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Investigating the influence of land-use change on soil microbial parameters in adjacent natural forests and agricultural fields on the Galápagos Islands

Masterarbeit

von

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der mich leider nicht mehr in meinem Leben begleiten kann,
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und es vergeht nicht ein Tag, an dem ich nicht an dich denke.
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Kurzfassung

Hinter der Kulisse des Weltnaturerbes, den Galapagos-Inseln, laufen die Dinge nicht immer so wie die traumhaften Bilder es uns suggerieren. Die Bewohner der Inseln stützen sich sehr auf den Tourismus, während parallel die Nachfrage nach Nahrung steigt. Um den Einfluss der Landwirtschaft auf bodenmikrobiologische Parameter zu untersuchen, wurden Bodenproben von landwirtschaftlichen Flächen (Dauer der landwirtschaftlichen Nutzung: ca. 5 bis 15 Jahre) und benachbarten Wäldern des Galapagos-Nationalparks auf zwei der Inseln (Santa Cruz und San Cristóbal) entnommen. Das experimentelle Design erlaubt uns, den Einfluss der Landnutzung auf Parameter wie Substrat-induzierte Respiration (SIR), den mikrobiellen Biomasse-Kohlenstoff (C_{mic}), -Stickstoff (N_{mic}) und -Phosphor (P_{mic}), die potentielle Aktivität verschiedener extrazellulärer Enzyme (*z.B.* Exoglucanase-, β-Glucosidase-, Exochitinase-, Protease-, Urease- und Phenoloxidase Aktivität), p*H*, C_{org}, DOC und Ammonium- bzw. Nitratgehalt zu untersuchen. Die Ergebnisse zeigten, dass der Nitratgehalt in landwirtschaftlichen Böden höher war, während der Ammoniumgehalt in Böden aus dem Wald höher war. C_{mic}, N_{mic} und P_{mic} waren in den landwirtschaftlich genützten Böden um ca. 60-70% geringer als in den Waldböden des Nationalparks. Auch SIR und die potentielle Aktivität der verschiedenen Enzymklassen waren in den Waldböden höher. Betrachtet man die mikrobielle Biomasse und SIR bezogen auf C_{org} war ebenfalls eine Abnahme in landwirtschaftlichen Böden festzustellen. Die spezifische Aktivität der Enzymklassen (bezogen auf C_{mic} und C_{org}) hingegen, wies Großteils keine signifikanten Unterschiede auf, bzw. waren diese abhängig vom jeweiligen Standort. Die Ergebnisse dieser Masterarbeit zeigen, dass in den beiden Untersuchungsstandorten die landwirtschaftliche Nutzung der Böden bereits nach wenigen Jahren zu deutlichen Veränderungen bodenmikrobiologischer Parameter geführt hat.

Abstract

Behind the scenes of the World Heritage for biodiversity, the Galapagos archipelago, things don´t always look as expected. The people rely strongly on tourism and at the same time the demand for food is increasing. To analyse the effects of agricultural land use, soil samples were taken from agricultural fields (duration of agricultural land use: ca. 5 to 15 years) and adjacent natural forests on two of the islands (Santa Cruz and San Cristóbal). The experimental design allows us to investigate the influence of land use on parameters like substrate induces respiration (SIR), microbial biomass carbon (C_{mic}), nitrogen (N_{mic}) and phosphorus (P_{mic}), the activity of different extracellular enzymes (*i.e.* exoglucanase, β-glucosidase, exochitinase, protease, urease, phenoloxidase), p*H*, C_{org}, DOC as well as ammonium and nitrate contents. The results show that the nitrate content was significantly higher in soils from the agricultural sites, whereas ammonium was higher in soils from the natural forest. C_{mic}, N_{mic} and P_{mic} in agricultural soils were about 60-70% lower compared to the soils from natural forest. In addition, SIR and the enzyme activities were higher in soils from the natural forest. Also, microbial biomass and SIR related to C_{org} showed a clear decrease in soils from agricultural fields. The specific enzyme activities (in relation to C_{mic} and C_{org}) tended to show no significance or their contents were dependent on the site, respectively. The results of this master's thesis show that on both investigated sites, few years of agricultural land use have led to clear changes in soil microbiological parameters.

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1. Introduction

The Galapagos Islands are located at the equator, 1,100 km west of the Ecuadorian coast and consist of 123 islands that differ in soil age due to volcanic activity (SNELL, STONE, AND SNELL 1996). The youngest soils are located on the western islands and the oldest on the eastern islands, so that the age increases from west to the east due to Nazca tectonic plate drifting (SIMKIN 1984). LARUELLE (1966) distinguished five soil zones on the windward side of Santa Cruz, whose age is around 1.3 Ma (GEIST, HARPP, AND D'OUVILLE 2011) and San Cristobal, one of the oldest island, has Lixisols (detailed soil information is given in STOOPS, 2014). This master thesis draws its attention to the inhabited islands Santa Cruz and San Cristobal.

The Galapagos Islands were annexed by Ecuador in 1832 under the name “Archipiélago del Ecuador”. At the beginning, the islands were only used as penal settlement, but over time the effort was set to ensure the ownership via colonisation with mainland habitants (JACKSON 1993). The Census of 2010 revealed that 25,124 inhabitants live on the islands with a 3.3% annual growth rate. 61% of the population lives on Santa Cruz and 30% on San Cristobal (LEÓN AND SALAZAR 2013). Over the years, dramatical changes have occurred; in 1974, 41% of the people lived in rural areas whereas in 1998, 86% lived in port towns (EPLER 2007). Over time, the tourism sector has strongly increased, the annual visitors flow jumped from 41,000 in 1990 to 72,000 in 2000 and has reached its maximum in 2015 with over 224,755 visitors (CONSERVANCY 2016) per year. If this trend remains, 969,000 visitors will be expected to arrive in the year of 2031, meanwhile the number of inhabitants will increase to 118,000 (EPLER 2007). TAYLOR, HARDNER, AND STEWART (2009) found out, that due to migration real per capita income is stagnating, so that tourism will not be able to bring salvation. Thus, the Galapagos Islands had experienced conflicts between local inhabitants and conservation efforts and it will likely become more dramatic. The UNESCO placed the Galapagos on the List of World Heritage in Danger in 2007 (UNESCO 2007). About 97% of the area is national park and 3.3%, which equals approximately 236.5 km^2, for human settlements (WWF 2003).

On the Galapagos Islands agriculture is intensive due to increasing needs; farmers till their soils manually, but the inputs are high incl. irrigation, mineral and organic fertilizers and pesticide applications. Alone on Santa Cruz, 74% of forest in the humid zone was clear-cut, which resulted in 11,448 ha of land that is now being cultivated and on San Cristobal it is 7,892 ha (MIT 2008).

Considering all these issues, including the invasion of alien species, agriculture plays a key role. Due to the periodical variation of weather, like warm a rainy season from January until May and a cool season from June until December imports are dependent on the mainland (ITOW 2003). If we look at the situation on Santa Cruz, during the hot season, 69% of the fruits and 80% of the vegetables must be imported. In wet seasons the numbers decline to 8% and 10% respectively (BREWINGTON 2011). Tourism generates 43% of the gross domestic product, while agriculture decreased by 31.3% (UTRERAS ET AL. 2014). This indicates the trend of abandonment, where the economically active population decreases significantly (GUZMÁN AND POMA 2013). After the abandonment of fields alien species invade and from there they spread further to the neighboring national park. This is an important factor why 600 alien species had the opportunity to invade the island (FALCONI 2001). A study from 2011 showed that of the 22% of farmers who had abandoned their fields, 84% described invasive species as a threat and as a reason to move (BREWINGTON 2011). Further, a survey in Santa Cruz showed that 67% of the farmers use agrochemicals in any form. An interesting fact about this survey was, that farmers had little awareness what exactly is contained in the agrochemicals they apply, for crop protection, i.e. insecticides against ants (O'CONNOR ROBINSON, SELFA, AND HIRSCH 2018). How intensive agricultural use affects the soil microbiology on Galapagos is largely unknown. Previous studies report on mycorrhizal fungi (SCHMIDT AND SCOW 1986), microbial populations at Fumaroles (MAYHEW, CHILDERS, AND GEIST 2005) or ascomycetes yeast species (JAMES ET AL. 2015) and none of the studies investigated the influence of land-use change. The study of SCHMIDT AND SCOW (1986) determined the presence and distribution of vesicular-arbuscular mycorrhizal fungi in association with plants from different communities on Santa Cruz. MAYHEW, CHILDERS, AND GEIST (2005) examined microbial communities at six fumarole fields on Sierra Negra and Alcedo volcanoes to test how extreme

geochemical conditions affect microbial biodiversity. And JAMES ET AL. (2015) found a *Kazachstania* strain from a sample of rotten wood from the tree *Scalesia pedunculata* at Los Gemelos (Santa Cruz).

It is well known that microbial biomass C may be strongly reduced with a conversion from forest to agriculture. For example, a decrease of about 52% in microbial biomass C from adjacent National Park to agricultural fields was reported for Cilento e Vallo di Diano, at Stio, Province of Salome, Italy (SCOTTI, IOVIENO, AND ZACCARDELLI 2015). Also in northwest of the Cofre de Perote volcano (Veracruz, Mexico) along an altitudinal gradient between 2550 – 3500 meters above sea level, GAMBOA AND GALICIA (2011) observed a decrease in microbial biomass C in deforested areas. At Perote, a former *Pinus patula* forest which was transformed 50 years ago to croplands, they observed a decrease in microbial biomass C about 88% and at Los Pescados a former *Pinus montezumae* forest which was transformed 45 years ago to croplands, a decrease about 44%.

While the effects of land use on enzyme activities is not as straightforward, different researchers suggest a very contradictory picture, concerning agricultural practices. For example, organic manure in comparison to mineral NPK fertilizer, was described to increase the microbial parameters like urease activity in all crop types by about 28-67% and alkaline phosphatase about 40-92% (KANDELER, STEMMER, AND KLIMANEK 1999), whereas high N inputs (poor quality) decreases the microbial biomass C about 17% compared to moderate N inputs (good quality) (SCHIPPER AND SPARLING 2000). On the other hand, there is evidence that inorganic fertilizers may inhibit enzyme synthesis (OLANDER AND VITOUSEK 2000) or increase it by stimulating plant growth and secretion of enzymes by roots (LYNCH AND PANTING 1980). Beside organic and inorganic fertilizer use, also the application of agrochemicals such as pesticides, can affect enzyme activities. In particular, the application of glyphosate for weed control was reported to decrease microbial biomass C by about 30-35%, urease 50-58%, β-glucosidase 28% and phosphatase 29-45% (TEJADA, 2009).

There is little knowledge on the effects of land-use change on microbial parameters on the Galapagos Islands. This is to our knowledge the first study that investigates the effect of land use (agricultural vs. natural forest Nation Park) on enzyme activities in this respective area.

In particular, this master's thesis aims to investigate the influence of land-use change from natural forests to agricultural use on soil microbiology. Properties like ammonium and nitrate content, enzyme activities of exoglucanase, β-glucosidase, exochitenase, phosphatase, protease, phenoloxidase, urease, microbial biomass C_{mic}, N_{mic}, P_{mic} and SIR were analyzed.

2. Materials and Methods

2.1 Sampling sites

Soil samples were collected from two sites, one on the island San Cristobal in Cerro Verde (13th September 2016) and one on Santa Cruz in El Cascajo (16th September 2016), for more details see Table 1. On each site, samples were taken from two different land-use forms, the Galapagos National Park forest and adjacent agricultural fields. On each site, four plots with a size of 5 x 5 m were established per land-use form, and five sub- samples from a depth of 0-10 cm were taken and composited on each plot. The samples were sieved (< 2 mm) under field moist conditions, transferred into plastic bags and frozen at -20° C. Samples were transported on ice by plane to the Austrian laboratory and stored in the freezer prior to further analysis.

2.2 Site description

Site description of the sampling locations is given in Table 1. The closest weather station to El Cascajo is Bellavista (0°41´46.53´´S, 90°19´37.20´´) with a mean annual temperature of 22.5°C while for Cerro Verde the weather station is not as closely located (calculated according to TRUEMAN AND D'OZOUVILLE *2010)*.

The fields in Cerro Verde have been cultivated for 15 years, dominantly with maize, yuca, beans and vegetables. Soil cultivation is via hoe, watering with drip irrigation, mineral NPK fertilisation since 8 years and pesticide use since 10 years. The vegetation of the adjacent national park area is composed mainly of *Hippomane mancinella* (native) and in lower abundance *Rubus niveus* (invasive) and *Lantana camara* (invasive).

Table 1. Site description and soil classification of El Cascajo and Cerro Verde.

Site	Elevation (m)	GPS coordinates	Soil information	Soil type	Stones at surface (%)
El Cascajo	260	LAT/LONG: S0 40.274 W90 15.759	10-20 cm A-horizon, below lava	Leptosol	50
Cerro Verde	220	LAT/LONG: S0 53.728 W89 25.845	Tephra deposit with profound soil depth (>100 cm)	Luvisol	0

In El Cascajo, the fields have been cultivated with vegetables for 4 years and before that it was an extensive coffee plantation. Soil cultivation is via hoe, watering by hand with brackish water, mineral fertilisation and poultry manure and common usage of pesticides. The vegetation of the national park area is comprised of the dominant species *Scalesia pedunculata* (endemic), *Psidium galapageium* (endemic), *Zanthoxylum fagara* (native), *Cestrum auriculatum* (invasive) and *Cedrela odorata* (invasive). There is no available data for precipitation, but the sites are located at the bottom of the humid zone.

In Table 2, the physical and chemical properties are shown. To determine soil bulk density, undisturbed soil samples were taken with cylinders (diameter: 8 cm, height: 5 cm), oven-dried and weighed. Total carbon and nitrogen (N_{tot}) were quantified by dry combustion (TABATABAI AND BREMNER 1983), and carbonate was measured gas-volumetrically (SOIL SURVEY STAFF 2004). Organic carbon (C_{org}) was calculated as the difference of total and carbonate carbon. P and K were extracted with the Mehlich-3 method (MEHLICH 1984) and measured by inductively coupled plasma atomic emission spectroscopy (ICP-AES). Cation exchange capacity (CEC) was estimated by summation of Mehlich-3-extractable basic cations plus exchangeable acidity (NGEWOH, TAYLOR, AND SHUFORD 1989).

Table 2. Main properties of the soils under different types of land use (National Park, NP and agricultural, Agri) and sites; values given are mean values ± standard error.

	El Cascajo		Cerro Verde	
	NP	Agri	NP	Agri
Water content (vol %)	**45.87*** ±0.74	42.25 ±1.07	**31.78*** ±1.26	27.07 ±0.34
p*H* $CaCl_2$	6.62 ±0.17	6.28 ±0.16	6.59 ±0.05	6.69 ±0.07
Bulk density (g/cm^3)	0.81 ± 0.04	0.85 ±0.02	0.94 ±0.02	**1.04*** ±0.03
C_{org} (%)	12.88 ±1.43	11 ±1.86	**7.33*** ±0.22	4.58 ±0.41
N_{tot} (%)	1.13 ±0.09	1.27 ±0.33	**0.59*** ±0.01	0.40 ±0.04
C_{org} / N_{tot}	11.4 ±0.76	9.3 ±0.83	12.5 ±0.43	11.4 ±0.41
P (mg/kg)	18 ±2.45	18.75 ±2.95	19.75 ±1.11	15.25 ±1.97
K (mg/kg)	**1.55*** ±0.03	1.15 ±0.10	3.68 ±0.44	2.65 ±0.09
CEC (meq/100g)	43.90 ±1.72	43.13 ±1.29	21.68 ±0.33	19.90 ±0.66

For each site, the asterisk (*) indicates that the mean value is significantly higher (P<0.05) for the respective land use. The bold written number point out significant values.

2.3 Soil acidity – p*H* Value and water content

The potential acidity was measured in a 0.01 M $CaCl_2$ solution. 2.0 g of frozen soil was put in a 50 ml beaker and 25 ml 0.01 M $CaCl_2$ solution was added. The solution was measured with a calibrated p*H*-meter (Mettler Toledo SG23). The sieved soil samples were oven dried for 24 hours at 105°C to determine the water content (SCHINNER et al. 1993).

2.4 Mineral nitrogen (N_{min}), chloroform fumigation extraction (CFE) for C_{mic}, N_{mic} and P_{mic} determination and dissolved organic carbon (DOC)

The frozen soil samples were gently thawed at 4°C over-night prior to chloroform fumigation extraction (CFE). Fumigated and non-fumigated soil samples were split into two subsamples, and transferred into plastic bottles. While one subsample (fumigated and non-fumigated) was extracted with 1 M KCl in a 1:10 w/v ratio for determination of C_{mic} and N_{mic}, the other subsample was extracted with 0.5 M $NaHCO_3$ pH of 8.5 (for P_{mic}). Plastic bottles were shaken on a horizontal shaker for 60 min and subsequently filtrated through nitrogen-free filter papers (Brand, Wertheim, Germany).

Aliquots of filtrates, from non-fumigated samples were transferred into cryo vials for NH_4 and NO_3 analysis (see section 2.4.1). All filtrates were stored in the freezer at -20°C prior to further analyses. Fumigated and non-fumigated samples were acidified with H_2SO_4 to remove remaining inorganic C, and then measured with an automated C_{org} /TN analyzer (C_{org} -V CPHE200V, linked with a TN-unit TNM-1 220 V, Shimadzu Corporation, Kyoto, Japan) according to (FERRETTI ET AL. 2018). Dissolved organic C (DOC) and extractable total nitrogen (ETN) was calculated from non-fumigated samples. For microbial biomass carbon (C_{mic}) and microbial biomass nitrogen (N_{mic}) no correction factor, according to BROOKES ET AL. (1985) was applied. To determine P_{mic} a digestion was conducted according to TIESSEN AND MOIR (1993) and the following determination based on VORONEY, BROOKES, AND BEYAERT (2008). Briefly, the $NaHCO_3$ extracts were treated with acid persulfate reagent mix in equal amounts in a 6 ml glas vial and capped prior to digestion in the autoclave at 120°C for 60 minutes. The persulfate reagent mix solution was prepared as follows, 12.5 g $K_2S_2O_8$ and approx. 150 ml Milli-Q water were added to a 250 ml flask and 15.5 ml of concentrated H_2SO_4 were added slowly (TIESSEN AND MOIR 1993). Phytate was used as a standard for P_{org} and KH_2PO_4 was used for P_{inorg} standards; they were treated as samples and used for further calibration purpose in the range of 0 ppm to 4 ppm. Buffer, digested samples, P_{org} and P_{inorg} –standards were pipped into clear microtiter plates. Phosphate was measured by using the molybdate blue method and colorimetric detection conducted at a wavelength of 712 nm with the plate reader (PerkinElmer® 2300 EnSpire™, China).

2.4.1 Nitrate- and ammonium determination (for microtiter plate)

The nitrate concentration was determined with vanadium chloride, as described in HOOD-NOWOTNY ET AL. (2010). Further, the ammonium concentration was determined by the modified indophenol reaction according to (SHAND, WILLIAMS, AND COUTTS 2008). The absorbance was measured with a plate reader (PerkinElmer® 2300 EnSpire™, China) for ammonium at a wavelength of 660 nm and nitrate at 540 nm.

2.5 Enzyme activity

Extracts for extracellular enzyme activities were prepared in 50 mM 4-Morpholineethanesulfonic acid sodium (MES-buffer) at p*H* 6.2 to mimic acidity of the natural soils. To prepare the homogenate, 1 g of frozen soil was put into an Erlenmeyer flask, and 100 ml of MES buffer was added. The suspension was homogenized with an ultra-homogenizer (Bandelin, Berlin, Germany). Following, absolute activities were measured using the following substrates: 4-Methylumbelliferyl β-D-cellobioside ("Exoglucanase", EC 3.2.1.91), 4-Methylumbelliferyl β-D-glucopyranoside ("β-Glucosidase", EC 3.2.1.21), 4-Methylumbelliferyl N-acetyl-β-D-glucosaminide ("Exochitinase", EC 3.2.1.201), 4-Methylumbelliferyl phosphate ("acid phosphatase", EC 3.1.3.2) and L-Leucine-7-amido-4-methylcoumarin hydrochloride ("Protease", EC 3.4.21). For more details, see also AMEUR ET AL. (2018). Briefly, 200 µl of the homogenate was pipetted into black microliter plates and 50 µl of the respective substrate was added. Then, the microtiter plates were incubated for 140 min at 20°C in the dark and measured at 450 nm emission wavelengths at an excitation at 365 nm and 30 flashes (PerkinElmer® type 2300 EnSpire™).

The same soil homogenate was used to determine the activities of phenoloxidase and peroxidase according to KEIBLINGER ET AL. (2018). The substrate L-3, 4-dihydroxyphenylalanin ("L-DOPA", EC 1.14.18.1) was added to a final concentration of 10 mM. Further, the solution was shaken for 10 min and then centrifuged 5 min at 5000 rpm. Thereafter, 250 µl of the solution were transferred into transparent microplates. For peroxidase activity, 10 µl 0.3 % H_2O_2 was added prior to incubation at 20°C for 20 hours. The absorption was read at 450 nm before and after the incubation. The enzyme activities were calculated according to GERMAN ET AL. (2011).

For the absolute urease activity (EC 3.5.1.5), the measurement was done according SINSABAUGH, REYNOLDS, AND LONG (2000) with minor modifications. An amount of 1 ml soil homogenate was pipetted into two 1.5 ml Eppendorf tubes (Eppendorf, Hamburg, Germany). One of the tubes received urea at a final concentration of ~20 mM as a substrate. After incubation for 18 hours at 20°C the tubes were centrifuged for 5 min at 5000 rpm. Supernatants were transferred into transparent microplates.

Background concentration of ammonium, and formation after addition of urea was measured according to SHAND, WILLIAMS, AND COUTTS (2008), as described above (section 2.4.1). Urease (amidohydrolase) activity was calculated according to SINSABAUGH, REYNOLDS, AND LONG (2000) by using standards of NH_4Cl in the range of 0 µM to 100 µM.

2.6 Substrate induced respiration (SIR)

The soil samples were gently thawed at 4°C overnight before analysis of SIR. The soil samples were of different moisture contents and relatively dry (dry matter content 69-79%), so similar soil moisture of 60% was adjusted for all soil samples. To ensure drainage of the soil, 20 ml GC vials were filled with 1 g of sterile silica sand. Then 2 g of field moist soil was added and moistened with MilliQ water (Millipore, City, Country) to reach the final water content of 60%, and the vials were sealed gas tight with a Rubber Butyl Stopper. Then, 200 µl of 800 ppm glucose solution were added and incubated for 4 hours at 22°C. The samples were analyzed immediately after amendment and after incubation with an Agilent Technologies 7890A GC system. The CO_2 was measured using a gas chromatograph (GC, Agilent 7890 A) connected with a headspace sampler (Agilent 7697 A) and a flame ionization detector (FID Ni-cat) for more details on the GC-procedure see KEIBLINGER ET AL. (2018).

2.7 Data evaluation and statistical analyses

All statistical and graphical work was conducted with Microsoft Excel 2010. To analyze if the variances were homogenous or heterogonous, Levene´s test was used. Further, data were tested for normal distribution, using the Kolmogorov-Smirnow-test. For data that fit the assumption of normal distribution and homogenous variances, the two-sample t-test was used; if the assumption was not met, Welch´s t-test was applied. For the data that did not fit normal distribution, the Mann-Whitney-test was used. Results were statistically significant when $P<0.05$. The tests were applied to compare the different land use areas at each of the two sites. For correlation analysis, the Pearson correlation was used for each site across the land use types.

3. Results

3.1 Soil physico-chemical properties

The water content was significantly (P<0.05) higher in soils from the National Park forest at each location (Table 1). Further, pH of the soils ranged from 6.28-6.69 and showed no difference between land-use type (Table 1). Also the bulk density showed no difference at El Cascajo, but at Cerro Verde a significant (P<0.05) increase was observed with agricultural use (Table 1). C_{org} (-37.5%) and total N (N_{tot}) where significantly (P<0.05) lower in agricultural soils in Cerro Verde. In El Cascajo the C_{org} and N_{tot} values were not changed significantly (Table 1). Also the C_{org} / N_{tot} ratio showed no differences, but there was a trend for higher values at the forest sites. A trend for higher K content in forest soils was observed, however only significant for El Cascajo, but not for Cerro Verde. The phosphorus content and CEC showed no significant differences.

3.2 Ammonium- and nitrate content

3.2.1 Ammonium and nitrate

For ammonium and nitrate we observed a clear pattern. The ammonium content was significantly (P<0.05) higher in forest soils at both sites, with significantly higher values of NH_4 by about 32.2% in El Cascajo and 25.7% in Cerro Verde in forest soils (Figure 1). However, the opposite pattern was observed for the nitrate content. The results showed that agricultural fields had significantly (P<0.05) higher nitrate contents, in El Cascajo and Cerro Verde by 152% and 680%, respectively (Figure 1).

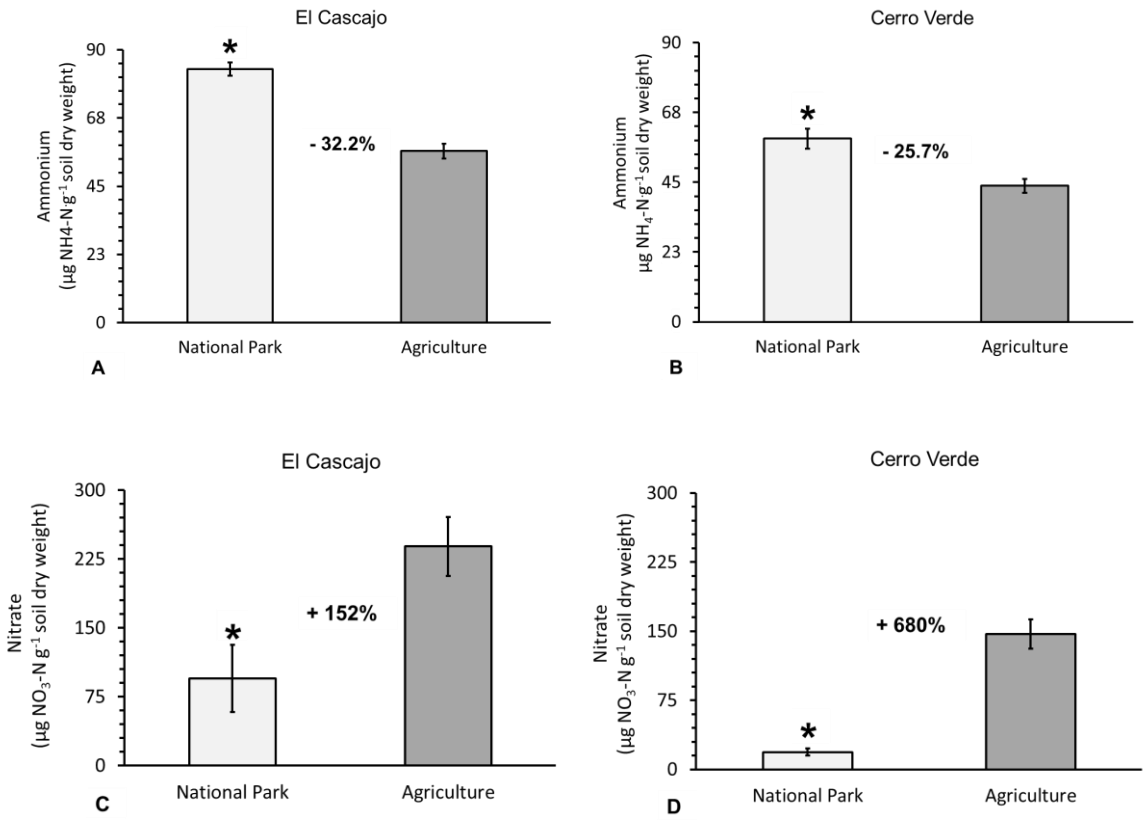


Figure 1. Ammonium and nitrate concentrations in soils from El Cascajo and Cerro Verde respectively of the National Park forest and agricultural fields. Values are mean and ± standard error (n=4). Asterisk (*) indicates a significant difference (P<0.05) between.

3.2.2 Ammonium- and nitrate content: Values in relation to the C_{org}

If we consider the values of ammonium and nitrate in relation to C_{org}, we can see that in general the mean values were significantly higher (P<0.05) for nitrate in soils from agricultural fields (Table 3). The ammonium content related to C_{org} however, did not show significant differences.

Table 3. Mean values and standard error (n=4) of ammonium and nitrate per unit C_{org} in the soils under different land use at the two sites.

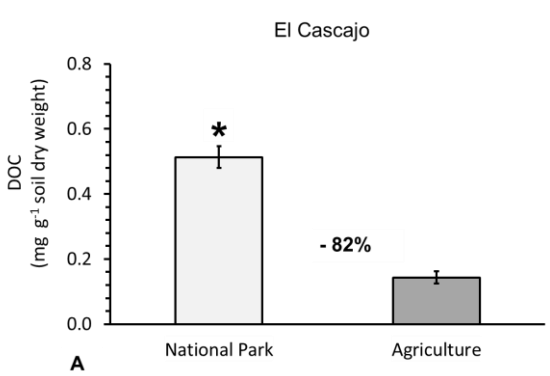
	El Cascajo		Cerro Verde	
	NP	Agri	NP	Agri
NH_4^+ / C_{org} (mg NH_4-N g^{-1} C_{org})	0.67 ±0.07	0.58 ±0.13	0.81 ±0.06	0.98 ±0.10
NO_3^- / C_{org} (mg NO_3-N g^{-1} C_{org})	0.74 ±0.34	**2.28*** ±0.37	0.26 ±0.05	**3.27*** ±0.41

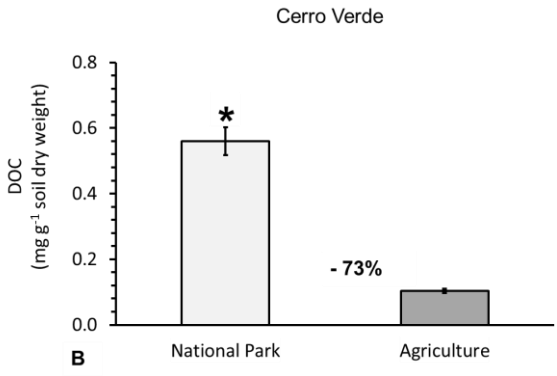
For each site, the asterisk (*) indicates that the mean value is significantly higher (P<0.05) for the respective land use. The numbers marked in bold visualise the significance. National Park (NP) and Agricultural land use (Agri).

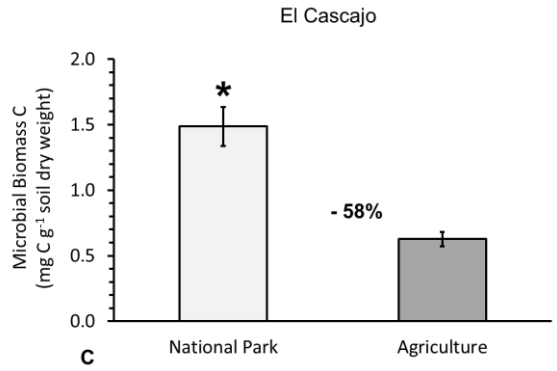
3.3 Microbial Parameters

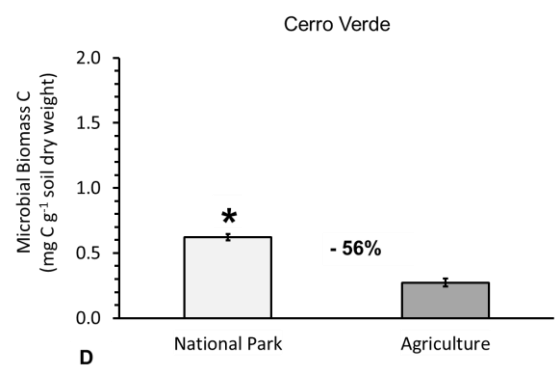
3.3.1 C_{mic}, N_{mic}, P_{mic} and DOC

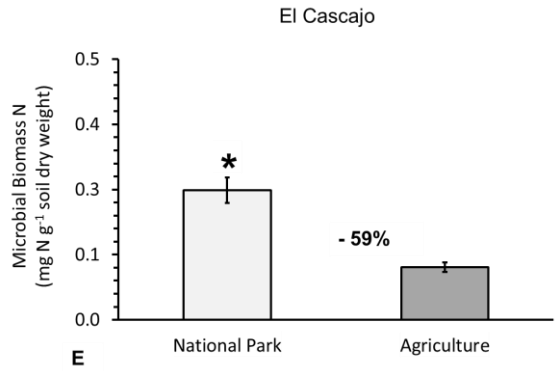
DOC values were significantly lower in agricultural fields by about 82% in El Cascajo) and 73% in Cerro Verde. In general, we observed a dramatical decrease of microbial biomass C, N and P in soils from agricultural fields (Figure 2). There was similar decline of C_{mic} in agricultural fields for both sites, with about 58% in El Cascajo and 56% Cerro Verde. Similarly, the N_{mic} decreased in a similar range by 59% in El Cascajo and 60% in Cerro Verde. A slightly stronger reduction was observed for P_{mic} with 71% in El Cascajo and 63% in Cerro Verde.

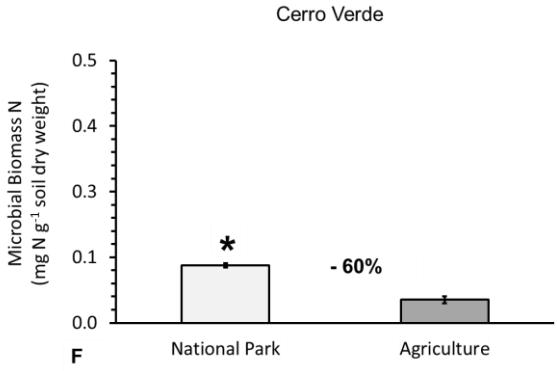

El Cascajo
DOC
(mg g-1 soil dry weight)
0.8
0.6
0.4
0.2
0.0
*
- 82%
National Park
Agriculture
A


Cerro Verde
DOC
(mg g-1 soil dry weight)
0.8
0.6
0.4
0.2
0.0
*
- 73%
National Park
Agriculture
B


El Cascajo
Microbial Biomass C
(mg C g-1 soil dry weight)
2.0
1.5
1.0
0.5
0.0
*
- 58%
National Park
Agriculture
C


Cerro Verde
Microbial Biomass C
(mg C g-1 soil dry weight)
2.0
1.5
1.0
0.5
0.0
*
- 56%
National Park
Agriculture
D


El Cascajo
Microbial Biomass N
(mg N g-1 soil dry weight)
0.5
0.4
0.3
0.1
0.0
*
- 59%
National Park
Agriculture
E


Cerro Verde
Microbial Biomass N
(mg N g-1 soil dry weight)
0.5
0.4
0.3
0.1
0.0
*
- 60%
National Park
Agriculture
F

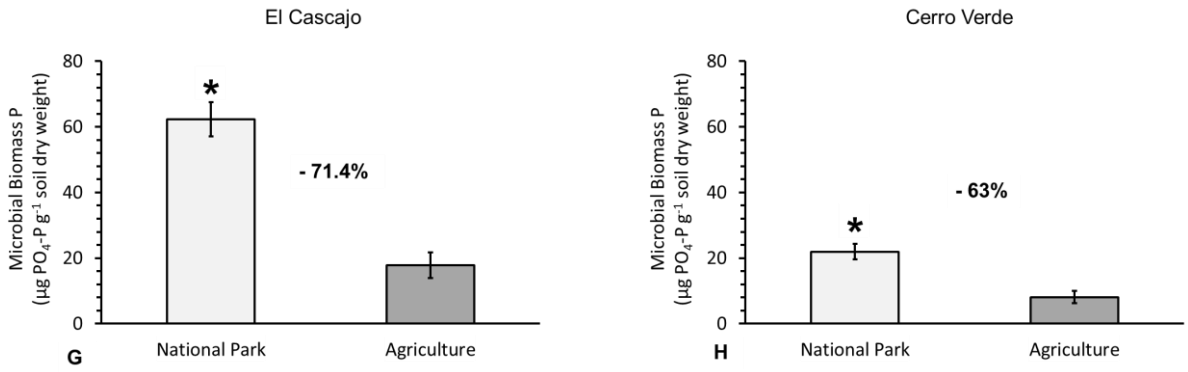


Figure 2. The DOC, C_{mic}, N_{mic} and P_{mic} values in the soils from El Cascajo and Cerro Verde respectively to National Park forest and adjacent agricultural fields. Values are mean and ± standard error (n=4). Asterisk (*) indicates a significant difference (P<0.05) between National Park forest and adjacent agricultural fields. (A, B) DOC values of El Cascajo and Cerro Verde (C, D) C_{mic} values of El Cascajo and Cerro Verde (E, F) N_{mic} values of El Cascajo and Cerro Verde (G, H) P_{mic} values of El Cascajo and Cerro Verde.

3.3.2 Microbial Biomass (C_{mic}, N_{mic} and P_{mic}): Values in relation to the C_{org}

Similar to the microbial biomass, also the relation to C_{org}, showed a strong decline in agricultural fields (Table 4). The C_{mic}/C_{org} decreased significantly ($P<0.05$) about 48% (El Cascajo) - 30% (Cerro Verde), the N_{mic}/C_{org} about 50% (El Cascajo) - 36% (Cerro Verde) and P_{mic}/C_{org} about 63% (El Cascajo) - 44% (Cerro Verde).

Table 4. Mean values and standard error (n=4) of microbial biomasses per unit C_{org} in the soils under different land use and site.

	El Cascajo		Cerro Verde	
	NP	Agri	NP	Agri
C_{mic} / C_{org} (mg C g $Corg^{-1}$)	**11.6*** ±0.6	6.0 ±0.7	**8.5*** ±0.2	5.9 ±0.2
N_{mic} / C_{org} (mg N g $Corg^{-1}$)	**1.9*** ±0.2	1.0 ±0.1	**1.5*** ±0.1	1.0 ±0.1
P_{mic} / C_{org} (µg P g $Corg^{-1}$)	**487.3*** ±21.3	180.1 ±46	**303.4*** ±29.6	170.2 ±27.4

For each site, the asterisk (*) indicates that the mean value is significantly higher ($P<0.05$) for the respective land use. The bold written number visualise the significance. National Park (NP) and Agricultural land use (Agri).

3.3.3 Pearson correlation coefficient between C_{mic} and N_{mic} with C_{org} and N_{tot}

The results (Table 5) show that all variables on Cerro Verde had significant ($P<0.05$) positive correlation, while on El Cascajo we observed no significant correlations.

Table 5. Pearson correlation coefficient between microbial biomass carbon (C_{mic}) and microbial biomass nitrogen (N_{mic}) with C_{org} and total nitrogen (N_{tot}) for each site across land uses.

	El Casajo		Cerro Verde	
	C_{org}	N_{tot}	C_{org}	N_{tot}
C_{mic}	0.56	0.02	**0.98**	**0.92**
N_{mic}	0.53	0.04	**0.95**	**0.91**

The bold written numbers visualise significance ($P<0.05$) of the correlations.

3.3.4 Microbial Biomass ratios: C_{mic}/N_{mic}, C_{mic}/P_{mic}, N_{mic}/P_{mic}

The ratios (Table 6) showed no significant differences, but for the C_{mic}/P_{mic} ratio a trend of higher values in agricultural sites was observed.

Table 6. Mean values of the ratios of the soils under different types of use and site.

	El Cascajo		Cerro Verde	
	NP	Agri	NP	Agri
C_{mic}/N_{mic}	6.0 ±0.1	6.2 ±0.2	5.7 ±0.2	6.3 ±0.4
C_{mic}/P_{mic}	24 ±0.5	31 ±6	29 ±3	37 ±5
N_{mic}/P_{mic}	4.0 ±0.1	4.8 ±0.9	5.1 ±0.7	6.0 ±1

No significant differences were detected between the land use types.

3.4 Substrate induced respiration

3.4.1 Substrate induced respiration (SIR)

The observed SIR values were significantly higher (P<0.05) at soils from forest sites. The values were reduced by about 54% (El Cascajo) and 52% (Cerro Verde) in agricultural sites (Figure 3).

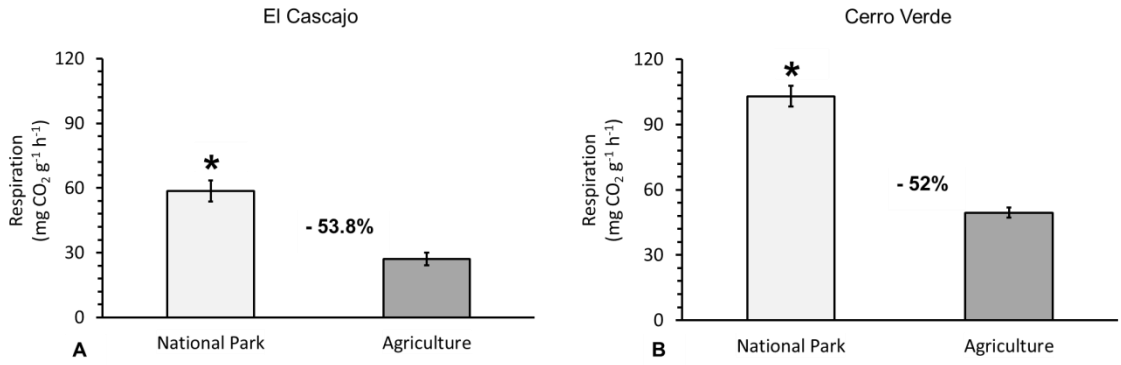


Figure 3. *The SIR values in soils from El Cascajo and Cerro Verde respectively to National Park forest and adjacent agricultural fields. Values are mean and ± standard error (=4). Asterisk (*) indicates a significant difference (P<0.05) between National Park forest and adjacent agricultural fields.(A) SIR value of El Cascajo (B) SIR value of Cerro Verde.*

3.4.2 Substrate induces respiration in relation to the C_{org} and C_{mic}

SIR in relation to C_{org} was significantly (P<0.05) lower in soils from agricultural fields (41% El Cascajo / 22% Cerro Verde) (Table 7). However, the SIR in relation to the C_{mic}, showed no significant differences between the land use types, but a strong difference between the sites El Cascajo and Cerro Verde, with about 4-fold higher values for Cerro Verde.

Table 7. Mean values and standard error of the substrate induced respiration (SIR) per unit C_{org} or C_{mic} in the soils under different land use and site.

	El Cascajo		Cerro Verde	
	NP	Agri	NP	Agri
SIR/C_{org} (g CO_2 g^{-1} C_{org} h^{-1})	**0.46*** ±0.04	0.27 ±0.06	**1.40*** ±0.03	1.09 ±0.06
SIR/C_{mic} (g CO_2 g^{-1} C_{mic} h^{-1})	40 ±2.1	44 ±5.5	166 ±6.4	185 ±13.1

For each site, the asterisk (*) indicates that the mean value is significantly higher (P<0.05) for the respective land use. The numbers marked in bold visualise the significance.

3.5 Enzyme activities

3.5.1 Absolute enzyme activities

We observed that the enzyme activities were generally higher at forest sites. Exceptions were observed for exoglucanase in Cerro Verde, exochitinase in El Cascajo and phenoloxidase at both sites, where values showed no significant change (Figure 4 and Figure 5). For carbon acquiring enzyme activities the activity of exoglucanase was reduced by 36% (El Cascajo), β-glucosidase 51% (El Cascajo) - 41% (Cerro Verde) and exochitinase 87% (Cerro Verde) in soils from agricultural fields.

Regarding the N-acquiring enzyme activities shown in Figure 5, agricultural soil management generally decreased activities, which was significant for urease activity in both sites, with a decrease of 44% in El Cascajo and 67% in Cerro Verde. For protease activity also a significant reduction was observed, however the decline was not as strong as for urease. Protease activities were reduced by 27% in El Cascajo and 21% in Cerro Verde due to agricultural land use.

In addition, the P-acquiring enzyme phosphatase (Figure 6) was significantly ($P<0.05$) reduced in soils from the agricultural field by 38% in El Cascajo and 29% in Cerro Verde.

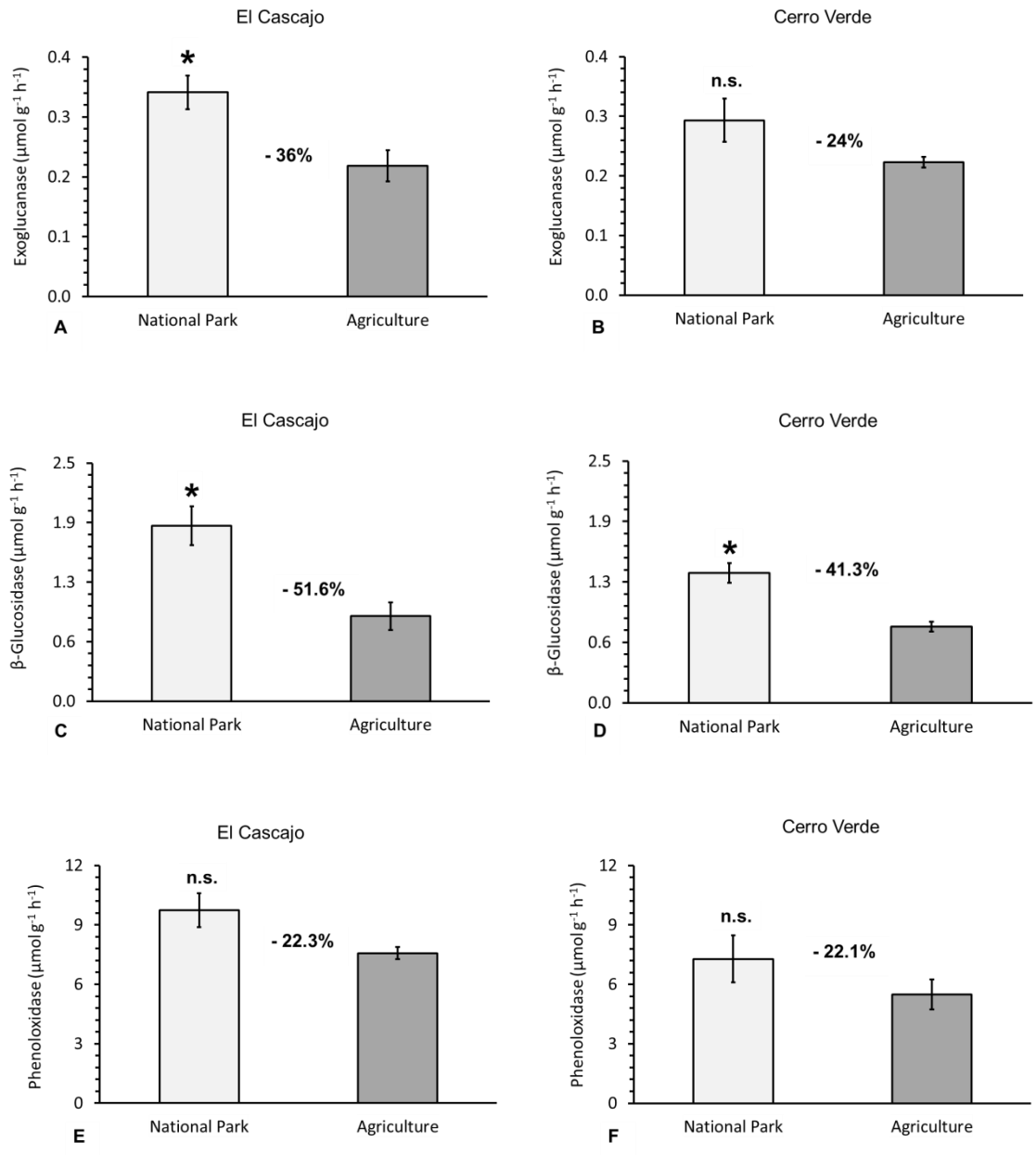


Figure 4. The C acquiring absolute enzyme activities in soils from El Cascajo respectively to National Park forest and adjacent agricultural fields. Values are mean and ± standard error (n=4). Asterisk (*) indicates a significant difference (P<0.05) between National Park forest and adjacent agricultural fields. (A, B) exoglucanase values (C, D) β-glucosidase values (E, F) phenoloxidase values.

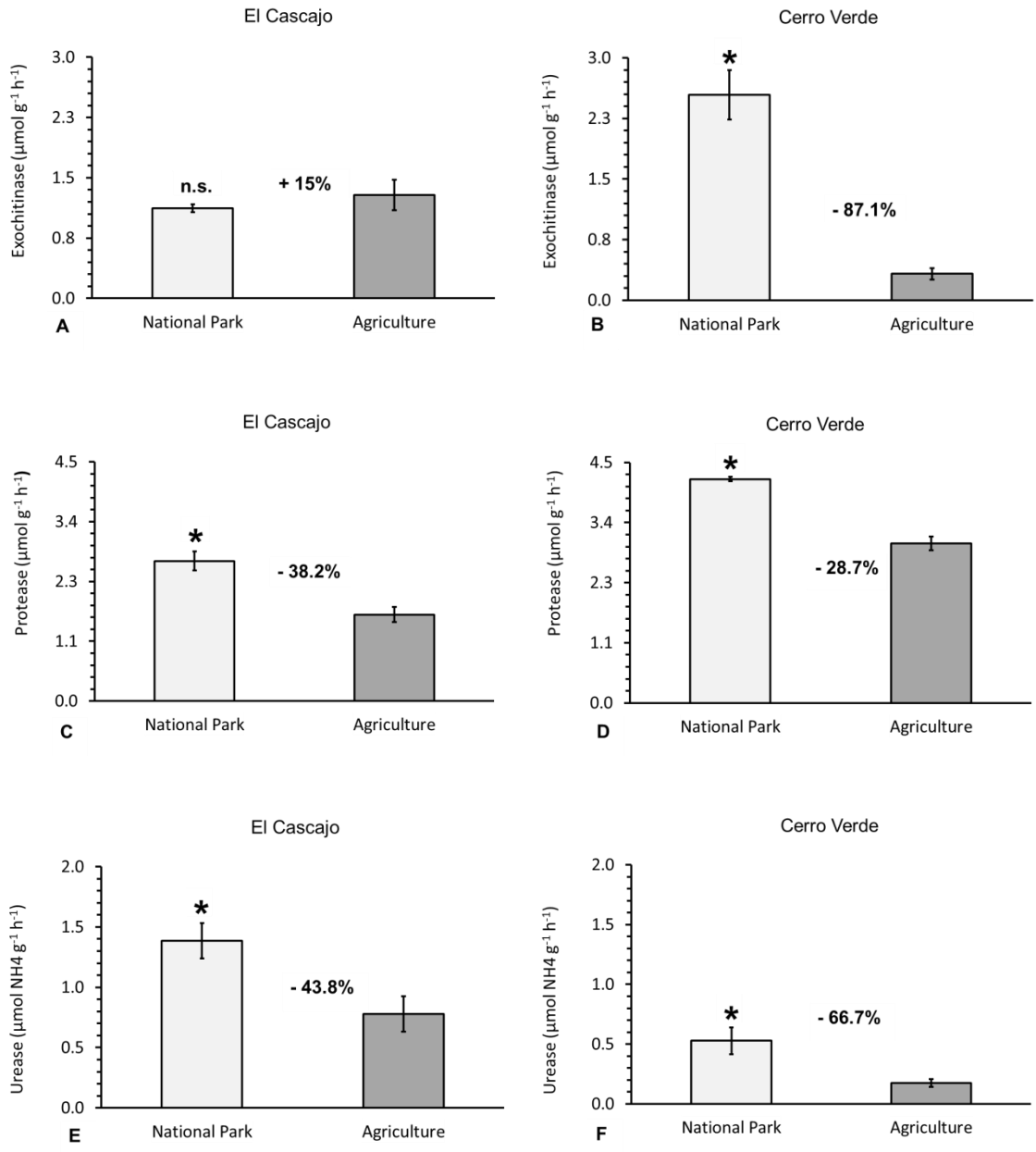


Figure 5. The N acquiring absolute enzyme activities in soils from El Cascajo respectively to National Park forest and adjacent agricultural fields. Values are mean and ± standard error (n=4). Asterisk (*) indicates a significant difference (P<0.05) between National Park forest and adjacent agricultural fields. (A, B) exochitinase values (C, D) protease values (E, F) urease values.

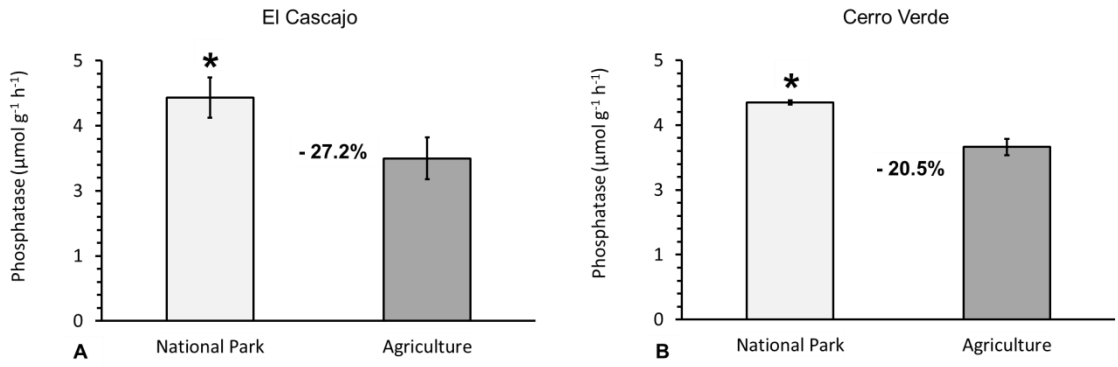


Figure 6. The P acquiring absolute enzyme activity in soils from El Cascajo respectively to National Park forest and adjacent agricultural fields. Values are mean and ± standard error (n=4). Asterisk (*) indicates a significant difference (P<0.05) between National Park forest and adjacent agricultural fields. (A, B) phosphatase values.

3.5.2 Specific enzyme activities: Values in relation to C_{org} and C_{mic}

If we consider the values of enzymatic activity in relation to C_{org} and C_{mic}, we can see that the specific enzyme activities differ notably from the "absolute" potential activities. In general, the specific activities showed less distinct patterns compared to absolute values, and only minor to no differences when related to C_{org}. For example, regarding the values in relation to the C_{org}, only β-glucosidase was reduced by 42% in El Cascajo and exochitinase by 79% in Cerro Verdo in the agricultural field whereas phosphatase was significantly (P<0.05) higher in soils from agricultural sites by 36% in Cerro Verde (Table 8).

However, the specific enzyme activities; values in relation to C_{mic} (Table 9) showed more differences than for the relation to C_{org}, with a trend for higher specific activities in agricultural sites. At the agricultural site C acquiring enzymes like exoglucanase activity was significantly higher by 79% in Cerro Verde and phenoloxidase activity by 78% in El Cascajo and 70% in Cerro Verde. The exochitinase activity was increased by 169% in agricultural fields of El Cascajo. Further, the N acquiring protease activity was increased by 41% in El Cascajo and the P acquring phosphatase activity by 100% in Cerro Verde in agricultural soils.

However, exochitinase activity was significantly higher in the National Park site of Cerro Verde with a reduction in activity by 70% in soils used agriculturally.

Table 8. Mean values and standard error of the potential enzyme activities per unit C_{org} in the soils under different land use and site.

	El Cascajo		Cerro Verde	
	NP	Agri	NP	Agri
Exoglucanase	2.75	2.07	3.97	4.95
(µmol g^{-1} C_{org} h^{-1})	±0.40	±0.20	±0.43	±0.36
β-Glucosidase	**14.36***	8.37	18.24	17.82
(µmol g^{-1} C_{org} h^{-1})	±0.90	±1.04	±0.86	±2.51
Phenoloxidase	79.37	74.47	98.79	118.66
(µmol g^{-1} C_{org} h^{-1})	±13.67	±11.43	±14.35	±7.87
Exochitinase	8.93	12.23	**34.40***	7.23
(µmol g^{-1} C_{org} h^{-1})	±0.73	±1.55	±3.41	±1.34
Protease	21.21	15.58	57.26	67.04
(µmol g^{-1} C_{org} h^{-1})	±2.66	±1.65	±1.58	±7.37
Urease	10.97	7.17	7.15	3.80
(µmol NH_4 g^{-1} C_{org} h^{-1})	±1.35	±1.22	±1.50	±0.53
Phosphatase	35.03	29.59	57.26	**78.07***
(µmol g^{-1} C_{org} h^{-1})	±6.09	±3.16	1.58±	±4.91

For each site, the asterisk (*) indicates that the mean value is significantly higher (P<0.05) for the respective land use. The numbers marked in bold visualise the significance. National Park (NP) and Agricultural land use (Agri).

Table 9. Mean values and standard error of the specific enzyme activities per unit C_{mic} in the soils under different land use and site.

	El Cascajo		Cerro Verde	
	NP	Agri	NP	Agri
Exoglucanase	0.24	0.35	0.47	**0.84***
(µmol mg^{-1} C_{mic} h^{-1})	±0.03	±0.04	±0.05	±0.08
β-Glucosidase	1.25	1.41	2.15	3.03
(µmol mg^{-1} C_{mic} h^{-1})	±0.12	±0.17	±0.11	±0.48
Phenoloxidase	6.91	**12.33***	11.78	**19.98***
(µmol mg^{-1} C_{mic} h^{-1})	±1.33	±1.02	±1.94	±1.15
Exochitinase	0.77	**2.07***	**4.05***	1.23
(µmol mg^{-1} C_{mic} h^{-1})	±0.07	±0.28	±0.39	±0.24
Protease	1.85	**2.61***	6.77	11.38
(µmol mg^{-1} C_{mic} h^{-1})	±0.27	±0.13	±0.26	±1.44
Urease	0.94	1.21	0.83	0.64
(µmol NH_4 mg^{-1} C_{mic} h^{-1})	±0.06	±0.16	±0.16	±0.08
Phosphatase	3.05	5.04	6.77	**13.56***
(µmol mg^{-1} C_{mic} h^{-1})	±0.60	±0.58	±0.26	±0.97

For each site, the asterisk (*) indicates that the mean value is significantly higher (P<0.05) for the respective land use. The numbers marked in bold visualise the significance. National Park (NP) and Agricultural land use (Agri).

3.5.3 Pearson correlation coefficient between C_{mic} and C_{org} with potential enzyme activities

At El Cascajo (Table 10) we observed significant (*P*<0.05) positive correlations between C_{mic} with exoglucanase (r=0.75), β-glucosidase (r=0.90), protease (r=0.76) and urease (r=0.89). However, no significant correlations were observed between C_{org} and potential enzyme activities. At Cerro Verde all variables showed strongly significant (*P*<0.05) with exception of the enzyme phenoloxidase.

Table 10. Pearson correlation coefficients between microbial biomass carbon (C_{mic}) and C_{org} with potential enzyme activities for each site across land uses.

	El Cascajo		Cerro Verde	
	C_{mic}	C_{org}	C_{mic}	C_{org}
Exoglucanase	**0.75**	0.48	**0.72**	**0.72**
β-Glucosidase	**0.90**	0.60	**0.89**	**0.85**
Phenoloxidase	0.48	0.19	0.52	0.65
Exochitinase	-0.12	0.34	**0.96**	**0.94**
Protease	**0.76**	0.41	**0.93**	**0.87**
Urease	**0.89**	0.57	**0.87**	**0.81**
Phosphatase	0.45	0.33	**0.94**	**0.95**

The bold written numbers visualise significance (*P*<0.05) of the correlations.

4. Discussion

4.1 Ammonium and Nitrate

In the present study, higher nitrate content was found at agricultural sites, while ammonium concentration was lower than in the forest sites. These observations were comparable to previous findings of GAMBOA AND GALICIA (2011) and BISSETT ET AL. (2011), who reported highest ammonium content at grassland and forest sites. In the forest areas, the higher ammonium concentrations can be explained by the higher organic matter content and higher mineralisation. Therefore, the soils from forest contained greater proportions of nitrogen in form of ammonium. This is supported by the fact that the NH_4/C_{org} values were not significantly different between national park and agricultural sites. It is likely that fertilization was the main cause of the high nitrate content in agricultural sites (BRACKIN ET AL. 2013), as neither p*H* nor bulk density (excepted in Cerro Verde) were different. Further, the NO_3 concentration related to C_{org} was significnantly higher in agricultural soils than in the national park, and the increase was even higher due to lower C_{org} values in the agricultural sites. This result further supports that fertilization may have caused the high nitrate concentrations in the agricultural soils.

4.2 Microbial biomass

A strong reduction of C_{mic} (El Cascajo -58% and Cerro Verde -56%), N_{mic} (El Cascajo -59% and Cerro Verde -60%) and P_{mic} (El Cascajo -71% and Cerro Verde -63%) on the agricultural field (Figure 2) in comparison to forest was found in this study. Similar results have been observed in many other studies (i.e. LI ET AL. 2018; SINGH AND GHOSHAL 2014; DENG ET AL. 2016).

In particular, the reduction in microbial biomass in the present study is similar to a study that compared soils from arboreal forest (*Populus simonii, Ulmus pumila and Pinus tabuliformis*) with arable land (*Zea mays*), with declines in C_{mic}, N_{mic} and P_{mic} by 42%, 25% and 89%, respectively, where also P_{mic} was affected strongest (QI ET AL. 2018). Due to continuous soil cultivation the C- mineralisation rate may be increased, which leads to a decrease of C_{org} and may have consequences on microbial biomass (GOVAERTS ET AL. 2007; KEMMITT ET AL. 2008).

However, also opposite findings were reported for a tropical dry land, where, for example grazed systems showed the highest C_{mic}, and even croplands had higher C_{mic} than natural forests. In the grazed system the root biomass of the grasses were very dominant, so that residue input, root exudation and elevated input of organic C were an important driver (CÂMARA ET AL. 2016).

Also MAHARJAN ET AL. (2017) observed in their study, that organic cropland had the highest, while conventional and forest had similar C_{mic} and N_{mic} values. On the one hand, organic cropland was fertilized with farmyard manure and vermicompost, which was an important resource of organic matter and hence increased activity of microbes. On the other hand, the forest site in the mentioned study had very low regeneration and crown density. Further, litter collection by villagers could have strongly affected the microbial biomass in forests in their study.

Although, changes in microbial biomass with land use form are different to our study, the results of correlation analyses were similar. They indicated a positive correlation of C_{mic} and N_{mic} with total organic matter and total nitrogen (MAHARJAN ET AL. 2017). In the present study, we also observed a significant positive correlation of C_{mic} and N_{mic} with C_{org} at Cerro Verde (Table 5), while only Cerro Verde showed a significant positive correlation of C_{mic} and N_{mic} with total nitrogen (N_{tot}). This leads us to the conclusion that microbial biomass is related to the quantity of organic matter.

This could also explain why in El Cascajo the microbial biomass was higher than in Cerro Verde, as the soil from the forest of El Cascajo showed higher C_{org} (12.88 %) and total nitrogen (1.13 %) values. In the study of GAMBOA AND GALICIA (2011), the specific C_{mic}/C_{org} content was higher in agricultural soils after deforestation, which suggests that losses of labile soil organic matter in response to land-use change can lead to an increase of C_{mic}/C_{org} in the soil. This is different from our results; we found a decline in C_{org} and an even stronger decline in dissolved organic matter (DOC) in agricultural soils at both sites; however, C_{mic}/C_{org} was still significantly lower in the agricultural areas compared to the forest areas.

As we can see from the results of MAHARJAN ET AL. (2017), it depends how forests are influenced through human activities. In our study the National Park forests on Galapagos are not used by humans; this has to be considered when comparing results on land use change of forests with national park.

4.3 Substrate induced respiration

In our study, both the SIR and SIR/C_{org} were higher in soils from National park forest at both sites. In addition, as SIR is another measure to determine microbial abundance in soil, it is not surprising that SIR/C_{mic} showed no significant changes.

4.4 Enzyme activity

4.4.1 Potential enzyme activities

Most enzyme classes showed a strong decline with agricultural land use at both sites, except for phenoloxidase activity, and exoglucanase activity in Cerro Verde and exochitinase activity in El Cascajo, where no significant changes were observed. Many studies showed similar results, where a major part of the absolute enzyme activities decreased after land-use change and a part of them was not affected (SAVIOZZI ET AL. 2001; SCOTTI, IOVIENO, AND ZACCARDELLI 2015; MOGHIMIAN ET AL. 2017; TRASAR-CEPEDA, LEIRÓS, AND GIL-SOTRES 2008). Soil cultivation is an important factor for enzyme activities. Due to long-term tillage organic matter content in soil may decrease rapidly and as a consequence, the soil biological activity decreases and crop productivity may be reduced (DICK 1984; BAYER ET AL. 2001). Also due to tillage, the three-dimensional network of roots, mycorrhizal hyphae and soil particles is disturbed. Further, this network could be a shelter for microorganisms and the glycoprotein, glomalin, of the arbuscular mycorrhiza stabilizes these aggregates (WRIGHT AND ANDERSON 2000). However, repeated application of inorganic fertilizers and the lower C_{org} content in cultivated soils could also decrease enzyme activities (BALIGAR, WRIGHT, AND HERN 2005). This is likely the case in the present study, where fertilization with inorganic fertilizer is a common practice for farmers, and a trend for lower C_{org} content already occurred. In addition, the soil tillage via hoe in agricultural sites could influence the enzyme activity, as forest soils are not tilled. The soil organic matter is positively correlated with the enzyme activity, which suggests that soil organic matter acts like a shelter for protection and preservation of enzymes in their active form (RAIESI AND BEHESHTI 2015). We observed a positive correlation between C_{mic} and C_{org} with most potential enzyme activities in Cerro Verde, with exception of exoglucanase and phenoloxidase where no significant correlation occurred (Table 10).

However, in El Cascajo only exoglucanase, β-glucosidase, protease and urease activity were positively correlated with C_{mic}. A positive correlation of enzyme activity with microbial biomass is supporting the idea that the decline of microbial biomass also reduces enzyme activity, since enzymes involved in C, N, P and S mineralization are mostly of microbial origin (TRIPATHI ET AL. 2007; RAIESI AND BEHESHTI 2015). Although the soil factors mentioned above are important, also crop species are an important factor for changes in enzyme activities (DENG AND TABATABAI 1994; DORAN AND PARKIN 1994). Factors like plant species, dead roots, root exudates, which are important for growth of microbes and litter input, may enhance enzyme activities (KANDELER AND MURER 1993). Therefore, differences between sites were observed for C – acquiring (Figure 4) enzymes, N – acquiring enzymes (Figure 5) and P – acquiring enzymes (Figure 6).

A trend of a slightly stronger reduction with agricultural land use was observed for El Cascajo, except for urease activity. In addition, for exochitinase, an opposite trend was observed and it seems that the effects of land use change from national park to agriculture are site specific for this enzyme class. Phenoloxidase showed a trend of lower activity in agricultural sites, albeit not significantly different in our study. It is suggested, that phenoloxidase activities, are reduced with more intensive land-use, due to their comparatively “narrow niche” in contrast to other enzymes which degrade simpler substrates (CHAER ET AL. 2009). Our results suggest that the absolute values are able to discriminate between land use systems.

4.4.2 Potential enzyme activities related to C_{org} and specific enzyme activities related to C_{mic}

We decided to also consider the relative enzyme activities related to C_{org} and C_{mic} (TRASAR-CEPEDA, LEIRÓS, AND GIL-SOTRES 2008). Relative enzyme activities related to C_{org} showed no significant declines with agricultural land use, except for β-glucosidase activity in El Cascajo and exochitinase activity in Cerro Verde. In contrast to that, phosphatase activities showed higher values in soil from the agricultural area in Cerro Verde.

Considering the relative enzyme activities related to C_{org}, the results of this study are contradictory to other studies. Most of the studies observed a change from high absolute values on forest sites to high specific values on agriculture sites (MEDEIROS ET AL. 2015; TRASAR-CEPEDA, LEIRÓS, AND GIL-SOTRES 2008; RAIESI AND BEHESHTI 2014). In the present study, the relative activities seemed to be compensated when C_{org} is taken into account. In other words, the values from agricultural sites increased and showed a compensation.

Alterations of “absolute” potential enzyme activities at El Cascajo and Cerro Verde were relatively similar. However, when we consider the changes in potential enzyme activities related to C_{org} at El Cascajo, we see a decrease in agricultural fields for exoglucanase (-25 %), phenoloxidase (-6 %), protease (-26 %) and phosphatase (-16 %); By contrast, at Cerro Verde, we see the opposite behavior for exoglucanase (+24 %), phenoloxidase (+20 %), protease (+17 %) and phosphatase (+36 %), with an increase in soils from agricultural fields. The β-glucosidase activity related to C_{org} decreased in both sites, while significantly only in El Cascajo (-42%). As only Cerro Verde showed a significant reduction in C_{org}, there was a trend for increasing enzyme activities for this site, where the reduction of C_{org} was strongest. In El Cascajo the trend was more in the opposite direction, due to the less pronounced (and non-significant) reduction in C_{org}.

This trend was the case for all enzyme activities with only two exceptions: Urease activity related to C_{org} decreased at both sites with agricultural land use (-34 % on El Cascajo and -47 % on Cerro Verde), however not significantly; exochinitase activity showed a different behaviour than other enzyme activites when related to C_{org}: at El Cascajo, it increased significantly by +36 %, while at Cerro Verde, it decreased by -79 % with agricultural land use. This could be related to N-limitation (AMEUR ET AL. 2018), as N_{tot} values were higher in El Cascajo compared to Cerro Verde. The observed compensation for most enzyme activities represents an ecological mechanism to retain soil metabolic activity (BURNS 1982), due to the loss of organic matter, especially the most labile organic matter (OGLE, BREIDT, AND PAUSTIAN 2005). Land use change may indeed cause considerable losses of organic matter, especially labile and least stabilized organic matter (TRASAR-CEPEDA, LEIRÓS, AND GIL-SOTRES 2008); this is also indicated in the present study by the significant decline in DOC after conversion of national park areas to agricultural land.

The picture is different when considering the specific enzymes activities related to C_{mic}. In general, we observed a trend of higher specific enzyme activities in agricultural soils. The specific enzyme activities like exoglucanase (+46 % in El Cascajo and +79 % $P<0.05$ in Cerro Verde), β-glucosidase (+13 % in El Cascajo and +41 % in Cerro Verde), phenoloxidase (+78 % in El Cascajo and +70 % $P<0.05$ in Cerro Verde), protease (+41 % $P<0.05$ in El Cascajo and +68 % in Cerro Verde) and phosphatase (+65 % in El Cascajo and +100 % $P<0.05$ in Cerro Verde) showed similar increases at both sites, but with considerably higher values at Cerro Verde.

Furthermore, the specific exochitinase activity showed significantly higher values in agricultural soils (+169 % $P<0.05$) at El Cascajo and significantly lower values (-70 % $P<0.05$) in agricultural soils at Cerro Verde.

This opposite trend for specific exochitinase activity in the two sites, also supports that absolute activities were only correlated with C_{org} in Cerro Verde (Table 10). It has been shown, that soil manipulation that resulted in a loss of C_{org}, such as soil warming (POLD ET AL. 2017) and litter removal (WEINTRAUB ET AL. 2013) resulted in reduced activities of exochitinase. The latter study even showed that also relative activities of exochitinase were related to changes in C_{org}. This is supported by the results of Cerro Verde in the present study, but in contrast to the site in El Cascajo. This might reflect substrate induced enzyme production by different availability of N-forms in the different sites. A similar trend as for exochitinase activity, was also observed for the urease activity related to C_{mic}, where values were higher (+29 %) in agricultural soils from El Cascajo and lower (-23 %) in Cerro Verde. By contrast, the protease activity, which is also an N-acquiring enzyme, did not show the same behavior as exochitinase and urease. Opposite trends for exochitinase and protease activity, were reported earlier and were related to the fact that these enzyme classes depolymerizes different carbon and nitrogen substrates (JIAN ET AL. 2016) as well as distinct turnover times of these substrates in soils (AMEUR ET AL. 2018)

The specific enzyme activities related to C_{mic} provide enzyme efficiency and are good indices of physiological capacity, assuming that the activities are caused by the currently viable microbial community (ALLISON ET AL. 2007; WALDROP, BALSER, AND FIRESTONE 2000).

A possible explanation for the observed increases in specific enzyme activities (related to C_{mic}) in agricultural fields is that (1) land use generates stress in the microbiota, which respond with increased activity related to their total biomass, and therefore cause the observed over-compensation of enzyme activities (DORAN 1980).

(2) The increase of specific enzyme activities related to C_{mic} in agricultural fields could also be due to the relative accumulation of a pool of organic matter in which hydrolytic enzymes have stabilized.

The most labile organic matter is lost and the most humified organic matter remains, which contains extracellular enzymes bound to humic or to clay-humic soil colloids (NOURBAKHSH 2007; TRASAR-CEPEDA, LEIRÓS, AND GIL-SOTRES 2008). Also, the breakup of soil aggregates after cultivation may have contributed to the release of entrapped and immobilized enzymes (RAIESI AND BEHESHTI 2014). By breaking up soil macro-aggregates by tillage, the contact between soil organic matter and soil enzymes increases, and this promotes the loss of C_{org}. (ALLISON AND JASTROW 2006).

5. Summary and Conclusions

Land-use change from natural forest to agricultural fields caused decreases in soil organic matter content. The results of this master's thesis show a decline in a range of soil (microbial) parameters with intensive agricultural use, such as ammonium content, microbial biomass carbon, nitrogen and phosphorus (C_{mic}, N_{mic} and P_{mic}), substrate induced respiration and potential hydrolytic enzyme activities. Specific enzyme activities (related to C_{org} and C_{mic}, respectively) did not show these clear changes in response to agricultural use, and in some cases even increased relative activities related to C_{mic}. For the moment, it is not clear to what extent the pesticide use influences the microbial parameters, because the pesticide analyses are still on-going. In general, the results of this thesis show that few years of agricultural use have influenced soil (microbial) parameters tremendously. First, if we consider the high content of nitrate in the agricultural soils along with their permeable nature, nitrate leaching and associated water contamination is a potential threat. Second, the potential enzyme activities showed clear reductions in agricultural soils; this could lead to a disturbance in the C, N and P cycle. One way to overcome this problem is to make the agriculture on the islands more sustainable through organic agriculture. Nevertheless, this would need more cooperation between all stakeholders on the islands, including the tourism industry, the Galápagos National Park Directorate, the Ministry of Agriculture and of course the farmers.

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7. Attachment: raw data of the performed laboratory analyses

Probenname	ProbenID	NPOC mg/L	EW (g)	DM (g)	NPOC (mg/gDW)		Probenname	ProbenID	NPOC mg/L	EW (g)	DM (g)	Einwaage FU	Auswaage FUM	korr DM	NPOC (mg/gDW)	Cmic
P unfum	Blank KCl	3,092														
P unfum	1,00	12,73	2,50	0,79	0,16		P fum	1,00	39,52	2,51	0,79	6,18	6,08	0,77	0,51	0,35
P unfum	2,00	10,91	2,50	0,79	0,14		P fum	2,00	27,64	2,51	0,79	6,46	6,29	0,77	0,36	0,22
P unfum	3,00	10,34	2,51	0,78	0,13		P fum	3,00	27,45	2,51	0,78	6,54	6,41	0,77	0,36	0,23
P unfum	4,00	11,08	2,52	0,79	0,14		P fum	4,00	34,33	2,51	0,79	6,46	6,34	0,78	0,44	0,30
P unfum	5,00	39,38	2,50	0,74	0,53		P fum	5,00	78,66	2,50	0,74	6,57	6,43	0,72	1,09	0,55
P unfum	6,00	40,91	2,50	0,76	0,54		P fum	6,00	88,92	2,51	0,76	6,55	6,41	0,74	1,20	0,66
P unfum	7,00	55,00	2,51	0,77	0,71		P fum	7,00	102,70	2,51	0,77	6,62	6,50	0,76	1,35	0,64
P unfum	8,00	47,53	2,51	0,77	0,62		P fum	8,00	94,29	2,50	0,77	6,63	6,52	0,75	1,25	0,63
P unfum	9,00	11,89	2,50	0,69	0,17		P fum	9,00	58,08	2,50	0,69	6,66	6,52	0,68	0,86	0,69
P unfum	10,00	16,68	2,50	0,70	0,24		P fum	10,00	61,50	2,51	0,70	6,55	6,40	0,68	0,90	0,66
P unfum	11,00	10,67	2,50	0,71	0,15		P fum	11,00	42,06	2,50	0,71	6,56	6,29	0,68	0,62	0,47
P unfum	12,00	13,36	2,51	0,71	0,19		P fum	12,00	61,10	2,51	0,71	6,55	6,34	0,69	0,88	0,70
P unfum	13,00	45,42	2,52	0,69	0,66		P fum	13,00	168,30	2,49	0,69	6,08	5,96	0,67	2,51	1,85
P unfum	14,00	36,21	2,51	0,68	0,53		P fum	14,00	130,20	2,50	0,68	6,12	5,89	0,65	1,99	1,46
P unfum	15,00	36,02	2,50	0,68	0,53		P fum	15,00	111,50	2,51	0,68	6,57	6,45	0,67	1,66	1,13
P unfum	16,00	35,74	2,50	0,69	0,51		P fum	16,00	135,30	2,50	0,69	6,50	6,28	0,67	2,02	1,50

Probenname	ProbenID	TDN mg/L	EW (g)	DM (g)	TDN (mg/gDW)		Probenname	ProbenID	TDN mg/L	EW (g)	DM (g)	Einwaage FUM	Auswaage FUM	korr DM	TDN (mg/gDW)	Nmic (mg/g)
P unfum	Blank KCl	2,179														
P unfum	1,00	7,08	2,50	0,79	0,09		P fum	1,00	11,94	2,51	0,79	6,18	6,08	0,77	0,15	0,06
P unfum	2,00	7,81	2,50	0,79	0,10		P fum	2,00	10,43	2,51	0,79	6,46	6,29	0,77	0,14	0,04
P unfum	3,00	9,78	2,51	0,78	0,12		P fum	3,00	12,43	2,51	0,78	6,54	6,41	0,77	0,16	0,04
P unfum	4,00	12,95	2,52	0,79	0,16		P fum	4,00	15,79	2,51	0,79	6,46	6,34	0,78	0,20	0,04
P unfum	5,00	11,40	2,50	0,74	0,15		P fum	5,00	18,80	2,50	0,74	6,57	6,43	0,72	0,26	0,11
P unfum	6,00	11,13	2,50	0,76	0,15		P fum	6,00	19,73	2,51	0,76	6,55	6,41	0,74	0,27	0,12
P unfum	7,00	12,55	2,51	0,77	0,16		P fum	7,00	19,92	2,51	0,77	6,62	6,50	0,76	0,26	0,10
P unfum	8,00	12,12	2,51	0,77	0,16		P fum	8,00	20,36	2,50	0,77	6,63	6,52	0,75	0,27	0,11
P unfum	9,00	12,23	2,50	0,69	0,18		P fum	9,00	20,10	2,50	0,69	6,66	6,52	0,68	0,30	0,12
P unfum	10,00	17,37	2,50	0,70	0,25		P fum	10,00	23,92	2,51	0,70	6,55	6,40	0,68	0,35	0,10
P unfum	11,00	9,23	2,50	0,71	0,13		P fum	11,00	14,12	2,50	0,71	6,56	6,29	0,68	0,21	0,08
P unfum	12,00	16,13	2,51	0,71	0,23		P fum	12,00	23,10	2,51	0,71	6,55	6,34	0,69	0,33	0,11
P unfum	13,00	13,58	2,52	0,69	0,20		P fum	13,00	33,19	2,49	0,69	6,08	5,96	0,67	0,50	0,30
P unfum	14,00	13,19	2,51	0,68	0,19		P fum	14,00	28,46	2,50	0,68	6,12	5,89	0,65	0,44	0,24
P unfum	15,00	12,16	2,50	0,68	0,18		P fum	15,00	24,34	2,51	0,68	6,57	6,45	0,67	0,36	0,18
P unfum	16,00	15,04	2,50	0,69	0,22		P fum	16,00	32,59	2,50	0,69	6,50	6,28	0,67	0,49	0,27

Probenname	ProbenID	NPOC mg/L	blank corrected	EW (g)	DM (g)	DOC (mg/gDW)
P unfum	Blank KCl	3,092				
P unfum	1	12,73	9,638	2,50	0,79	0,12
P unfum	2	10,91	7,818	2,50	0,79	0,10
P unfum	3	10,34	7,248	2,51	0,78	0,09
P unfum	4	11,08	7,988	2,52	0,79	0,10
P unfum	5	39,38	36,288	2,50	0,74	0,49
P unfum	6	40,91	37,818	2,50	0,76	0,50
P unfum	7	55	51,908	2,51	0,77	0,67
P unfum	8	47,53	44,438	2,51	0,77	0,58
P unfum	9	11,89	8,798	2,50	0,69	0,13
P unfum	10	16,68	13,588	2,50	0,70	0,19
P unfum	11	10,67	7,578	2,50	0,71	0,11
P unfum	12	13,36	10,268	2,51	0,71	0,14
P unfum	13	45,42	42,328	2,52	0,69	0,61
P unfum	14	36,21	33,118	2,51	0,68	0,49
P unfum	15	36,02	32,928	2,50	0,68	0,48
P unfum	16	35,74	32,648	2,50	0,69	0,47

Probenname	ProbenID	TN mg/L	blank korr	EW	DM	TDN (mg/gDV
P unfum	Blank KCl	2,179				
P unfum	1	7,079	4,9	2,50	0,79	
P unfum	2	7,81	5,631	2,50	0,79	0,07
P unfum	3	9,784	7,605	2,51	0,78	0,10
P unfum	4	12,95	10,771	2,52	0,79	0,14
P unfum	5	11,4	9,221	2,50	0,74	0,12
P unfum	6	11,13	8,951	2,50	0,76	0,12
P unfum	7	12,55	10,371	2,51	0,77	0,13
P unfum	8	12,12	9,941	2,51	0,77	0,13
P unfum	9	12,23	10,051	2,50	0,69	0,15
P unfum	10	17,37	15,191	2,50	0,70	0,22
P unfum	11	9,232	7,053	2,50	0,71	0,10
P unfum	12	16,13	13,951	2,51	0,71	0,20
P unfum	13	13,58	11,401	2,52	0,69	0,17
P unfum	14	13,19	11,011	2,51	0,68	0,16
P unfum	15	12,16	9,981	2,50	0,68	0,15
P unfum	16	15,04	12,861	2,50	0,69	0,19

Tara	Proben Name	m, feucht [g]	m, trocken [g]	Wassergehalt (%)	m,subtrahiert	Dry matter (%)
50.99	CV_A_I_1	2.28	52.78	27.37	1.79	0.79
49.50	CV_A_II_1	2.39	51.39	26.46	1.89	0.79
58.72	CV_A_III_1	2.43	60.62	27.89	1.90	0.78
45.24	CV_A_IV_1	2.24	47.01	26.55	1.77	0.79
47.35	CV_F_I_1	2.26	49.02	35.33	1.67	0.74
45.26	CV_F_II_1	2.24	46.96	31.76	1.70	0.76
47.99	CV_F_III_1	2.44	49.87	29.79	1.88	0.77
46.80	CV_F_IV_1	2.24	48.52	30.23	1.72	0.77
48.10	EC_A_I_1	2.47	49.81	44.76	1.71	0.69
47.80	EC_A_II_1	2.56	49.59	43.26	1.79	0.70
50.08	EC_A_III_1	2.47	51.84	40.19	1.76	0.71
59.38	EC_A_IV_1	2.34	61.05	40.77	1.66	0.71
48.34	EC_F_I_1	2.49	50.05	45.76	1.71	0.69
49.67	EC_F_II_1	2.41	51.30	47.49	1.63	0.68
54.94	EC_F_III_1	2.42	56.59	46.31	1.65	0.68
50.74	EC_F_IV_1	2.45	52.44	43.92	1.70	0.69

Cerro Verde agriculture	p*H*	Cerro Verde forest	p*H*
CV_A_I_1	6,502	CV_F_I_1	6,534
CV_A_II_1	6,705	CV_F_II_1	6,488
CV_A_III_1	6,854	CV_F_III_1	6,696
CV_A_IV_1	6,689	CV_F_IV_1	6,622
El Cascajo agriculture		El Cascajo forest	
EC_A_I_1	6,466	EC_F_I_1	6,804
EC_A_II_1	6,264	EC_F_II_1	6,417
EC_A_III_1	5,829	EC_F_III_1	6,262
EC_A_IV_1	6,567	EC_F_IV_1	7,01

	Vollprobe 1	Vollprobe 2			Vollprobe 1	Vollprobe 2	
	Wert* Verd.	Wert* Verd.			tats. Wert	tats. Wert	Mittelwert
ProbenBez.	µg NH4-N	µg NH4-N	% dry matter	Einwaage (g)	µg NH4-N/gTS	µg NH4-N/gTS	Voll1/Voll2
P1	3.105	3.103	78.51	2.496	39.62	39.58	39.60
P2	3.149	3.164	79.08	2.5	39.82	40.01	39.92
P3	3.642	3.680	78.19	2.51	46.45	46.94	46.69
P4	3.858	3.966	79.02	2.52	48.53	49.89	49.21
P5	4.641	4.703	73.89	2.50	62.78	63.62	63.20
P6	4.497	4.490	75.89	2.50	59.19	59.09	59.14
P7	3.858	3.758	77.05	2.51	49.93	48.63	49.28
P8	4.960	4.996	76.79	2.51	64.31	64.77	64.54
P9	3.519	3.444	69.08	2.50	50.92	49.84	50.38
P10	3.960	4.027	69.80	2.50	56.74	57.70	57.22
P11	4.382	4.597	71.33	2.50	61.43	64.45	62.94
P12	3.971	4.014	71.04	2.51	55.72	56.33	56.02
P13	5.607	5.735	68.60	2.52	81.17	83.03	82.10
P14	6.038	6.159	67.80	2.51	88.88	90.66	89.77
P15	5.689	5.763	68.35	2.50	83.20	84.29	83.75
P16	5.430	5.509	69.49	2.50	78.17	79.32	78.74

	Vollprobe 1	Vollprobe 2			Vollprobe 1	Vollprobe 2	
	Wert* Verd.	Wert* Verd.			tats. Wert	tats. Wert	Mittelwert
ProbenBez.	µg NO3-N	µg NO3-N	% dry matter	Einwaage (g)	µg NO3-N/gTS	µg NO3-N/gTS	Voll1/Voll2
P1	8.879184862	8.976225133	78.51	2.496	113.28	114.52	113.90
P2	9.946627851	10.2862688	79.08	2.5	125.78	130.08	127.93
P3	11.79039301	12.13003396	78.19	2.51	150.37	154.70	152.54
P4	15.13828239	15.52644347	79.02	2.52	190.44	195.32	192.88
P5	1.018922853	0.96069869	73.89	2.50	13.78	13.00	13.39
P6	1.276079573	1.193595342	75.89	2.50	16.79	15.71	16.25
P7	2.523047065	2.295002426	77.05	2.51	32.65	29.70	31.18
P8	1.145075206	1.077147016	76.79	2.51	14.85	13.97	14.41
P9	15.13828239	15.47792334	69.08	2.50	219.05	223.96	221.51
P10	18.48617176	21.93110141	69.80	2.50	264.84	314.19	289.52
P11	10.57738962	10.8199903	71.33	2.50	148.29	151.69	149.99
P12	20.52401747	21.39737991	71.04	2.51	287.99	300.25	294.12
P13	9.170305677	9.315866084	68.60	2.52	132.77	134.87	133.82
P14	2.804463852	2.819019893	67.80	2.51	41.28	41.49	41.39
P15	1.154779233	1.159631247	68.35	2.50	16.89	16.96	16.92
P16	12.80931587	13.24599709	69.49	2.50	184.42	190.71	187.56

	Phenolox	"Perox"	Start (T1)	End (T2)	Duration	TM	Phenoloxidase activity	"Perox"	Real peroxidase activity
	Absorption	Absorption	MM-DD-YY HH-MM	MM-DD-YY HH-MM	h	g	µmol g-1 h-1	µmol g-1 h-1	µmol g-1 h-1
P1	0.116	0.125	3.14.16 13:50	3.15.16 9:50	20.00	0.77	6.81	7.0	0.2
P2	0.063	0.066	3.14.16 13:50	3.15.16 9:50	20.00	0.76	3.71	3.8	0.1
P3	0.089	0.093	3.14.16 13:50	3.15.16 9:50	20.00	0.83	4.79	4.8	0.0
P4	0.108	0.112	3.14.16 13:50	3.15.16 9:50	20.00	0.73	6.67	6.6	0.0
P5	0.107	0.112	3.14.16 13:50	3.15.16 9:50	20.00	0.69	6.91	6.9	0.0
P6	0.077	0.085	3.14.16 13:50	3.15.16 9:50	20.00	0.73	4.74	5.0	0.3
P7	0.110	0.118	3.14.16 13:50	3.15.16 9:50	20.00	0.71	6.98	7.2	0.2
P8	0.185	0.187	3.14.16 13:50	3.15.16 9:50	20.00	0.79	10.49	10.2	-0.3
P9	0.123	0.129	3.14.16 13:50	3.15.16 9:50	20.00	0.65	8.44	8.6	0.1
P10	0.114	0.122	3.14.16 13:50	3.15.16 9:50	20.00	0.69	7.34	7.6	0.2
P11	0.110	0.118	3.14.16 13:50	3.15.16 9:50	20.00	0.70	7.08	7.3	0.2
P12	0.118	0.124	3.14.16 13:50	3.15.16 9:50	20.00	0.71	7.43	7.5	0.1
P13	0.140	0.139	3.14.16 13:50	3.15.16 9:50	20.00	0.67	9.33	9.0	-0.4
P14	0.130	0.133	3.14.16 13:50	3.15.16 9:50	20.00	0.66	8.81	8.7	-0.1
P15	0.181	0.180	3.14.16 13:50	3.15.16 9:50	20.00	0.66	12.27	11.7	-0.5
P16	0.129	0.134	3.14.16 13:50	3.15.16 9:50	20.00	0.67	8.59	8.6	0.0

	meanUrease	Start (T1)	End (T2)	Duration	TM	Slope/extinktion coefficient	Urease activity
	Absorption	MM-DD-YY HH-MM	MM-DD-YY HH-MM	h	g		nmol NH4 g-1 h-1
P1	0.325	7.24.14 12:50	7.25.14 9:06	20.27	0.766	0.16	65.96
P2	0.131	7.24.14 12:50	7.25.14 9:06	20.27	0.761	0.16	26.71
P3	0.234	7.24.14 12:50	7.25.14 9:06	20.27	0.834	0.16	43.56
P4	0.184	7.24.14 12:50	7.25.14 9:06	20.27	0.729	0.16	39.35
P5	0.270	7.24.14 12:50	7.25.14 9:06	20.27	0.695	0.16	60.45
P6	0.925	7.24.14 12:50	7.25.14 9:06	20.27	0.732	0.16	196.49
P7	0.649	7.24.14 12:50	7.25.14 9:06	20.27	0.709	0.16	142.31
P8	0.655	7.24.14 12:50	7.25.14 9:06	20.27	0.792	0.16	128.60
P9	0.873	7.24.14 12:50	7.25.14 9:06	20.27	0.652	0.16	208.11
P10	1.104	7.24.14 12:50	7.25.14 9:06	20.27	0.695	0.16	247.13
P11	0.394	7.24.14 12:50	7.25.14 9:06	20.27	0.699	0.16	87.73
P12	1.084	7.24.14 12:50	7.25.14 9:06	20.27	0.715	0.16	235.97
P13	1.712	7.24.14 12:50	7.25.14 9:06	20.27	0.672	0.16	395.93
P14	1.299	7.24.14 12:50	7.25.14 9:06	20.27	0.660	0.16	305.98
P15	1.129	7.24.14 12:50	7.25.14 9:06	20.27	0.664	0.16	264.64
P16	1.810	7.24.14 12:50	7.25.14 9:06	20.27	0.673	0.16	418.49

		nmol g-1 h-1	nmol g-1 h-1	nmol g-1 h-1	nmol g-1 h-1	nmol g-1 h-1
		Exoglucanase	β-Glucosidase	Exochitinase	Phosphatase	Protease
	1	227.36	783.32	221.41		3151.63
	2	229.98	921.16	238.18	3444.89	3133.91
	3	197.02	784.47	326.93	2974.58	3034.64
CV_A	4	237.34	662.76	529.73	3563.19	2620.51
	5	187.12	1076.26	1640.29	4154.12	4154.12
	6	339.66	1309.31	2679.95	4206.79	4206.79
	7	304.44	1449.49	2838.61	4098.22	4098.22
CV_F	8	341.90	1534.88	3007.49	4291.27	4291.27
	9	230.61	828.70	1197.18	3224.75	1695.32
	10	286.43	1253.87	1848.45	4215.57	1927.43
	11	171.80	561.19	1025.97	2504.17	1243.11
EC_A	12	184.50	924.36	1075.02	2552.06	1644.94
	13	371.93	2163.83	1263.49	3777.40	2392.46
	14	257.03	2220.07	1048.92	4353.86	3065.99
	15	376.85	1515.29	1110.99	5368.38	2789.97
EC_F	16	359.00	1465.85	1065.14	3672.80	2287.13

Proben ID		mg CO2/g TS.h	mg CO2/g TS.h
CV_A_I_1	P1	55.88	33.65
CV_A_II_1	P2	47.23	26.97
CV_A_III_1	P3	45.03	28.28
CV_A_IV_1	P4	49.55	38.62
CV_F_I_1	P5	93.16	92.51
CV_F_II_1	P6	96.94	92.62
CV_F_III_1	P7	111.17	109.85
CV_F_IV_1	P8	110.85	100.85
EC_A_I_1	P9	29.73	25.73
EC_A_II_1	P10	19.44	21.37
EC_A_III_1	P11	25.91	16.94
EC_A_IV_1	P12	33.49	26.53
EC_F_I_1	P13	69.38	64.55
EC_F_II_1	P14	51.44	45.94
EC_F_III_1	P15	49.44	44.66
EC_F_IV_1	P16	64.49	53.06

	Pmic µg PO4-P g-1
	12.57
	5.00
	4.65
CVA	10.27
	15.95
	23.95
	25.93
CVF	
	8.26
	28.31
	18.73
ECA	15.97
	75.32
	64.26
	48.37
ECF	61.13