

The Local Impact of Macrofauna and Land-Use Intensity on Soil Nutrient Concentration and Exchangeability in Lowland Tropical Peru

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**The Local Impact of Macrofauna and Land-Use Intensity on Soil
Nutrient Concentration and Exchangeability in Lowland Tropical
Peru**

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ABSTRACT

Agricultural expansion is a major driver of deforestation which has negative consequences for biodiversity and habitat stability. While sustainable farming is known to be beneficial for biodiversity and crop resilience, little is known about the impact of macrofauna and land-use intensity on soil quality. In this study, we examine the relative effects of (1) soil macrofauna and (2) land-use (primary forest, agroforestry, annual crop) on element depletion rates, concentration, and exchangeability in standardised soil. We used microcosms with two different mesh sizes, 0.25mm and 5mm, to exclude and include macrofauna, respectively. The microcosms were incubated for up to a year throughout which samples were collected without replacement. Macrofauna did not have a significant impact on any of the soil parameters which is likely to be due to the low diversity of termites in the sites. Land-use intensity significantly affected cation depletion rates whose effects increased in order of primary forest < agroforestry < annual crop. At the end of the study soil Mg^{+2} concentration and Ca/Mg ratio in the agroforestry site differed from other land-use sites. Our results suggest that both bottom-up and top-down interactions have major effects on soil conditions and the results should therefore be used to advice future research and policy around land-use management.

Keywords: agroforestry; annual crop; land-use; macrofauna; Peru; primary forest; soil.

RESUMEN

La expansión Agrícola es una de las causas principales de deforestación y tiene consecuencias negativas para la biodiversidad y estabilidad del suelo. Aunque se sabe que la agricultura sostenible es beneficiosa para la biodiversidad y para la resiliencia agrícola, tenemos un conocimiento mínimo acerca del papel que tienen la macrofauna y la intensidad del uso del suelo en su calidad. En este estudio examinamos los efectos relativos de (1) la macrofauna del suelo y (2) del uso de suelo (bosque primario, agroforestería, cosechas anuales) en las tasas de agotamiento de elementos del suelo, su concentración y su capacidad de intercambio catiónico en suelos estandarizados. Para nuestros análisis usamos microcosmos con diferentes tamaños de grilla, 0.25mm y 5mm, para así respectivamente poder excluir o incluir la macrofauna. Los microcosmos fueron incubados hasta por un año a lo largo del cual muestras fueron tomadas aleatoriamente y sin remplazo. Encontramos que la macrofauna no tuvo un efecto significativo en ninguno de los parámetros de suelo analizados, esto es posiblemente el resultado de la baja diversidad de termitas en los lugares de muestreo. La intensidad del uso de suelo presentó un efecto significativo en la tasa de agotamiento catiónico, estos efectos se incrementaron partiendo de bosques a agroforestería y a cosechas anuales. Al final del estudio la concentración de Mg^{+2} y la proporción de Ca/Mg en el sitio de agroforestería fueron diferentes a los de los otros sitios. Nuestros resultados indican que las dos interacciones, tanto como de enfoque ascendente como descendente, tienen un efecto importante en las condiciones del suelo y por lo tanto los resultados podrían ser usados para guiar nuevas rutas de investigación y asesorar las políticas sobre el manejo de uso de suelo.

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2
3 AGRICULTURAL expansion, due to an increased demand for products, is one of the major
4 contributors to deforestation in tropical regions (Defries *et al.* 2010, Tilman *et al.* 2011) and has
5 been shown to affect soil quality by reducing carbon (C) availability and increase bulk density
6 (Murty *et al.* 2002). Additionally, soil macrofauna diversity has been shown to decline with land-
7 use intensity in order of forest > agroforestry > pasture > annual crop (Barros *et al.* 2002). Soil
8 macrofauna plays a key role in maintaining soil stability as it regulates nutrient cycling,
9 bioturbation and soil erosion (Thiele-Bruhn *et al.* 2012, Jouquet *et al.* 2011, 2006, Siegrist *et al.*
10 1998). Hence, less intense agricultural systems (agroforestry) with potentially higher macrofauna
11 diversity may promote self-regulatory habitats (Thiele-Bruhn *et al.* 2012, Black & Okwakol
12 1997) and enhance crop resilience against disturbance, stress and soil-borne diseases (Brussaard
13 *et al.* 2007).

14
15 Soil macrofauna, in particular termites, are highly abundant in tropical terrestrial regions
16 (Bignell & Eggleton 2000), and vital for ecosystem functioning. Termites are ecosystem
17 engineers that alter the physical and chemical structure of their habitats (Jouquet *et al.* 2014,
18 2011, Jones 1990, Jones *et al.* 1994); however, termite diversity is highly sensitive to disturbance
19 (Jones *et al.* 2003, Vaessen *et al.* 2011). Kagezi *et al.* (2011) showed that farmland consistently
20 had lower cellulose removal rates by termites than forest habitats or grasslands. Hence, the
21 reduction of termite mediated decomposition with agricultural intensification may reduce the
22 prosperity of farmland compared with agroforestry where biodiversity is higher (Asare *et al.*
23 2014, Evans *et al.* 2011). While there is a general consensus that sustainable farming is beneficial
24 for biodiversity and crop resilience, little is known about the impact of macrofauna or land-use
25 intensity on soil quality (but see Herrick [2000] for a general discussion).

26
27 In this study, we aim to examine the relative impacts of (1) soil macrofauna and (2) land-
28 use intensity on element depletion rates and concentration, and cation exchangeability. We

hypothesise that macrofauna will have a significant impact on soil element depletion rates, concentrations and exchangeability with its impact declining with land-use intensity (primary forest > agroforestry > annual crop) (Murty *et al.* 2002). Further, we hypothesise that element depletion rates will increase and concentrations decrease with land-use intensity due to the reduction of trees and root biomass (Fukuzawa *et al.* 2006).

METHODS

STUDY SITE – The study was conducted between May 2015 - May 2016 in three areas of different land-use intensity in the province of Ucayali in Peru. The region has mean annual temperature and rainfall of 26.1°C and 3,329 mm, respectively (climate-data.org). One site per land-use intensity was established and the sites were located 2 km - 30 km apart. The soil type in all sites was identified as Inceptisols, Dystrudepts (Soil Survey Staff 1999) and neither fertilisers, pesticides nor insecticides were used in any of the sites prior to, or during, the sampling. The land-use intensity was ranked from low to high as follows:

- Primary forest: well-preserved natural forest owned and managed by Universidad Nacional de Ucayali (UNU), Pucallpa. The forest was selectively logged in recent history but never clear-cut and has, to our knowledge, no history of burning. The topography was relatively flat with shallow streams surrounding the plot (see Table 1 for site specific information).
- Cocoa agroforestry: managed mature (ca 15 years old) plantation with regular cutting of the herbaceous understory. Common tree species found on-site were *Inga edulis*, *Calycophyllum spruceanum*, *Guazuma crinita*, *Phytelephas macrocarpa*, *Atallea phalerata*, and *Bactris gasipaes*. Trees were planted for shade, fruit, timber, firewood, and thatching

material (Vebrova *et al.* 2014). The topography was flat except for the interception of a shallow stream at the edge of the plot.

- Annual maize crop: The maize field was burned in August 2014 after which maize was planted and harvested in March 2015. At the start of the experiment the field had been untouched for two months and harboured dense but short undergrowth. The topography was flat with steep sections where streams formed in the wet season.

EXPERIMENTAL DESIGN AND MICROCOSM PREPARATION – In each site an 80 m × 80 m plot was established at least five meters from the site boundary. Due to the elongated outline of the agroforestry site the shape of the plot resulted in an expansion of the sampling area (= 200 m²). A soil macrofauna exclusion experiment was conducted using soil microcosms where macrofauna was included and excluded with mesh of two different sizes (see below). In each site the two microcosm treatments were positioned in pairs at random at least 10 m apart (60 microcosms per site and 180 microcosms in total).

Standardised soil was prepared using a combination of two parts Inceptisol, Eutrudept soil, (Soil Survey Staff 1999) and one-part humus collected from two secondary forests at the UNU in Pucallpa, Peru, at an altitude of 150 m (S8°23'58.9", W74°34'36.6"). The average (±SD) pH of the soil mixture was 5.3 ± 0.3 and the proportion of C and N were 4.2% ± 1.5% and 0.3% ± 0.07%, respectively. The soil texture was loam to sandy loam with an average sand, silt and clay content of 50.4%, 39.7% and 9.9% respectively. The soil was homogenised and then sterilised in an autoclave at a maximum temperature of 120°C and pressure of 15 psi. Sterilisation was conducted to enable the soil to be inhabited by organisms that were specific to the sites which enabled us to fully decipher the role of microorganisms and macrofauna invertebrates in the different land-use sites.

Microcosms were constructed using 500 ml cylindrical (6.4 cm height and 10 cm diameter) plastic pots with lids. The bottom and top of each pot were cut out and replaced with fine (0.25 mm) and coarse (5 mm) stainless steel mesh to exclude and include macrofauna, respectively (see Dahlsjö *et al.* 2014a). Each microcosm was buried a couple of centimetres below ground (Fig. S1). Soil macrofauna activity is highest in the top ten centimetres (Lavelle *et al.* 2006) and so the height of the microcosms allowed soil macrofauna to enter both from the top and bottom while the soil was retained within the microcosm.

SAMPLING – Sampling took place at five sampling occasions (3, 6, 12, 24 and 48 weeks after installation) during which six microcosms of each mesh treatment were collected at each site without replacement. Soil temperature and moisture were recorded in each microcosm as they were extracted from the ground during sampling. This was done to detect relative microclimatic differences between the mesh treatments and the potential impact they may have had on the results. All macrofauna from the microcosms were collected and placed in >70% ethanol and used as a determinant of treatment effectiveness (if macrofauna was detected in microcosms with fine mesh the samples were not used). Soil samples were air dried to constant temperature and processed through a 2 mm sieve at the UNU in Pucallpa after which they were transported to the Czech Republic for chemical analysis.

Termite abundance is high in tropical ecosystems with an average of 130 individuals m⁻² recorded in Peru (Dahlsjö *et al.* 2014). While termite biomass may be exceeded by that of earthworms (Köning & Varma 2006), a similar study found termite biomass to be higher than that of other taxa in the soil (Dahlsjö *et al.* 2014b). For better understanding of the functional diversity of termite species we therefore conducted termite specific sampling using a standardised belt transect (100 m × 2 m) in each study site following Jones & Eggleton (2000). Each transect

was split into twenty 10 m² sections (2 m × 5 m) in which termites were collected from a range of micro-habitat including leaf-litter, dead wood (logs and branches), runways, nests and mounds, at the base of plants, and in twelve soil pits (12 cm × 12 cm × 10 cm). In each 10 m² section termites were searched for during one person-hour (active searching by two people for 30 min) and preserved in >70% ethanol.

Environmental data from two data loggers (TOMST®) in each site provided ambient temperature (12 cm above the ground), soil surface temperature (ground level), and soil temperature and soil moisture (6 cm depth) data that were recorded with 15 minute intervals throughout the 48 week experiment. Canopy cover was measured at each sampling location in all sites using a spherical convex densitometer. The densitometer was preferred above other methods due to its wide angle (120°) that includes both canopy cover and light penetration (Fiala *et al.* 2006). Light penetration was deemed to be an important parameter as macrofauna may be sensitive to temperature and moisture extremes affected by the amount of sun penetrating the canopy (see e.g. Eggleton *et al.*, 1996). Five random soil samples from each site were collected for determination of soil type and quality (see Table 1).

SOIL CHEMICAL AND STRUCTURAL ANALYSES – Soil chemical and structural analyses were conducted by J. H., J.J. and M. Z. at the Department of Soil Science and Soil Protection, Czech University of Life Sciences in Prague, Czech Republic. Elemental analyses of nitrogen (N) and carbon were conducted using a Thermo Scientific Flash 2000 NCS Analyser while soil pH was recorded using an inoLab Level 1 pH-meter with 1:5 (w/v) ratio of soil and water solution (ISO 10390:2005). Particular main alkaline (Na⁺, K⁺, Mg²⁺, Ca²⁺) and acid (Al³⁺, Fe³⁺, Mn²⁺) elements were determined via inductively coupled plasma mass spectrometry (ICP-OES iCAP

7000 Thermo Scientific USA) in a BaCl₂ solution following the ICP Forest protocol (Cools & De Vos 2010). In the same BaCl₂ solution pH was recalculated to determine the H⁺ values of the soil (Cools & De Vos 2010). Further, exchangeable acidity (EA) was calculated as the sum of all acid elements including H⁺, whereas Cation Exchange Capacity (CEC) was calculated as the sum of all elements both acid and alkaline. Base saturation is given by the ratio EA/CEC * 100 and soil texture was defined by an aerometric method following Rzaşa and Owczarzak, (2013) and samples were classified according to the USDA texture triangle.

MACROFAUNA IDENTIFICATION – Macrofauna that was encountered in the soil microcosms were identified to Order for all insects and to Class for other invertebrate taxa by C. A. L. D (Table S1). Due to the functional importance of termites, and the high abundance in some samples, termites were identified to the highest possible resolution. Soldiered termites were identified to genus using Constantino's (2002) key to Neotropical genera. Species were identified using keys for specific genera (e.g. Bourguignon & Roisin 2011) or the reference collection at the Natural History Museum (NHM) in London. When soldiers were not available, gut morphology and enteric valve structures were used to identify the worker caste. Soldierless termites were identified to species by their gut morphology and enteric valve structures described in Bourguignon et al. (2010 and 2015) and in the unpublished key to Apicotermitinae species of the Guiana Shield (Hernandez L. M. unpubl. data) (see Table S2 for a list of termite species and morphospecies). Termite feeding-groups (FG) were identified following Donovan et al. (2001) and Inward et al. (2007) where the feeding substrates of the different groups are defined as follows: FGI- sound wood, FGII- wood and leaf litter, FGIII- soil and humus with visible plant structures, and FGIV- mineral soil without visible plant structures.

DATA ANALYSIS – Soil samples were taken before and after sterilisation to examine its effects on soil quality. The differences in carbon and nitrogen concentrations in the sterilised and unsterilised soils were analysed using ANOVA. ANOVA was also used to examine the impact of the mesh-treatments (fine and coarse mesh) on the physical conditions of the soil by comparing the variance in temperature and moisture between the two treatments.

Element depletion rates and ratios were generated by analysing the changes in soil quality over time. The time between each sampling occasion increased exponentially (3, 6, 12, 24, and 48 weeks after the start of the experiment) and was log-transformed along with the soil data to generated log-normal distributions. Macrofauna effects were examined by comparing soil quality in the control (including macrofauna) and exclusion treatments (excluding macrofauna) while the impact of land-use intensity on soil quality was examined using data from the control treatment only. The difference in depletion rates between mesh treatments and among land-use sites were examined using analysis of covariance (ANCOVA) (*lm*, R) for all soil element concentrations, cation exchangeability, and pH. Untransformed data were used to explore the difference in soil chemical composition among sites at the end of the experiment after 48 weeks; these analyses were conducted using ANOVA and *post hoc* TukeyHSD tests for each of the soil elements (*aov* and *TukeyHSD*, R). Significant data from the ANCOVA and *post hoc* analyses were visualised using the [graphics] package in R. Termite species richness was generated from the transect surveys in each site and represent the number of species found in each transect. Species richness was pooled for each feeding-group and site and visualised using the [ggplot2] package in R.

RESULTS

We found that the sterilisation of the soil baits reduced C and N content by approximately 25% and the mesh treatments showed significant differences in soil moisture (ANOVA, $F = 4.7$, $P < 0.05$) with soil in the coarse mesh treatment being wetter than the soil in the fine mesh treatment (coarse mesh mean (\pm SD) $29\% \pm 14\%$ moisture; fine mesh mean (\pm SD) $24\% \pm 10\%$ moisture).

Land-use intensity had a significant impact on cation depletion rates and end-of-experiment concentration, while the macrofauna exclusion treatment did not have a significant impact on soil quality (ANCOVA, $P > 0.05$, for all analysed elements, cation exchangeability and pH). The depletion rates differed significantly among sites with the highest number of differences between the primary forest and annual crop site, followed by the primary forest and the agroforestry site, and then the agroforestry site and annual crop (Fig. 1). Depletion rates of the cations manganese (Mn^{2+}) and magnesium (Mg^{2+}) in the primary forest were significantly different to the depletion rates in the agroforestry site and the annual crop (lm , Mg^{2+} : primary forest – agroforestry, $F = 3.61$, $P < 0.01$; primary forest – annual crop, $F = 2.96$, $P < 0.05$, Mn^{2+} : primary forest – agroforestry, $F = 35.07$, $P < 0.05$; primary forest – annual crop, $F = 40.55$, $P < 0.01$) (Fig. 1). The depletion rates of both cations were higher in the agroforestry site and annual crop than in the primary forest where Mg^{2+} increased, and Mn^{2+} decrease at a slower rate than in the other land-use sites. Cation Exchange Capacity (CEC) and sulphur cations (S^{2+}) in the annual crop declined significantly faster than in the primary forest where CEC was shown to increase and S^{2+} decrease at a slower rate (lm , CEC: primary forest – annual crop, $F = 2.05$, $P < 0.05$, S^{2+} : primary forest – annual crop, $F = 6.82$, $P < 0.01$) (Fig. 1). Zinc cation (Zn^{2+}) concentration was relatively stable throughout the experiment in the primary forest and in the agroforestry site which were significantly different from the depletion of Zn^{2+} in the annual crop (lm , Zn^{2+} : primary forest – annual crop, $F = 6.82$, $P < 0.01$, agroforestry – annual crop, $F = 8.47$, $P < 0.05$) (Fig. 1). The Ca^{2+}/Mg^{2+} ratio showed a significant increase in the agroforestry site compared

with the stable ratios in the primary forest and the annual crop (Fig. 1). At the end of the experiment the cation concentration of magnesium (Mg^{2+}) was significantly lower in the agroforestry site than in the primary forest (*TukeyHSD*, Mg^{2+} : primary forest – agroforestry, $F = 0.029$, $P < 0.05$) and the calcium/magnesium cation ratio (Ca^{2+}/Mg^{2+}) in the agroforestry site was significantly higher than in the primary forest and in the annual crop (*TukeyHSD*, Ca^{2+}/Mg^{2+} : primary forest - agroforestry, $F = 0.0006$, $P < 0.05$; agroforestry – annual crop, $F = 0.008$, $P < 0.05$) (Fig. 2).

Termite species richness was low in all study sites with the highest number of species recorded in the primary forest (9 species) followed by the annual crop (4 species) and then the agroforestry site (3 species) (Fig. 3, Table S2). No true soil-feeding termites (FGIV) were recorded in the study and the agroforestry site showed the lowest diversity of feeding-groups with only FGIII (humus-feeding termites) being present.

DISCUSSION

In this study we have explored the top-down effects of macrofauna diversity and abundance, and land-use intensity on soil quality in an agricultural region in lowland Peru. We found that bottom-up effects of soil quality had an unexpected impact on the role of macrofauna in our samples suggesting that soil processes in the region are dominated by microbial activity. Additionally, we found that the properties of the standardised soil were more stable in the primary forest followed by the agroforestry and then the annual crop demonstrating the effects of land-use intensity on soil quality.

MACROFAUNA AND NUTRIENT CYCLING – Macrofauna did not show a significant impact on soil nutrient depletion in any of the land-use sites which may be due to (1) the impact of the mesh

treatments on the microhabitat of the microcosms, (2) the quality of the standardised soil, or (3) the low termite diversity in the study region.

Firstly, the moisture content of the soil in the coarse mesh treatment was on average 20% higher than the moisture content in the fine mesh treatment. The significant difference was unexpected as finer mesh has been shown to be prone to waterlogging (Richardson *et al.* 2010). A possible explanation may be that less water was able to enter the microcosms with fine mesh due to the small aperture. While macrofauna is sensitive to waterlogging (Martius 1994, Martius *et al.* 1994) the total soil water content in the coarse mesh was less than 30% which is not likely to have had an impact on the macrofauna. We therefore conclude that the difference in microcosm moisture, albeit significant, was too small to have had a major impact on the results.

Secondly, the standardised soil was low in organic matter ($C = 4.2\% \pm 1.5\%$; $N = 0.3\% \pm 0.07\%$) due to the inaccessibility of organic rich soil as well as the reduction of C and N following sterilisation. Note that the latter should be considered before sterilisation takes place in future research. The quality of the soil attracts organisms to the soil baits which increases the chance of seeing the relative difference between soil with and without macrofauna. In Dahlsjö *et al.* (2014), macrofauna was shown to have a significant impact on soil C and N depletion rates, over a period of four months, where C concentration in the standardised soil was high (15%). While the standardised soil in this study was more representative of regional soils, nutrient turnover in lowland tropical forests is high which means that the soils themselves may have low nutrient concentration at any one time (Quesada *et al.* 2011). Changes in soil nutrient concentration may therefore be difficult to detect over relatively short (≤ 1 year) time periods. We believe that higher organic content in the standardised soil may therefore have increased the detectability of differences between the two treatments within the time-frame of the study.

Thirdly, the diversity of termites, one of the most prominent decomposer organisms in lowland tropical ecosystems (Jouquet *et al.* 2011), was surprisingly low in all study sites. Only nine species were found in the primary forest which is low compared with other South American studies, e.g. an average (\pm SD) of 43 ± 1.7 species was found per transect in a Peruvian primary forest site (Dahlsjö *et al.* 2014). The low termite species richness (13 species in total) may be due to regional degradation and fragmentation, however, as long as primary forest patches are present in the landscape the original species pool have been found to be somewhat intact (Bourguignon *et al.* 2017). Bottom-up effects such as soil quality, on the other hand, may have a major impact on soil dwelling invertebrates. Jones *et al.* (2010) showed that termite diversity was radically lower in forests where soil cation concentration and pH were high. While cations were not measured in the study sites, the standardised soil was of a similar soil type (Inceptisol) and showed higher levels of Mg^{+2} and Ca^{2+} , and higher pH than in Tambopata, the study region in Dahlsjö *et al.* (2014) where termite species richness has been shown to be high. According to Jones *et al.* (2010) the high concentration of cations in the soil may cause metal toxicity in termites and the relatively high pH may interfere with the microbial symbionts that are vital for the breakdown of organic matter in the termite gut (Hongoh & Ohkuma 2010). The low diversity of termites is therefore the most likely cause of the non-significant results of the macrofauna exclusion experiment. The above should be considered in future studies and better understanding of the impact of soil quality on invertebrate communities is called for due to their importance in ecosystem functioning.

LAND-USE INTENSITY AND NUTRIENT CYCLING – As hypothesised, the difference in nutrient depletion rates was higher between the lowest (primary forest) and highest (annual crop) land-use intensity sites while the two farmed sites (agroforestry and annual crop) showed the lowest

number of significant differences. Among the six significant relationships, the trends of nutrient availability were predominantly positive (slower) in the primary forest than in the agroforestry site or the annual crop. In contrast, depletion rates were highest in the annual crop.

The low impact of macrofauna suggests that microbial communities played a major role in soil nutrient cycling in the study region. Forest habitats, even when logged, have been shown to have higher microbial biomass than degraded land such as plantations (Araújo *et al.* 2013) with the removal of vegetation showing a major impact (Zhao *et al.* 2011). Microbial organisms, such as bacteria and fungi, break down organic matter into forms that are available for plant uptake (Lavelle *et al.* 2006). The absence of vegetation in the soil baits, and the potentially higher microbial biomass in the forested site, may explain the accumulation of some soil elements in the primary forest.

At the site level, a reduction in vegetation biomass has been shown to increase nutrient leaching due to the reduced root biomass and increased water flow (Fukuzawa *et al.* 2006). The lack of trees, coupled with potentially lower microbial biomass, may explain the high depletion rates in the annual crop site. Despite the presence of cocoa trees and native trees in the agroforestry site, depletion rates were still similar to that of the annual crop. This may have been due to the regular cutting of the understory creating spikes in nutrient input which has been shown to lead to increased levels of leaching (Poudel *et al.* 2002). The potential difference in microbial biomass and the difference in vegetation among sites are therefore likely to be the main reasons for the significant differences in nutrient depletion rates among sites.

EFFECT OF LAND-USE INTENSITY ON SOIL NUTRIENT CONCENTRATION – While depletion rates increased with increasing land-use intensity, the concentration of soil nutrients at the end of the

experiment differed relatively little with only Mg^{2+} and $\text{Ca}^{2+}/\text{Mg}^{2+}$ ratio being significantly different among sites. While the depletion rates suggested that nutrient availability in the primary forest was more closely related to the agroforestry site than the annual crop, agroforestry was the only site that was significantly different in nutrient concentration at the end of the study with lower Mg^{2+} concentration than the primary forest and higher Ca/Mg ratio than the primary forest and the annual crop. In the primary forest and annual crop, Ca^{2+} changed with the concentrating of Mg^{2+} over time whereas the concentration of Ca^{2+} in the agroforestry site stayed the same. It is unclear why Ca^{2+} concentration in the agroforestry site did not change throughout the study, although it might be due to the presence of decomposing cut weed biomass and harvested cocoa pods coupled with a certain level of leaching. The high $\text{Ca}^{2+}/\text{Mg}^{2+}$ ratio in the agroforestry site was higher than the ratio that is considered suitable for optimal plant growth due to the adverse effect that Ca^{2+} has on Mg^{2+} availability (Vootman & Bindraban 2015). Mg^{2+} is a vital component of chlorophyll which plays a major role in photosynthesis and plant growth (Hao & Papadopoulos 2004) which suggests that soil fertility in the agroforestry site at the end of the study may have been low. Agroforestry was also the only site with one termite feeding-group, which is low even for disturbed habitats (Neoh *et al.* 2015, Eggleton *et al.* 1996).

The relative similarity in nutrient concentration and exchangeability among sites may, as discussed above, be due to the generally low biodiversity in the study region. This may have had an impact on nutrient cycling resulting in slower soil processes than in areas with higher soil biodiversity (Dahlsjö *et al.* 2014b). The soil incubation time in this study may therefore have been too short to see a substantial change in nutrient availability. To further the understanding of the resilience of ecosystems to deforestation and climate change we encourage studies to examine the long-term impact of land-use intensity on soil functioning.

CONCLUSION- This study examined standardised soil to gauge how external conditions and decomposer organisms affect soil quality in sites with different land-uses. The low diversity of termites, and other macrofauna, is likely to be due to the high levels of trace metals and pH across the sites. Additionally, while the soil in the agroforestry site had a high $\text{Ca}^{2+}/\text{Mg}^{2+}$ ratio, unfavourable for plant growth, the annual crop site showed the highest rates of element depletion. Our results suggest that both bottom-up (effect of soil quality on the functional role of macrofauna decomposers) and top-down (land-use intensity on soil quality) interactions have major effects on soil conditions. While some management regimes, such as understory removal or burning, are carried out to increase crop productivity, they may inadvertently reduce soil nutrient retention and biodiversity, thereby creating agro-systems that are less resilient to global change. These insights should be used to advice future research and policy around land-use management.

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.jj3ft18>
(Dahlsjö, Stiblik, Jaklová, Zídek, Huaycama, Lojka, and Houška, 2019).

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TABLES

Table 1. Site specific information. Temperature and moisture data are from the experimental period between May 2015 and May 2016. All measurements were taken from the localities and are not linked to the soil used in the soil microcosms. PF = primary forest, AF= cocoa agroforestry, AC = maize annual crop.

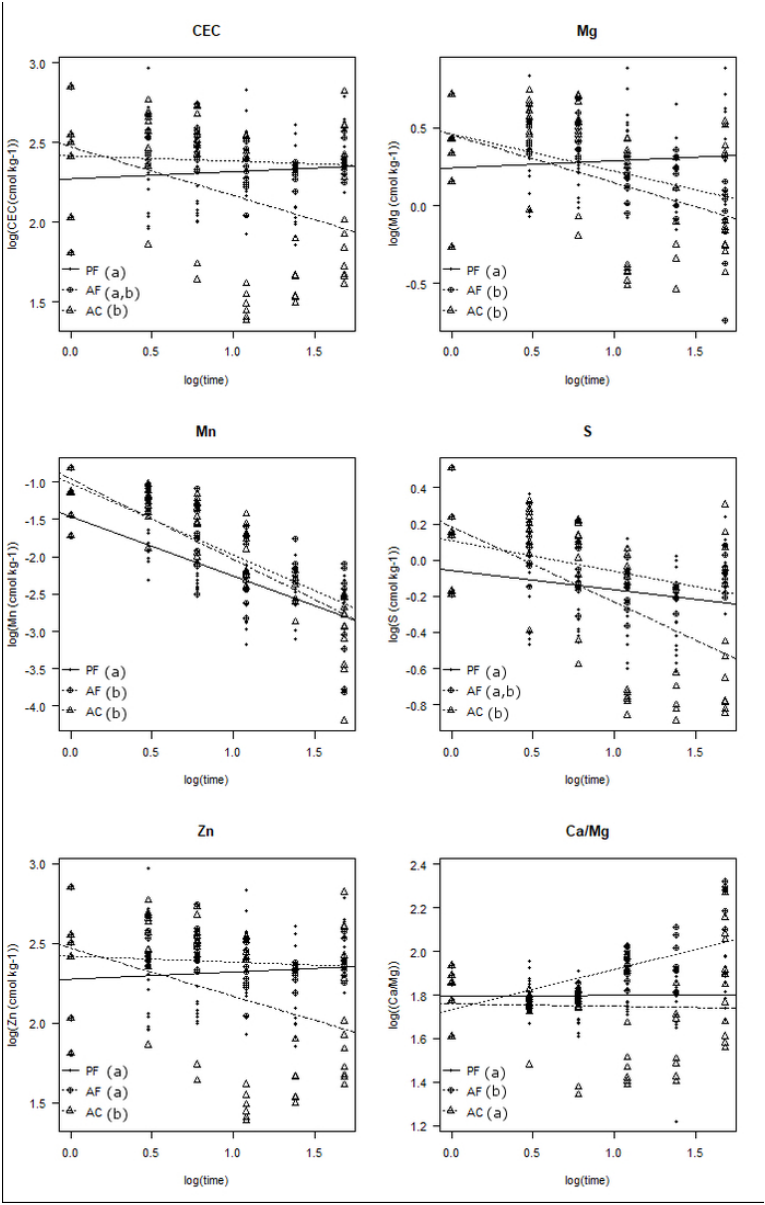
Site	Latitude	Longitude	Area	Soil temp °C	Soil moisture %	Canopy cover %	O-horizon	Soil pH	Carbon %	Nitrogen %
			(ha)	(mean±SD)	(mean±SD)	(mean± SD)	(cm)		(mean± SD)	(mean± SD)
PF	-8.87S	-75.01W	2469	25.3 ± 0.8	40.0 ± 7.8	98.4 ± 1.3	<10	6.2 ± 0.6	3.9 ± 0.6	0.3 ± 0.02
AF	-8.81S	-75.23W	1	26.2 ± 0.8	29.1 ± 10.6	91.5 ± 4.7	20	5.7 ± 0.1	2.8 ± 0.8	0.2 ± 0.07
AC	-8.90S	-75.13W	6	26.4 ± 1.3	26.9 ± 12.0	69.6 ± 6.0	<10	6.7 ± 0.5	3.3 ± 1.6	0.2 ± 0.07

FIGURE LEGENDS

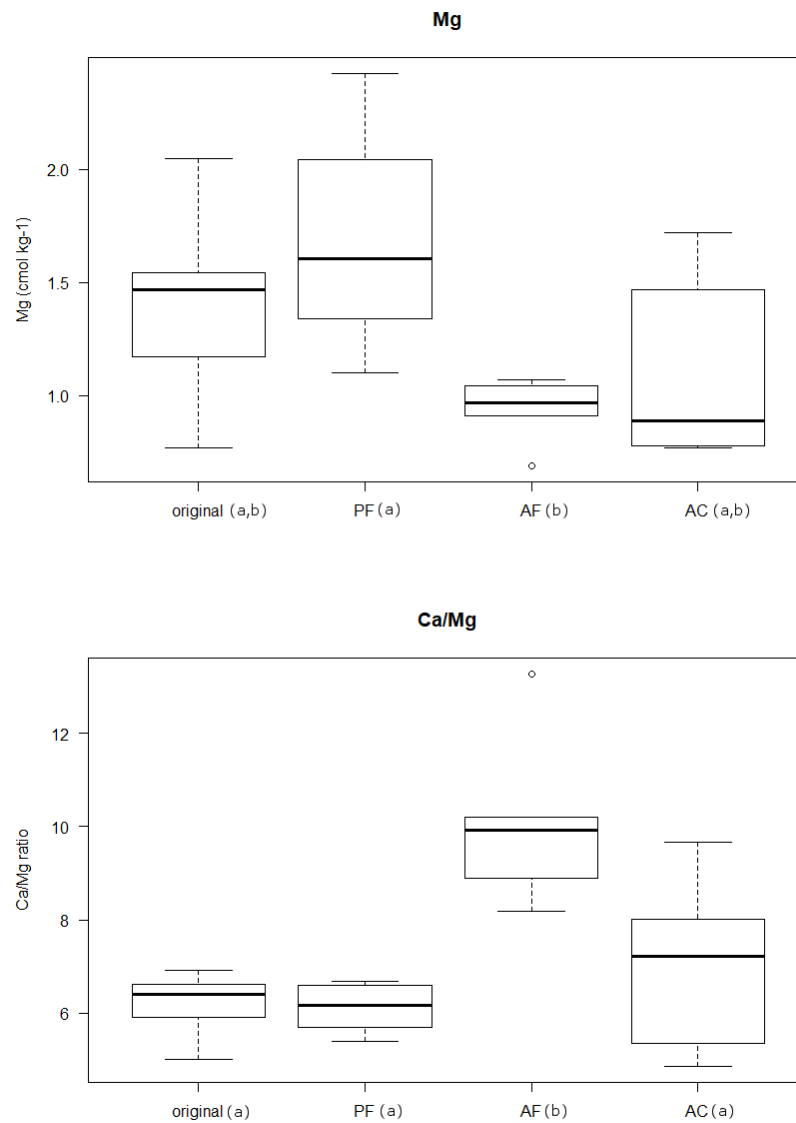
FIGURE 1. Models (ANCOVA) of log-transformed time and nutrient concentration in the three study sites (PF: primary forest, AF: agroforestry, AC: annual crop) indicating trends in nutrient concentration and exchangeability over time. Different letters (in brackets) indicate significant differences among depletion rates indicated by the solid and dashed lines.

FIGURE 2. Mg^{2+} concentration and Ca^{2+}/Mg^{2+} ratio in the soil baits at the end of the experiment (48 weeks). Different letters (in brackets) indicate significant differences. The whiskers show the minimum and maximum observed values and the black line is the median. PF: primary forest, AF: agroforestry, AC: annual crop.

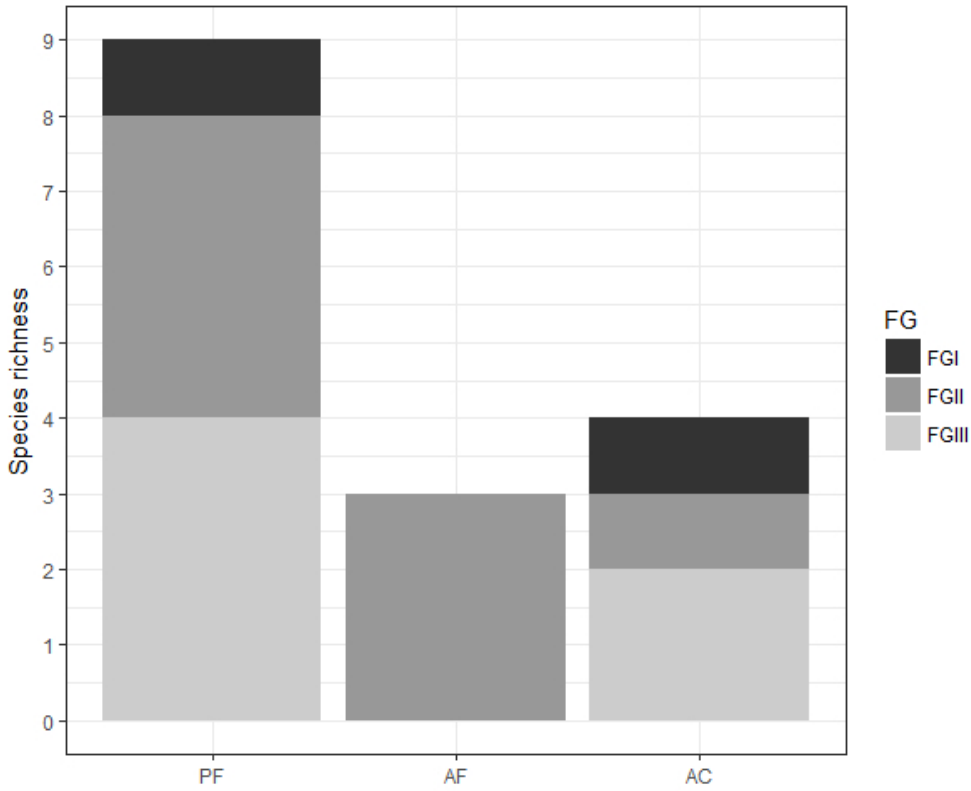
FIGURE 3. Termite species richness of feeding-groups. PF: primary forest, AF: agroforestry, AC: annual crop. FGI: wood-feeding termites, FGII: wood and litter-feeding termites, FGIII: humus-feeding termites.



59x92mm (300 x 300 DPI)



71x101mm (300 x 300 DPI)



50x42mm (300 x 300 DPI)

SUPPORTING INFORMATION

The Local Impact of Macrofauna and Land-Use Intensity on Soil Nutrient Concentration and Exchangeability in Lowland Tropical Peru

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Table S1. Abundance (mean \pm SD) of taxa (order and class) per microcosm across sampling occasions in the three land-use sites.

Class	Order	Primary Forest	Agroforestry	Annual Crop
INSECTA				
	Termitoidea	2.78 \pm 11.78	-	64.11 \pm 245.02
	Hymenoptera	0.11 \pm 0.47	1.00 \pm 2.11	0.833 \pm 2.41
	Coleoptera	-	-	0.11 \pm 0.47
ARACHNIDS		0.06 \pm 0.24	0.89 \pm 2.01	0.22 \pm 0.73
DIPLOPODA		0.11 \pm 0.32	0.50 \pm 0.86	0.06 \pm 0.24
CHILOPODA		0.06 \pm 0.24	-	0.06 \pm 0.24
ISOPODA		0.39 \pm 1.42	4.11 \pm 6.53	2.06 \pm 3.84
CLITELLATA		0.056 \pm 0.24	0.33 \pm 0.77	-
GASTROPODA		-	0.06 \pm 0.24	-
TOTAL		3.72 \pm 11.73	7.17 \pm 8.21	67.44 \pm 245.14

Table S1. List of termite species and morphospecies that were encountered in each of the transects. Feeding-group

classification from Donovan *et al.* (2001), FGI = wood-feeders (non-Termitidae), FGII = wood-feeders (Termitidae),
FGIII = humus-feeders.

	Feeding-group	Primary forest	Agroforestry	Annual crop
RHINOTERMITIDAE				
<i>Heterotermes sp. I</i>	I	√	-	√
TERMITIDAE				
APICOTERMITINAE				
<i>Anoplotermes pacificus</i>	III	-	-	√
<i>Anoplotermes sp. F</i>	III	√	-	√
<i>Anoplotermes sp. K</i>	III	√	-	-
<i>Anoplotermes grp. GL</i>	III	√	-	-
<i>Anoplotermes sp. new</i>	III	√	-	-
NASUTITERMITINAE				
<i>Nasutitermes sp. I</i>	II	√	-	-
<i>Nasutitermes sp. II</i>	II	√	√	√
<i>Nasutitermes sp. III</i>	II	-	√	-

1					
2					
3	<i>Nasutitermes sp. V</i>	II	-	√	-
4					
5					
6	TERMITINAE				
7					
8					
9	<i>Microcerotermes sp. I</i>	II	√	-	-
10					
11					
12	<i>Microcerotermes sp. II</i>	II	√	-	-
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Figure S1. Soil microcosms with coarse (left) and fine (right) mesh in their respective locations in the ground. The microcosms were subsequently covered with soil and a brightly coloured flag was placed between them to indicate their position in the plot.

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