN	4.80 (0.14) ^a	20.29 (13.48) ^b	7.03 (1.18) ^a	0.042*
C min (kg ha ⁻¹ r ⁻¹) ⁵	2526 (1131) ^a	2418 (103) ^a	2818 (1080) ^b	0.048*
N min (kg ha ⁻¹ yr ⁻¹) ⁶	24.34 (18.31) ^a	54.11 (20.62) ^a	172.9 (93.00) ^b	0.011*

¹ Percentage of water stable aggregates of 1–3 mm; ² Total soil organic carbon; ³ Hot-water-extractable carbon;

⁴ Potential mineralisable nitrogen; ⁵ Carbon mineralisation rate; ⁶ Nitrogen mineralisation rate

Table 3. Biological parameters at the three different sites in the Koiliaris Critical Zone Observatory (Crete, GR) (I = intensively cultivated olive orchard, E = extensively used olive orchard, P = pasture): biomasses (in kg C ha⁻¹) of the trophic and taxonomic groups in the soil food webs, bacterial activity and microarthropod diversity. Values represent mean and standard deviation (between brackets), nd: not detected. The *p* values represent significance levels from an ANOVA for repeated measures, where the superscript letters denote statistically significant differences between sites, and number of ** denotes statistical significance level (*: *p* < 0.05, **: *p* < 0.01). All measurements were done in the topsoil (0–10 cm).

Site	I	E	P	rmANOVA (<i>p</i> value)
Bacteria	63.31 (11.95) ^b	14.60 (3.79) ^a	38.17 (5.83) ^b	0.003**
Thy (pmol g ⁻¹ h ⁻¹) ¹	5.52 (3.56) ^b	0.77 (0.46) ^a	7.27 (0.98) ^b	0.026*
Leu (pmol g ⁻¹ h ⁻¹) ²	229.3 (89.78) ^b	86.26 (21.22) ^a	294.4 (45.02) ^b	0.014*
Fungi	50.19 (10.82)	24.94 (11.73)	34.70 (10.35)	0.095
Fungal : bacterial biomass ratio	0.79 (0.05)	1.75 (0.87)	0.91 (0.23)	0.121
Flagellates	0.65 (0.32)	0.51 (0.16)	0.32 (0.26)	0.52
Amoebae	23.34 (22.30)	6.39 (4.10)	9.45 (3.22)	0.587
Fungivore Nematodes	0.05 (0.02)	0.007 (0.006)	0.04 (0.02)	0.148
Bacterivore Nematodes	0.10 (0.03)	0.03 (0.005)	0.06 (0.06)	0.241
Herbivore Nematodes	0.18 (0.02) ^b	0.01 (0.006) ^a	0.28 (0.12) ^b	0.015*
Omnivore Nematodes	0.23 (0.17)	0.12 (0.04)	0.10 (0.14)	0.620
Predaceous Nematodes	0.09 (0.09)	0.03 (0.03)	0.08 (0.06)	0.564
Total nematode biomass	0.65 (0.22)	0.20 (0.06)	0.57 (0.33)	0.152
Enchytraeids	0.003 (0.006)	0.03 (0.06)	0.003 (0.006)	0.545
Herbivore mites	0.0002 (0.0003)	0.0003 (0.0003)	0.0008 (0.0007)	0.329
Herbofungivore mites	0.0001 (0.0001)	0.002 (0.001)	0.008 (0.007)	0.152
Fungivore mites	nd	0.003 (0.004)	0.02 (0.02)	0.174
Nematovore mites	nd	0.002 (0.001)	nd	0.112
Omnivore mites	0.05 (0.03)	0.17 (0.24)	0.31 (0.22)	0.374
Predaceous mites	0.0005 (0.0008) ^a	0.003 (0.004) ^a	0.08 (0.04) ^b	0.016*
Herbivore collembola	0.001 (0.002)	nd	0.001 (0.002)	0.689
Herbofungivore collembola	0.002 (0.003)	0.006 (0.008)	0.05 (0.07)	0.426
Fungivore collembola	0.0006 (0.001)	0.01 (0.02)	0.14 (0.10)	0.057
Symphyla	nd	0.03 (0.06)	0.03 (0.03)	0.418
Total biomass	137.0 (16.99) ^b	46.20 (6.01) ^a	82.98 (10.63) ^{ab}	0.024*
Total microarthropod biomass	0.06 (0.02)	0.23 (0.21)	0.62 (0.47)	0.133
Microarthropod taxa richness	6.67 (2.52) ^a	15.33 (7.51) ^a	27.67 (1.53) ^b	0.037*
Shannon <i>H</i> index	1.25 (0.50)	1.35 (0.77)	2.44 (0.18)	0.281
Pielou evenness <i>J</i>	1.52 (0.34)	1.12 (0.51)	1.69 (0.12)	0.322

¹ bacterial activity: Thymidine incorporation rate; ² bacterial activity: Leucine incorporation rate

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Table A1. Biomasses (kg C ha^{-1}) of the microarthropod taxa in the soil food web at three different sites on Crete, Greece (I = intensively cultivated olive orchard, E = extensively used olive orchard, P = pasture). Trophic groups: omnivorous mites (Omni), fungivorous mites (Fumi), nematovorous mites (Nemi), predatory mites (Prmi), herbivorous mites (Hemi), herbofungivorous mites (HFmi), herbofungivorous collembolans (HFco), fungivorous collembolans (Fuco) and Symphylans (Symp). Numbers represent mean and standard deviation (between brackets), measured in the topsoil (0–10 cm).

Site		I	E	P
Acari				
Astigmata	Omni	0.0003 (0.0005)	0.0025 (0.0044)	0.0021 (0.0037)
<i>Tyrophagus</i>	Omni	0.0018 (0.0031)	0.2417 (0.3952)	
Mesostigmata	Omni			0.0007 (0.0012)
<i>Epicriopsis</i>	Fumi		0.0001 (0.0002)	
<i>Hypoaspis</i>	Prmi	0.0005 (0.0008)	0.0005 (0.0008)	0.0087 (0.0076)
<i>Leiioseius</i>	Prmi			0.0069 (0.0088)
<i>Macrocheles</i>	Prmi			0.0045 (0.0079)
<i>Pachylaelaps</i>	Prmi			0.0045 (0.0079)
Rhodacaridae	Prmi			0.0110 (0.0129)
Zercon	Nemi		0.0009 (0.0008)	
Oribatida	Omni		0.0213 (0.0097)	0.0400 (0.0542)
<i>Aphelacarus acarinus</i>	HFmi			
Brachychthoniidae	HFmi	0.0001 (0.0001)	0.0005 (0.0008)	0.0014 (0.0016)
Ceratozetidae	Omni		0.0008 (0.0014)	0.0103 (0.0104)
<i>Cosmochthonius</i>	Hemi	0.0002 (0.0003)	0.0003 (0.0002)	0.0008 (0.0007)
Damaeidae	Fumi		0.0003 (0.0003)	0.0005 (0.0009)
<i>Hermanniella</i>	HFmi			0.0005 (0.0009)
<i>Licnodamaeus pulcherrimus</i>	HFmi		0.0011 (0.0008)	0.0002 (0.0003)
Mycobatidae	HFmi			0.0024 (0.0034)
Nanhermanniidae	HFmi		0.0005 (0.0009)	
Oppliidae	Omni		0.0005 (0.0009)	0.0200 (0.0271)
Oribatellidae	HFmi			0.0008 (0.0006)
Pelopsidae	Fumi			0.0003 (0.0006)
<i>Rhinoppia</i>	Fumi		0.0021 (0.0030)	
<i>Tectocephesus</i>	Omni			0.0275 (0.0110)
Prostigmata				
Alicorhagiidae	Omni	0.0136 (0.0058)		
Erythraeidae	Prmi		0.0005 (0.0009)	
<i>Eupodes</i>	Omni		0.0013 (0.0023)	0.0080 (0.0121)
<i>Microtydeus</i>	Omni	0.0090 (0.0020)	0.0125 (0.0084)	0.0942 (0.0837)
<i>Nanorchestes</i>	Omni			0.0119 (0.0154)
Paratydeidae	Prmi		0.0015 (0.0026)	0.0287 (0.0151)
<i>Pyemotes</i>	Prmi			0.0072 (0.0068)
<i>Pygmephorus</i>	Fumi		0.0010 (0.0010)	0.0177 (0.0188)

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Table A1. Continued.

<i>Rhagidia</i>	Prmi		0.0010 (0.0009)	0.0041 (0.0042)
<i>Scutacarus</i>	Ommi		0.0041 (0.0064)	0.0212 (0.0200)
<i>Speleorchestes</i>	Ommi	0.0013 (0.0012)		0.0182 (0.0225)
Stigmaeidae	Prmi			0.0014 (0.0024)
<i>Tarsonemus</i>	Ommi	0.0006 (0.001)	0.0018 (0.0030)	0.2529 (0.1300)
Tydeidae	Ommi	0.0516 (0.0439)	0.0003 (0.0004)	0.0032 (0.0038)
Collembola				
Entomobryomorpha				
<i>Lepidocyrtus</i>	HFco		0.0011 (0.0087)	0.0188 (0.0214)
<i>Lepidocyrtus lignorum</i>	HFco		0.0050 (0.0087)	
Poduromorpha				
<i>Friesea</i>	Fuco			0.0096 (0.0167)
<i>Hypogastrura</i>	Fuco		0.0046 (0.0030)	
<i>Mesaphorura</i>	Fuco			
Onychiuridae	HFco	0.0017 (0.0030)		0.0289 (0.0501)
<i>Onychiurus</i>	Fuco	0.0006 (0.001)		0.0967 (0.0670)
<i>Paratullbergia</i>	Fuco		0.0079 (0.0136)	0.0084 (0.0110)
Symphyleona				
Sminthuridae	Heco	0.0011 (0.0020)		0.0014 (0.0024)
Protura	Fuco		0.0005 (0.0009)	0.0251 (0.0287)
Symphyla	Symp		0.0336 (0.0582)	0.0250 (0.0284)

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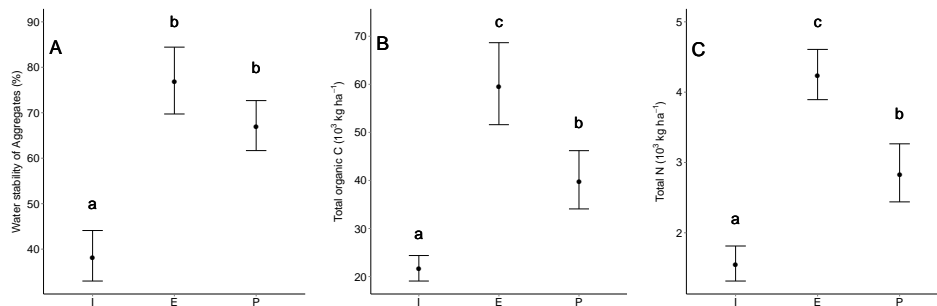


Figure 1. Water stability of aggregates of 1–3 mm (%) **(A)**, total organic C in 10^3 kg ha^{-1} **(B)**, and total N in 10^3 kg ha^{-1} **(C)**, for the three land use types in the Koiliaris Critical Zone Observatory (Crete, GR) (I = intensively cultivated olive orchard, E = extensively used olive orchard, P = pasture), points represent back transformed means, error bars depict standard deviations, and small letters in the graphs (a–c) represent significant differences between sites.

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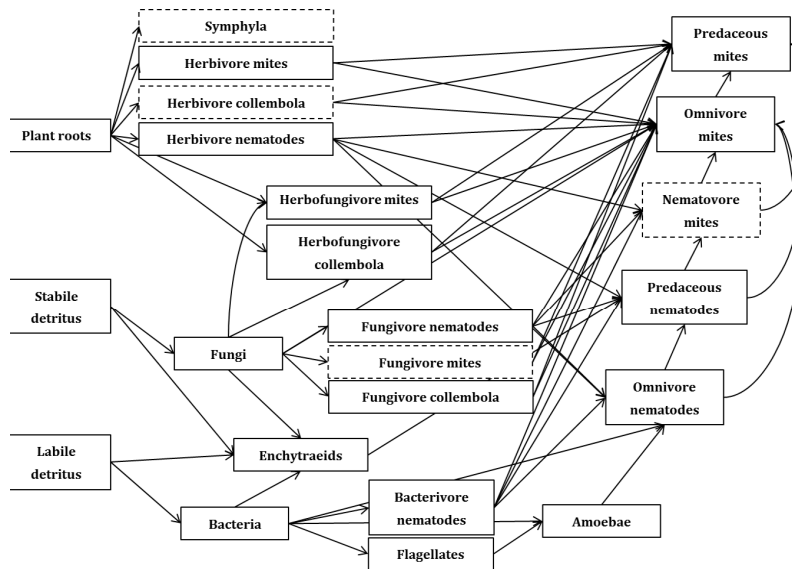


Figure 2. Soil food web diagram representative for all three land use types in the Koiliaris Critical Zone Observatory (Crete, GR). Boxes represent the presence of trophic groups in the soil food web, arrows represent feeding interactions based on diet information (the arrow points from the group eaten to the group that eats). Groups with drawn boxes were present at all sites, groups with dashed boxes were only present at some sites.

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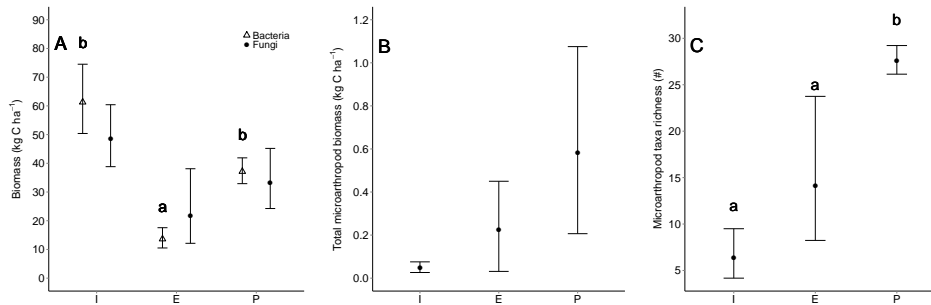


Figure 3. Bacterial (open triangles) and fungal biomass (closed points) in kg C ha^{-1} **(A)**, total microarthropod biomasses in kg C ha^{-1} **(B)**, and microarthropod taxonomic richness **(C)**, for the three land use types in the Koiliaris Critical Zone Observatory (Crete, GR) (I = intensively cultivated olive orchard, E = extensively used olive orchard, P = pasture), points represent back transformed means, error bars depict standard deviations, and small letters in the graphs (a–c) represent significant differences between sites.

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