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Induced response of soil properties and Oribatid mites (Acari, Cryptostigmata) community structure after the conversion of tropical secondary forests into oil palm and rubber plantations

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Abstract

The aim of investigation was to address the impacts of tropical forests conversion into agricultural land on changes in Oribatid mites' communities as well as soil physico-chemical properties across 2–4 texturally distinct soils in La Mé and Grand Lahou, Côte d'Ivoire. The fieldwork was conducted in the humid period on two study sites: 1– rubber landscape (secondary forest, 7-, 12- and 25-year-old rubber plantations) and 2– oil palm landscape (secondary forest, 13-, 20- and 39-year-old oil palm plantations). Three sampling areas were established on each land-use type and age class, for a total of 24 sampling areas. In each sampling area, soil cores for Oribatid mite's extraction were taken at a depth of 10 cm across a 40–50 m transect. The soil physical and chemical properties were also measured. The results showed a decrease in Oribatid density (–29% and –71%), species richness (–29% and –42%), diversity (–29% and –59%), soil organic carbon (–56% and –17%), total nitrogen (–55% and –12%) and soil organic matter (–56% and –17%), and an increase in bulk density (+28% and +21%), respectively after the conversion of the secondary forests into rubber and oil palm plantations. Whatever the study site, the soil physico-chemical and biological properties were more stabilized in the clay and clay sandy textures compared to sandy clay and sandy soil textures. Our findings suggest the incorporation of woody trees with an understory of nitrogen-fixing legume species as a cover crop, which can create a sustainable agroforestry system with improved land quality.

Keywords: Soil physico-chemical properties, Oribatid mite communities, secondary forests conversion, rubber and oil palm plantations, soil quality

Introduction

With an estimated area of 4.06 billion hectares (FAO, 2020), the forests are the most species-rich and diversified ecosystems on the planet (Köhl *et al.*, 2015). Forests are so important because they harbor 50–80% of world's biodiversity (Le Danff, 2002). Soils and their inhabitants are fundamental for life since they contribute to the terrestrial ecosystem's functionality and they provide different ecosystem services, in particular, those related to food provisioning (Conti, 2015). Forests provide water, mitigate climate change, provide habitat for many invertebrates and also protect soils, that is a set of essential services for food production and a sustainable economic development (Köhl *et al.*, 2015).

Nonetheless, the transformation and degradation of landscapes is rapidly increasing worldwide. Due to the increase in the human population and increased resource demand, pressure on ecosystems is increasing strongly (Krause, 2020). Tropical deforestation has become a global environmental concern and a major cause of biodiversity loss as well as climate change (Swarnalatha, 2010; Allen, 2015). The original extent of tropical rain forests was 15 million km². There remains about 7.5–8 million km² with a current rate of loss estimated at near 2% annually (Swarnalatha, 2010). Data from 2010 to 2020 indicated a destruction of 3.9 million hectares of forests annually in Africa (FAO, 2020). During the latter half of the last century, monoculture plantations of rubber (*Hevea brasiliensis*) and oil palm (*Elaeis guineensis*) began to dominate the landscape (Allen, 2015). The large scale transformation of rainforests into monoculture plantation systems such as oil palm and rubber, is one of the main drivers for biodiversity modification (Krause, 2020). Therefore, it is important to understand the long-term effects produced by continued deforestation and subsequent cultivation on these transforming systems (Allen, 2015).

With over 16 million hectares at the beginning of the 20th century, currently the residual areas of forests in Côte d'Ivoire represent only about 2.97 million hectares (IFFN, 2021). The main perennial crops that cause deforestation in the country remain cocoa, coffee, rubber and oil palm (Tondoh *et al.*, 2015; Yéo *et al.*, 2020; Adiko, 2021). In recent decades, these crops have boomed in the humid tropics due to growing



demand from the population. The financial returns provided by these crops are considerable and decisive for the economies of producing countries (Despréaux and Nicolas, 2001). The rubber production system occupied 165 000 farmers and an area of 600 000 hectares (Commodafrica, 2018) with an annual production estimated at 990 000 tones in 2019 (Ndiaye and Fainke, 2020), which makes Côte d'Ivoire the leading African producing country and the sixth world producer of natural rubber (Adiko, 2021). Planted on an area of 250 000 hectares in Côte d'Ivoire, the average annual production of crude palm oil is estimated at 550 000 tones (Fages, 2019). With a 3.13% contribution to the gross domestic product, oil palm has become a major component in the country's economy (Palmafrique 2017).

Despite their major roles in the economy of Côte d'Ivoire, the conversion of forests into agricultural lands, unsustainable forest management and climate change are all having negative impacts on forest biological diversity (Swarnalatha, 2010), and may also affect the short- and long-term nutrient status of the converted land-use systems (Allen, 2015). The highest SOC losses in the upper layer were caused by the conversion of primary forests into tree plantations such as cocoa, coconut, rubber and oil palm (Chiti *et al.*, 2014). Likewise, DeBlécourt *et al.* (2013) pointed out a decline in soil carbon stocks of 37% on average following the conversion of tropical forests into rubber plantations in southern Yunnan Province, China; thus leading to a decrease in organic matter and soil fertility (Krashevskaya *et al.*, 2015). Soil organic matter influences soil structure. Indeed, the higher the organic matter, the more soil aggregation will be enhanced, promoting stable environments (Conti, 2015). Intensive agriculture is one of the anthropogenic activities that stimulate erosion with the loss of nutrient-rich upper soil layers (Conti, 2015). This degradation lowers the resilience of forest ecosystems and makes it more difficult for them to cope with changing environmental conditions (Swarnalatha, 2010). The intensification of agriculture and the traditional techniques based on extensive tillage have seriously affected the soils, degrading their physical and chemical parameters and causing loss of biodiversity (Conti, 2015).

Most of the work on the soil biological components, carried out simultaneously in rubber and oil palm plantations, only concerns bacteria, fungi, and enzymes (Krashevskaya *et al.*, 2015; Kerfahi *et al.*, 2016; Nurulita *et al.*, 2016), nematodes (Kerfahi *et al.*, 2016), and protists (Krashevskaya *et al.*, 2016). Yet, Oribatid mites with body size usually range between 100-1000 µm play a significant role in the process of decomposition and mineralization and are considered as the most successful among all soil arthropods (Lisafitri *et al.*, 2015; Mandal *et al.*, 2019). They possess a diverse mode of feeding starting from the degraded plant materials to decaying faecal matter. Several species of oribatid mites are instrumental in biodegradation because they consume large amounts of plant materials and digest them with enzymes (such as cellulose and cellobiase) produced by microbial colonies in mite guts (Haq, 2016; Mandal *et al.*, 2019). Due to low mobility, high population density and species richness oribatid mites have been proposed as a potential bio-indicator for soil health and land use, reflecting impacts of land use intensification (Sulistiyorini *et al.*, 2018; Mandal *et al.*, 2019). Their composition reflects the state of stress in the ecosystems. Oribatida are extremely sensitive towards all sorts of soil disturbance; their long life span, gradual development, low fecundity and dispersion indicate the status of the environment (Mandal *et al.*, 2019).

Apart from Drescher *et al.* (2016), information related to the impact of tropical rainforest transformation into oil palm and rubber plantations on Oribatid mites' diversity and community composition are rather unexplored. Some of the studies did not provide complete systematic information on soil properties such as texture and nutrients status (Vrignon-Brenas *et al.*, 2019). Similarly, the soil physico-chemical and biological properties responses to the combination of land-use change and soil texture have not yet been investigated in Cote d'Ivoire. In such landscapes, the most important factor affecting soil N availability is soil texture (Allen, 2015). The loss of soil nutrient depends on climatic factors, soil texture, the form of fertilizer applied, and agricultural practices (Vrignon-Brenas *et al.*, 2019). Soil biochemical characteristics, nutrient stocks and gross soil-N cycling rates in the reference land uses were higher in the clay than the loam Acrisol soils (Allen, 2015). Clay soils are known to have higher nutrient ion availability, higher water holding capacity, and higher soil-N cycling rates compared to sandy soils (Silver *et al.*, 2000; Sotta *et al.*, 2008). Soil type also influences organic matter turnover due to differences in soil clay content (Demessie *et al.*, 2013).

Previous studies demonstrated that the monoculture plantations have a negative impact on soil quality (Conti, 2015; Vrignon-Brenas *et al.*, 2019; Hemati *et al.*, 2020). Nonetheless, it is possible to maintain or improve soil conditions on a site by maintaining or increasing organic matter, nutrients and soil organism diversity (Vrignon-Brenas *et al.*, 2019; Hemati *et al.*, 2020). Conservation agriculture and the related management practices have demonstrated in the last decades to be an efficient tool to combine food productivity with environmental protection around the world (Conti, 2015; Vrignon-Brenas *et al.*, 2019; Hemati *et al.*, 2020).

The aim of investigation was to address the impacts of tropical forest conversion into agricultural land on changes in Oribatid mite's communities as well as soil physico-chemical properties across 2-4 texturally distinct soils in La Mé and Grand Lahou, Côte d'Ivoire. We hypothesized that (i) the Oribatid mite's

abundance, species richness and diversity will be higher in the reference land uses (secondary forests of Grand Lahou; secondary forests of La Mé) compared to agricultural lands (rubber plantations; oil palm plantations), (ii) soil carbon, total nitrogen, organic matter and soil water content will be higher in the reference land uses compared to agricultural lands, and (iii) soil physico-chemical and biological properties will be more stabilized in the clay and clay sandy textures compared to sandy clay and sandy soil textures.

Materials and Methods

Study sites description

This investigation was carried out in 2013 and 2017 in Côte d'Ivoire through two study sites. The first site hosting the rubber landscapes is based in the department of Grand Lahou (5°13'N; 5°03'W) situated in southern Côte d'Ivoire about 140 km of Abidjan. The second site, characterized by the oil palm landscape is located in the La Mé Station (5°26'N, 3°50'W) in south-eastern of Côte d'Ivoire, -30 km from Abidjan (Fig. 1). The climate of the two study sites is an equatorial type with four seasons: a long dry season from December to March, a long wet season from April to July, a short dry season from August to September, and a short wet season from October to November (Péné and Assa, 2003; Ettian *et al.*, 2009). During the fieldwork on the site of Grand Lahou (site 1), the monthly rainfall ranged from 0 mm in January to 282 mm in June, with an annual total of 1,085 mm. Monthly mean temperature varied between 25°C in August and 29°C in February and March, with an annual average of 27°C. This site is characterized by a rainforest vegetation type, and various land uses such as secondary forests, rural domains and fallow systems

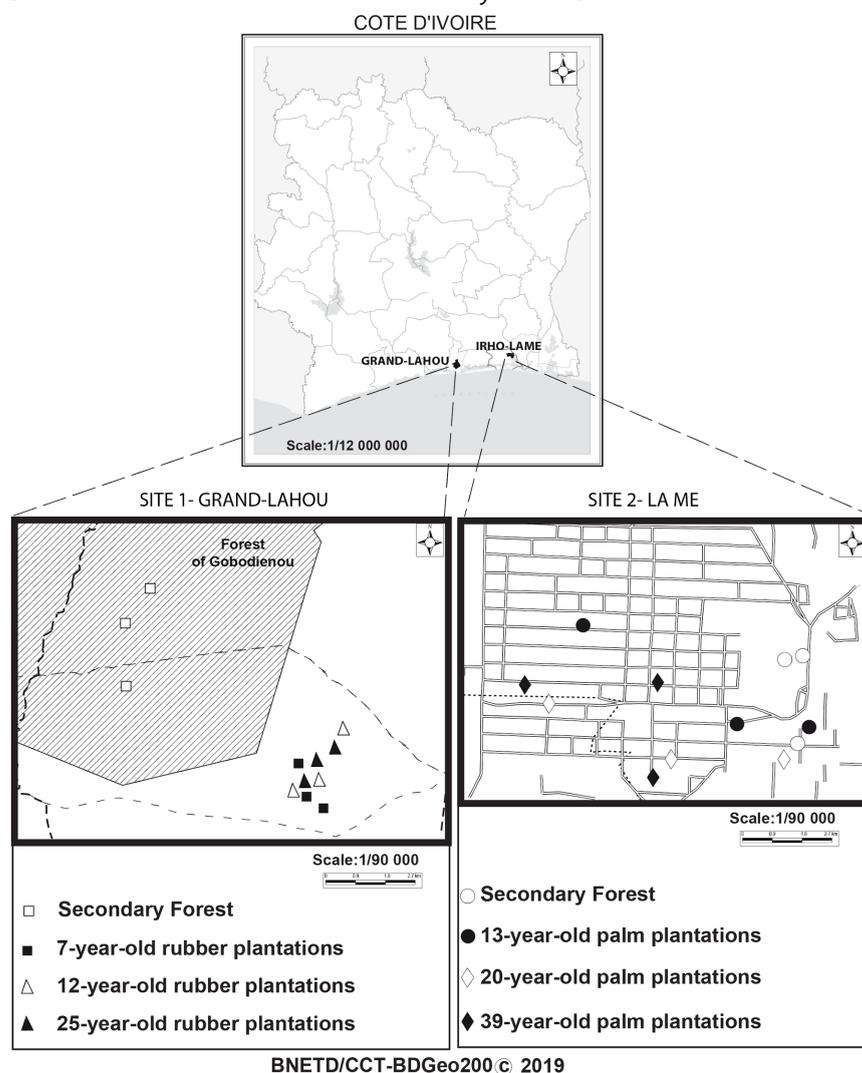


Figure 1. Location of the two study sites in Côte d'Ivoire, and details of the selected plots for the field works

(Ettian *et al.*, 2009). It contains various tree species more than 25 m high with several lianas and herbaceous plants. *Diospyros* spp and *Mapania* spp. are among the dominant plants. On the La Mé site (site 2), the monthly rainfall during the sampling ranged from 18 mm in January to 486 mm in June, with an

annual total of 1,915 mm. Likewise, the monthly mean temperature varied between 25°C in August and 29°C in February and March, with an annual average of 27°C. The natural vegetation of this site is ombrophilous type dominated by the woody species *Turraeanthus africanus* and *Heisteria parvifolia* (Traoré and Péné, 2016). These forests have been highly degraded since the past half century, and this due to many agricultural activities carried out there. Indeed, a part of these forests has been transformed into agricultural land dominated by the rubber and oil palm plantations. In the rubber plantations, litter is abundant, whereas undergrowth and herbaceous stratum are absent, even if few species of *Elaeis guineensis* (Arecaceae), *Pueraria phaseoloides* (Papilionaceae), *Thaumatococcus daniellii* (Marantaceae), *Uapaca guineensis* (Euphorbiaceae), and *Turraeanthus africanus* (Meliaceae) are observed in some places. Weed species characterize the principal understory vegetation in the oil palm plantations (Traoré and Péné, 2016), and it was twice as tall in young plantations, but leaf litter depth and total epiphyte abundance were double in old plantations. The topsoils of the two study sites are ferrallitic type (Perraud, 1971; Yeboua and Ballo, 2000) with variable textures. Clay, clay sandy, sandy clay and sandy textures characterize the soils of the site of Grand Lahou, whereas clay sandy and sandy textures make up the soils of the site of La Mé.

Rubber and oil palm plantations management in Côte d'Ivoire

Rubber plantations: Land preparation depends on the type of initial vegetation (forest, fallow, savannah) colonizing the plot (FIRCA, 2012). In the case of a forest, the land is cleared from October to December and consists of cutting the undergrowth and then the shrubs and tall trees. After clearing, plant debris should be burned and gathered in between the lines in January. Concerning shrub fallows, the clearing is done during the period from December to January and picketing in February–March depending on the planting design. If it is a savannah (herbaceous fallow), the clearing is done during the period from February to March. In this last case, if *Imperata cylindrica* is dominant, the use of herbicide (Round Up, Arsenal) is necessary. However, if *Chromolaena odorata* is dominant, it must be cleared in January or February and burnt in March and the treatment must be made in March with one of the herbicides (Obouayeba *et al.*, 2006). In pure culture, the sowing of cover crops, in particular *Pueraria phaseoloides* is recommended to avoid soil erosion and weeds (Obouayeba *et al.*, 2006). The tree densities recommended for planting are: (i) 510 trees per hectare « 7 m inter-rows and 2.80 m between plants », (ii) 555 trees per hectare « 6 m inter-rows and 3 m between plants », and (iii) 666 trees per hectare « 5 m inter-rows and 3 m between plants » (Obouayeba *et al.*, 2006). After the first rains, holes of 40 cm × 40 cm × 60 cm or 40 cm × 40 cm × 40 cm are dug to receive the plants (FIRCA, 2012). The planting is done by hand and takes place at the beginning of the rainy seasons. During the year of planting, phosphate fertilizer must be brought into the planting hole; nitrogen and potassium fertilizers applied directly above the crown (November–December). For the second and third year of planting, fertilizers should be applied in a circle directly above the crown. Thereafter, bring the fertilizers on the fly in the inter-rows (Obouayeba *et al.*, 2006). The fertilization of the soils of the rubber trees in production is done on warning, after the leaf diagnosis and soil analysis to determine the needs. (Obouayeba *et al.*, 2006). The maintenance of the plots consists in undergrowth regular weeding. Chemical (with fungicide) and preventive control is recommended to treat the diseases that attack the leaves and stems, while curative control is recommended to treat the diseases that attack the roots (root rot). The harvest of the latex is done by an incision in the bark (bleeding) (Obouayeba *et al.*, 2006). After the productive period (35–40 years), rubber trees are uprooted and a new crop is planted after a few years of lying fallow.

Oil palm plantations: Site preparation including clear-cutting, burning and terracing takes place between October and February (Konan *et al.*, 2006). Then, a leguminous cover (*Pueraria javanica*) is sown to protect the soil from erosion and direct exposure to sunshine (Yeboua and Ballo, 2000) and to inhibit the growth of invasive plants (Jacquemard, 2011). After 9–10 months of seedling growth, the oil palm planting takes place during the humid period, particularly in April, May and June. All plantations are carried out with identical 9 m × 9 m palm spacing in a triangular formation by offsetting every second row (Yeboua and Ballo, 2000; Konan *et al.*, 2006; Luskin and Potts, 2011), for a density of 143 palms trees per hectare. Simple or compound fertilizers with nitrogen (N), phosphorus (P), potassium (K) and magnesium (Mg) are applied to soil under the plants during the first 2 years and at the end of the fifth year. Clearing is done twice per year and within a radius of 1.5–2 m around the plants during the first 4 years of planting, and then once a year beyond the fourth year. Pruning is practiced at the end of the third year and it takes place once every 12 months in 4–12-year-old plantations and then once every 6–8 months in plantations older than 12 years. This operation consists in cleaning the palm crown to prepare the first harvest, and suppressing all dry low palm fronds, old male inflorescences and small rotten fruit bunches. All organic residues (palm fronds and understory vegetation) from clear-cutting and pruning are stacked in the inter-row to improve soil fertility for future crop rotation. Harvest can be done one to three times per month, using bags, baskets, wheelbarrows and carts (Konan *et al.*, 2006). Three management zones are observed in oil palm plantations: weeded circle zone; understory vegetation with pruned fronds in

inter-row areas; and harvest paths. Fusarium wilt is treated by replacing diseased trees with a more tolerant variety (Diabaté *et al.*, 2014, 2015). Oil palm pests are most commonly treated by application of deltamethrin, cypermethrin and maneb (Konan *et al.*, 2006).

Sampling design and soil cores collection

The study was conducted during the wet period on two forest sites. For a better understanding of the response of Oribatid mites' communities and soil physico-chemical properties following the transformation of secondary forests into agrosystems, three secondary forests (reference land use) and nine rubber plantations (7-, 12- and 25-year-old) were selected on the site of Grand Lahou, for a total of 12 sampling areas. In each sampling area of this site, a 40 m transect was defined and five sampling points were allocated every 10-m interval between two consecutive points. The same method was applied on the site of La Mé, where the oil palm plantations were 13-, 20-, and 39-year-old. However, the sampling was performed along a 50 m transect with 12.5-m interval between two consecutive points. This difference in the length of transects allowed the collection of soil data in the inter-rows of plantations; zones very often occupied by crop residues and therefore assumed to be more fertile. On both sites, a total of 24 sampling areas (Table 1) was defined. For each sampling point, soil cores including litter thickness were taken with a steel corer (\varnothing 5 cm) at 0–10 cm soil depth (Noti *et al.*, 2003). In total, 120 soil cores were taken through the 24 sampling areas and brought to the laboratory for mite extraction.

Table 1. Differences in characteristics of the plots sampled on the two study sites

Plots	Age (years)	Soil type	Soil textures	Previous cropping
Site of Grand Lahou				
rubber	7	ferrallitic	sandy clay	secondary forest–older palm tree
rubber	7	ferrallitic	clay sandy	secondary forest–coffee
rubber	7	ferrallitic	sandy	secondary forest–older palm tree
rubber	12	ferrallitic	clay	secondary forest–older palm tree
rubber	12	ferrallitic	sandy clay	secondary forest
rubber	12	ferrallitic	sandy clay	secondary forest–cocoa
rubber	25	ferrallitic	clay	secondary forest–older palm tree
rubber	25	ferrallitic	sandy clay	secondary forest
rubber	25	ferrallitic	sandy clay	secondary forest
secondary forest	100	ferrallitic	sandy clay	primary forest
secondary forest	100	ferrallitic	sandy clay	primary forest
secondary forest	100	ferrallitic	sandy clay	primary forest
Site of La Mé				
oil palm	13	ferrallitic	sandy	primary forest–older palm tree
oil palm	13	ferrallitic	sandy	primary forest–older palm tree
oil palm	13	ferrallitic	sandy clay	primary forest–older palm tree
oil palm	20	ferrallitic	sandy	primary forest–older palm tree
oil palm	20	ferrallitic	sandy	primary forest–older palm tree
oil palm	20	ferrallitic	sandy clay	primary forest–older palm tree
oil palm	39	ferrallitic	sandy clay	primary forest–maize–fallow
oil palm	39	ferrallitic	sandy clay	primary forest–cassava–fallow
oil palm	39	ferrallitic	sandy clay	primary forest
secondary forest	150	ferrallitic	sandy clay	primary forest
secondary forest	150	ferrallitic	sandy clay	primary forest
secondary forest	150	ferrallitic	sandy clay	primary forest

Oribatid mites extraction and identification

The Oribatid mites were extracted from the soil sample using Berlese-Tullgren for 10 days. A stereo binocular Loup was used for sorting out the extracted soil Oribatida. The specimens were mounted in semi-permanent (using lactic acid) slides and observed with a digital camera VC.5000 mounted on a NOVEX light microscope. Adult Oribatid mites were identified at the family, genus, and morphospecies levels by using keys and illustrations provided in Balogh and Balogh (1992 a,b), Krantz and Walter (2009) and Walter *et al.* (2013). Oribatida and Acaridida were defined in the recent sense found in Krantz and Walter (2009).

Soil physico-chemical characterization

The Tropical Soil Biology and Fertility method recommended by Anderson and Ingram (1993) was used for the chemical analysis. Composite soil samples were obtained by mixing five cores taken in quadrats (50 cm × 50 cm × 10 cm) and at 0.5–1 m from the sampling point. In each sampling area and following the transect established, three composite soil samples were taken with a 20-m (site 1) or 25-m (site 2) interval between two consecutive points. At the Station, soil composite samples were air-dried for 2 weeks to steady weight and passed through a 2-mm sieve to remove plant parts and other debris. Throughout the same transect, three soil cores (non-composite samples) were taken at 0–10 cm soil depth and at 50 cm from the sampling point, using the cylinder method (Yoro and Godo, 1990) for physical measurements. Before measurements, soil cores were oven-dried at 105°C for 48 hrs. On the 24 sampling stands, 72 composite soil samples and 72 non-composite soil samples were taken for the physico-chemical measurements.

Data analysis

The data were analyzed considering four land use types: *SFC* secondary forests of Grand Lahou, *RBP* rubber plantations of 7–25 years, *SFL* secondary forests of La Mé, and *OPP* oil palm plantations of 13–39 years. The Oribatid mite abundance was expressed as the mean number of individuals per square meter (ind m⁻²). The species richness, Shannon index, Margalef diversity index and evenness allowed the Oribatid mites diversity study. The non-parametric estimators such as the observed species (Sobs) and expected species (the first-order jackknife) were determined in order to assess the discovery rate of the species (Colwell *et al.*, 2004). The community structure of Oribatid mites was studied by using the abundance and species richness of cohorts or infraorders. The dominance and frequency indices of Oribatid species were classified following the Napierała and Błoszyk (2013) method. Thus, five dominance and frequency classes have been defined according to the partition below:

- Dominance: eudominants (>30% of the total number of individuals), dominants (15.1–30.0%), subdominants (7.1–15.0%), residents (3.0–7.0%), and subresidents (<3%).
- Frequency: euconstants (>50% of presence), constants (30.1–50%), subconstants (15.1–30.0%), accessory species (5.0–15.0%), and accidents (<5%).

Soil bulk density was measured by using the cylinder method (Yoro and Godo, 1990). Soil water content was determined after oven-drying at 105°C for 48 hrs. Soil pH_{H2O} was determined by means of a glass electrode in 1:2.5 soil: water (Tondoh *et al.*, 2015). The Walkley and Black (1934) method was used to determine soil organic carbon (SOC), that is, a wet oxidation of organic carbon in an acid dichromate solution, followed by back-titration of the remaining dichromate with ferrous ammonium sulfate. Total N was determined by the Kjeldahl method (Waneukem and Ganry, 1992). Soil organic matter (SOM) was estimated through the formula organic C × 1.7, as per Noti *et al.* (2003). The C:N ratio was also estimated. The response of soil properties to the impact of soil texture changes as well as an effect of sites and land use types was studied. An ordination (canonical correspondence analysis) was performed between the soil physico-chemical and biological parameters and the land use types.

The anthropic disturbance (rubber and oil palm production) on soil Oribatid mites was estimated by using an index of change V (Wardle, 1995) for each organism group. This index compares the relative increase or decrease in Oribatid mite's abundance and species richness between plantations and secondary forests. The index was calculated by the formula:

$$V = \frac{2M_{CN}}{M_{CN} + M_{NT}} - 1$$

where M_{CN} and M_{NT} were the abundance or species richness observed respectively in the plantations and the secondary forests. The index V ranges from -1 when organisms occur only in secondary forests to +1 when organisms occur only in plantations with 0 representing equal abundance or species richness in both secondary forests and plantations. The magnitude of response to human interference was expressed by the following categories: extreme inhibition by plantations $V < -0.67$; moderate inhibition by

plantations $-0.67 < V < -0.33$; mild inhibition by plantations $-0.33 < V < 0$; mild stimulation by plantations $0 < V < 0.33$; moderate stimulation by plantations $0.33 < V < 0.67$; extreme stimulation by plantations $V > 0.67$.

Statistical analysis

After verification of the homogeneity test (Batlett test), the values of soil properties were normalized if necessary following the formula $\ln(x+1)$. A one-way analysis of variance (ANOVA) associated with the post-hoc Tukey's test was performed to examine the effects of land-use types on soil physico-chemical and biological characteristics. This analysis was carried out both within and between land use types. The same test (one-way ANOVA) was used to assess the impact of soil texture on the soil properties in the site of Grand Lahou whilst on the site of La Mé, a t-test of Student was applied. All tests were realized by using R software (R Development Core Team, 2008). With the software Statistica 7.1 (StatSoft Inc., Tulsa, USA), the factorial Anova associated to general linear mixed model (GLMM) was used to explore the effects of land use types and study sites on the soil properties. In order to establish possible relationship between the abundance of Oribatid morphospecies in land use types and their environmental variables, we performed a multivariate analysis, specifically a canonical correspondence analysis. The CCA was made by using PAST software (Hammer, 2001). Rare morphospecies, occurring in fewer than three samples were omitted because they do not improve the CCA analysis (Skubala and Maslak, 2009). A Monte Carlo permutation test was used to determine statistically whether the Oribatid morphospecies composition depended of the soil physical and chemical parameters. Pearson's correlation was applied in the analyses of the relationships between soil physico-chemical descriptors and the abundance of each Oribatid morphospecies included in the CCA analysis. The cumulative species richness was estimated after 500 randomizations by using the software EstimateS 7.5. The first-order jackknife non-parametric estimator was used to determine the expected species richness.

Results

Species composition and community structure

A total of 80 morphospecies was recorded across the land use types. Respectively, 31, 34, 31 and 34 species were observed in the secondary forests of Grand Lahou, rubber plantations, secondary forests of La Mé and the oil palm plantations. The expected species richness (the first-order jackknife) indicated that the total species richness could reach 33, 47, 32 and 36 species, respectively, in the secondary forests of Grand Lahou, rubber plantations, secondary forests of La Mé and the oil palm plantations. Thus, the observed species would represent 72–96% of the expected species, indicating that the sampling effort was not sufficient to complete the Oribatid species inventories.

The observed species were structured into five cohorts or infraorders (Palaeosomata, Mixonomata, Desmonomata, Brachypylina and Poronota). The abundance of Brachypylina ($F = 7.68$; $p = 0.0014$) and Palaeosomata ($F = 3.50$; $p = 0.0393$) varied significantly within the rubber plantations whereas those of Poronota ($F = 4.37$; $p = 0.0374$) significantly differed within the secondary forests of La Mé. The data revealed a significant variation between the land use types in the abundance of Palaeosomata ($F = 3.50$; $p = 0.0212$), Mixonomata ($F = 5.84$; $p = 0.0015$) and Poronota ($F = 6.12$, $p = 0.0011$), except for the Desmonomata ($F = 0.43$; $p = 0.7320$) and Brachypylina ($F = 0.16$; $p = 0.9230$) (Fig. 2). The Poronota (41%) and Brachypylina (43%) represented the major cohorts through the two sites and land use types (secondary forests of Grand Lahou: Poronota 50%, Brachypylina 29%; rubber plantations: Poronota 51%, Brachypylina 30%; secondary forests of La Mé: Poronota 35%, Brachypylina 51%; and oil palm plantations: Poronota 22%, Brachypylina 69%). The study sites influenced significantly the abundance of Mixonomata (GLMM, $F = 13.24$; $p = 0.0004$) and Poronota (GLMM, $F = 22.20$; $p = 0.0001$). The land use types (GLMM, $F = 3.50$; $p = 0.0178$) and the Site \times Lut interaction (GLMM, $F = 3.50$; $p = 0.0178$) significantly affected the abundance of Palaeosomata. The Poronota (10, 10, 14 and 9 species) and Brachypylina (11, 12, 11 and 13 species) were the more diversified groups, respectively, in the secondary forests of Grand Lahou, rubber plantations, secondary forests of La Mé and the oil palm plantations.

On the 24 sampling areas, species dominance analysis indicated four clusters: 1 dominant specie (Acaridida sp.1), 1 subdominant specie (Haplozetidae sp.1), 8 resident species (Damaeidae sp.1, *Oppia* sp.1, *Oppia* sp.13, Oppiidae sp.4, *Galumna* sp.1, *Galumna* sp.2, Mycobatidae sp.1, and Mycobatidae sp.2) and 70 subresident species. The distribution frequency of Oribatid species presented three clusters: 2 subconstant species (*Galumna* sp.2 and Haplozetidae sp.1), 17 accessory species and 61 accidental species (Appendix 1). In other words, the observed species were (i) dominant and accidental: 1 specie (Acaridida sp.1), (ii) subdominant and subconstant: 1 specie (Haplozetidae sp.1), (iii) resident and subconstant: 1 specie (*Galumna* sp.2), (iv) resident and accessory: 7 species (Damaeidae sp.1, *Oppia* sp.1, *Oppia* sp.13, Oppiidae

sp.4, *Galumna* sp.1, Mycobatidae sp.1 and Mycobatidae sp.2), (v) subresident and accessory: 10 species (*Javacarus* sp.1, *Meristacarus* sp.2, *Phthiracarus* sp.1, *Dolicheremaeus* sp.1, Damaeidae sp.1, *Neoliodes* sp.1, *Oppia* sp.6, *Oppia* sp.10, *Oppia* sp.15 and Ceratozetidae sp.1), and (vi) subresident and accidental : 60 species.

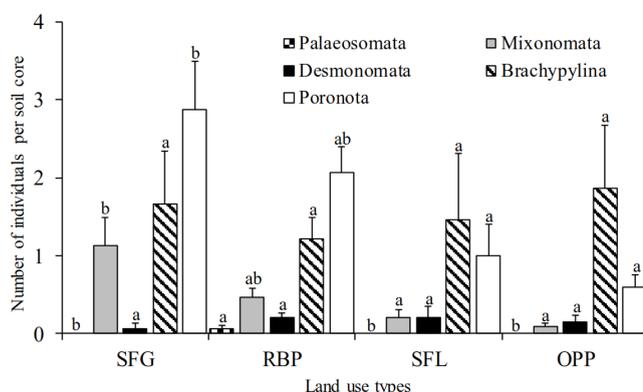


Figure 2. Abundance (mean and standard error) of Oribatid mite major groups observed across the land use types. *SFG* secondary forests of Grand Lahou, *RBP* rubber plantations of 7–25 years, *SFL* secondary forests of La Mé, *OPP* oil palm plantations of 13–39 years. $N = 120$, One-way ANOVA test, $P < 0.05$. Means followed by the same lowercase letter are not significantly different at the 0.05 level (Tukey's HSD test)

Oribatid mites' abundance

The mean density of Oribatid mites varied significantly within the rubber plantations ($F = 4.53$; $p = 0.0164$), except the secondary forests of Grand Lahou ($F = 1.78$; $p = 0.2100$), secondary forests of La Mé ($F = 0.64$; $p = 0.5420$) and the oil palm plantations ($F = 0.60$; $p = 0.5520$). The mean density significantly differed between the land use types ($F = 4.73$; $p = 0.0051$). Higher densities were recorded in the secondary forests of Grand Lahou ($4617 \pm 930 \text{ ind m}^{-2}$) and La Mé ($4862 \pm 3348 \text{ ind m}^{-2}$) (Fig. 3). The density of Oribatida decreased by -29% and -71% , respectively, after conversion of the secondary forests into rubber and oil palm plantations. The study sites (GLMM, $F = 1.73$; $p = 0.1900$), land use types (GLMM, $F = 2.45$; $p = 0.0671$) and the Site \times Lut interaction (GLMM, $F = 0.30$; $p = 0.8245$) did not influence significantly the Oribatid mite's density.

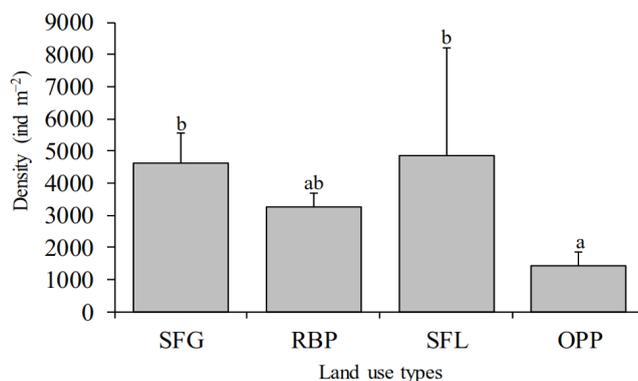


Figure 3. Density (mean and standard error) of Oribatid mites recorded along the land use types.

SFG secondary forests of Grand Lahou, *RBP* rubber plantations of 7–25 years, *SFL* secondary forests of La Mé, *OPP* oil palm plantations of 13–39 years. $N = 120$, One-way ANOVA test, $P < 0.05$. Means followed by the same lowercase letter are not significantly different at the 0.05 level (Tukey's HSD test)

Oribatid mite diversity indices

Mean values of the species richness did not change significantly within the land use types: the secondary forests of Grand Lahou ($F = 2.02$; $p = 0.1750$); rubber plantations ($F = 2.69$; $p = 0.0795$); secondary forests of La Mé ($F = 2.51$; $p = 0.1220$) and the oil palm plantations ($F = 1.15$; $p = 0.3270$). At the scale of the four land use types, a significant variation ($F = 4.14$; $p < 0.0500$) of the species richness was recorded (Table 2). The mean number of species determined on the site of Grand Lahou (secondary forests: 4.00 ± 0.69 species; rubber plantations: 2.84 ± 0.31 species) was superior to those recorded in the site of La Mé (secondary forests: 2.53 ± 0.82 species; oil palm plantations: 1.49 ± 0.31 species).

Table 2. Oribatid mites' diversity (mean \pm standard error) parameters determined among the land use types

Diversity parameters	Land use types				P value
	SFG	RBP	SFL	OPP	
Species richness	4.00 \pm 0.69 ^b	2.84 \pm 0.31 ^{ab}	2.53 \pm 0.82 ^{ab}	1.49 \pm 0.31 ^a	0.0101*
Shannon–Wiener Index H'	1.15 \pm 0.16 ^c	0.81 \pm 0.09 ^{bc}	0.64 \pm 0.21 ^{ab}	0.30 \pm 0.09 ^a	0.0013**
Margalef Diversity Index	3.12 \pm 0.53 ^a	2.94 \pm 0.28 ^a	10.79 \pm 9.44 ^a	2.32 \pm 0.76 ^a	0.311
Evenness J	0.82 \pm 0.08 ^c	0.66 \pm 0.07 ^{bc}	0.40 \pm 0.13 ^{ab}	0.22 \pm 0.06 ^a	0.0001***

SFG secondary forests of Grand Lahou, RBP rubber plantations of 7–25 years, SFL secondary forests of La Mé, OPP oil palm plantations of 13–39 years. $N = 120$. One-way ANOVA test

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; different superscript lowercase letters indicate significant variations between the land use types (Tukey's HSD test)

The species richness dropped by –29% and –42%, respectively, after conversion of the secondary forests into the rubber and oil palm plantations. The Shannon index varied significantly within the secondary forests of La Mé ($F = 4.50$; $p = 0.0347$), except the rubber plantations ($F = 2.02$; $p = 0.1450$), oil palm plantations ($F = 1.33$; $p = 0.2750$) and the secondary forests of Grand Lahou ($F = 3.23$; $p = 0.0751$). It significantly differed between the land use types ($F = 5.94$; $p < 0.0100$). The site of Grand Lahou (secondary forests: 1.15 ± 0.16 ; rubber plantations: 0.81 ± 0.09) was more diversified than those of La Mé (secondary forests: 0.64 ± 0.21 ; oil palm plantations: 0.30 ± 0.09). The Shannon index decreased by –29% and –59%, respectively, after transformation of the secondary forests into rubber and oil palm plantations. The Margalef diversity index did not vary significantly ($F = 1.22$; $p > 0.0500$) between the land use types, whereas the evenness differed significantly ($F = 8.54$; $p < 0.0010$). Equally, the total number of individuals in the site of La Mé was distributed less evenly among the species (secondary forests: 0.40 ± 0.13 ; oil palm plantations: 0.22 ± 0.06) compared to the site of Grand Lahou (secondary forests: 0.82 ± 0.08 ; rubber plantations: 0.66 ± 0.07). The study site significantly influenced the species richness (GLMM, $F = 9.66$; $p = 0.0023$), Shannon index (GLMM, $F = 18.73$; $p = 0.0001$) and the evenness (GLMM, $F = 31.03$; $p = 0.0001$). The land use types significantly affected the species richness (GLMM, $F = 3.73$; $p = 0.0133$) and Shannon index (GLMM, $F = 4.13$; $p = 0.0080$). This was not the case with the Site \times Lut interaction (species richness: GLMM, $F = 0.02$, $p = 0.9961$; Shannon index: GLMM, $F = 0.03$, $p = 0.9914$; evenness: GLMM, $F = 0.06$, $p = 0.9779$).

Soil physical properties

Apart from the oil palm plantations ($F = 0.89$; $p = 0.4216$); secondary forests of La Mé ($F = 4.36$; $p = 0.0676$) and the rubber plantations ($F = 2.10$; $p = 0.1441$), the mean values of bulk density measured within the secondary forests of Grand Lahou varied significantly ($F = 19.46$; $p = 0.0023$). The bulk density was lower in the soil of forests (secondary forests of Grand Lahou: $0.95 \pm 0.05 \text{ g cm}^{-3}$; secondary forests of La Mé: $0.91 \pm 0.04 \text{ g cm}^{-3}$) compared to plantations, and changed significantly ($F = 9.22$; $p < 0.0010$) between the land use types (Table 3). The values of the soil bulk density increased by +28% and +21%, respectively, after conversion of the secondary forests into rubber and oil palm plantations. The soil water content differed significantly ($F = 3.87$; $p = 0.0347$) within the rubber plantations, except the oil palm plantations ($F = 1.26$; $p = 0.3003$), and the secondary forests of La Mé ($F = 0.73$; $p = 0.5170$) and Grand Lahou ($F = 1.01$; $p = 0.4156$). It varied significantly ($F = 9.97$; $p < 0.0010$) between the land use types.

Table 3. Soil physical measurements (mean \pm standard error) through the land use types

	Bulk density (g cm^{-3})		Water content (%)	
SFG	0.95	\pm 0.05 ^{bc}	29.12	\pm 3.95 ^a
RBP	1.22	\pm 0.01 ^a	16.70	\pm 1.61 ^b
SFL	0.91	\pm 0.04 ^c	12.02	\pm 1.21 ^b
OPP	1.10	\pm 0.05 ^{ab}	13.77	\pm 1.40 ^b
P value	0.0001***		0.0001***	

SFG secondary forests of Grand Lahou, RBP rubber plantations of 7-25 years, SFL secondary forests of La Mé, OPP oil palm plantations of 13-39 years. *N* = 72, One-way ANOVA test

*** *P* < 0.001; different superscript lowercase letters indicate significant variations between the land use types (Tukey's HSD test)

The soils from the secondary forests of Grand Lahou retained more water ($29.12 \pm 3.95\%$) compared to other land use types. The conversion of secondary forests into agrosystems led to a decrease in soil water content of -43% in the site of Grand Lahou and to an increase of $+15\%$ in the site of La Mé. The soil physical parameters were significantly influenced by the study sites (bulk density: GLMM, *F* = 5.55; *p* = 0.0214; water content: GLMM, *F* = 12.53; *p* = 0.0007) and land use types (bulk density: GLMM, *F* = 8.04; *p* = 0.0001; water content: GLMM, *F* = 4.83; *p* = 0.0042). The Site \times Lut interaction impacted significantly the soil water content (GLMM, *F* = 4.23; *p* = 0.0085).

Soil chemical measurements

Except the secondary forests of Grand Lahou (*F* = 1.35; *p* = 0.3266), values of the soil pH varied significantly within the secondary forests of La Mé (*F* = 6.44; *p* = 0.0320), rubber plantations (*F* = 35.93; *p* = 0.0001) and the oil palm plantations (*F* = 8.08; *p* = 0.0020). Values of the soil pH differed significantly (*F* = 10.28; *p* < 0.0010) between the land use types. Whatever the site, soils were acids with values ranged from 4.43 ± 0.08 (secondary forests of Grand Lahou) to 5.37 ± 0.13 (oil palm plantations). The amount of soil organic carbon varied significantly within the land use types (SFG: *F* = 5.19, *p* = 0.0490; SFL: *F* = 5.23, *p* = 0.0483; RBP: *F* = 8.08, *p* = 0.0351; OPP: *F* = 4.84, *p* = 0.0170). The total nitrogen changed significantly within the rubber plantations (*F* = 4.02; *p* = 0.0310) except the other land use types (SFL: *F* = 0.73, *p* = 0.5176; SFG: *F* = 4.75; *p* = 0.0579; OPP: *F* = 0.22; *p* = 0.8034). The amount of organic carbon (*F* = 7.80; *p* < 0.0010) and total nitrogen (*F* = 7.92; *p* < 0.0010) differed significantly between the land use types. The reverse trend was observed with the C:N ratio (*F* = 1.50; *p* > 0.0500), which remains inferior to 15 (Table 4). Whatever the study site, organic carbon and total nitrogen were higher in the forest soils (secondary forests of Grand Lahou: COS 22.90 ± 3.31 g kg⁻¹ soil, NT 2.00 ± 0.29 g kg⁻¹ soil; secondary forests of La Mé: COS 19.55 ± 1.33 g kg⁻¹ soil, NT 1.60 ± 0.09 g kg⁻¹ soil) and decreased after their conversion into agrosystems. The COS and NT contents from the

Table 4. Chemical variables (mean \pm standard error) measured across the land use types

	SOC (g kg ⁻¹ soil)		TN (g kg ⁻¹ soil)		C/N		SOM (g kg ⁻¹ soil)		pH-H ₂ O	
SFG	22.90	\pm 3.31 ^a	2.00	\pm 0.29 ^a	11.46	\pm 0.30 ^a	38.93	\pm 5.63 ^a	4.43	\pm 0.08 ^b
RBP	10.00	\pm 0.70 ^{ab}	0.91	\pm 0.05 ^{ab}	10.70	\pm 0.15 ^a	17.01	\pm 1.19 ^{ab}	5.11	\pm 0.12 ^a
SFL	19.55	\pm 1.33 ^b	1.60	\pm 0.09 ^b	12.21	\pm 0.30 ^a	33.23	\pm 2.27 ^b	5.00	\pm 0.15 ^a
OPP	16.15	\pm 1.26 ^b	1.40	\pm 0.09 ^b	12.66	\pm 1.31 ^a	27.46	\pm 2.14 ^b	5.37	\pm 0.13 ^a
<i>P</i> value	0.0004***		0.0004***		0.2318		0.0004***		0.0001***	

SFG secondary forests of Grand Lahou, RBP rubber plantations of 7-25 years, SFL secondary forests of La Mé, OPP oil palm plantations of 13-39 years, SOC soil organic carbon, TN total nitrogen, C/N carbon nitrogen ratio, SOM soil organic matter, pH-H₂O potential of hydrogen-water. *N* = 72, One-way ANOVA test

*** *P* < 0.001; different superscript lowercase letters indicate significant variations between the land use types (Tukey's HSD test)

soil of forests represented respectively (rubber plantations: 2.3 and 1.2 times) and (oil palm plantations: 2.2 and 1.1 times) the amounts recorded in the agrosystems. The soil organic matter varied significantly within (SFG: *F* = 5.19, *p* = 0.0490; SFL: *F* = 5.23, *p* = 0.0483; RBP: *F* = 3.86, *p* = 0.0351; OPP: *F* = 4.84, *p* = 0.0170) and between the land use types (*F* = 7.80; *p* < 0.0010). Whatever the study site, organic matter was higher in the forest soils (secondary forests of Grand Lahou: 38.93 ± 5.63 g kg⁻¹ soil; secondary forests of La Mé: 33.23 ± 2.27 g kg⁻¹ soil) and dropped after their transition into agrosystems. Apart from C:N ratio, the sites and land use types affected significantly the soil chemical properties (Table 5). The Site \times Lut interaction impacted significantly the soil organic carbon, total nitrogen and soil organic matter.

Table 5. Anova table of general linear mixed model (GLMM) effects on soil characteristics across the site and land use type. F-values and the corresponding *p*-values are displayed.

		SOC	TN	SOM	C/N	pH-H ₂ O
	df	F	F	F	F	F
Site	1	8.28 **	5.60 *	8.28 **	2.81	10.10 **
Lut	3	13.54 ***	8.38 ***	13.54 ***	2.44	28.78 ***

Site × Lut	3	3.73 *	4.28 **	3.74 *	1.74	1.03
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* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; SOC soil organic carbon, TN total nitrogen, C/N carbon nitrogen ratio, SOM soil organic matter, pH-H₂O potential of hydrogen-water

Impact of soil texture on soil physico-chemical and biological parameters

Overall, the soil physico-chemical and biological properties varied significantly on the four soil textures recorded in the site of Grand Lahou (site 1): total density ($F = 9.59$; $p < 0.0010$), species richness ($F = 9.14$; $p < 0.0010$), bulk density ($F = 17.70$; $p < 0.0010$), soil water content ($F = 31.62$; $p < 0.0010$), SOC ($F = 15.19$; $p < 0.0100$), TN ($F = 11.62$; $p < 0.0100$), C:N ratio ($F = 10.96$; $p < 0.0100$), SOM ($F = 15.19$; $p < 0.0100$) and pH ($F = 10.60$; $p < 0.0010$). The clay soils allowed the development of Oribatid mites, and materialized by an increase in abundance (6129 ± 1042 ind m⁻²) and species richness (4.50 ± 0.52 species) (Table 6). The reverse trend was recorded in the sandy soils, where a decrease of these variables was observed (density: 955 ± 771 ind m⁻²; species richness: 0.80 ± 0.58 species).

Table 6. Modification in soil physico-chemical and biological (mean \pm standard error) characteristics along the soil textures of the site of Grand Lahou

Soil characteristics	Soil textures				P value
	CS	CL	SC	SA	
Total density (10 ³ ind m ⁻²)	3.50 \pm 0.53 ^{ab}	6.12 \pm 1.04 ^b	1.91 \pm 0.40 ^a	0.95 \pm 0.77 ^a	0.0007***
Species richness	3.17 \pm 0.41 ^{bc}	4.50 \pm 0.52 ^c	2.40 \pm 0.51 ^{ab}	0.80 \pm 0.58 ^a	0.0009***
Bulk density (g cm ⁻³)	1.10 \pm 0.01 ^a	1.24 \pm 0.01 ^b	1.25 \pm 0.04 ^b	1.33 \pm 0.01 ^b	0.0006***
Water content (%)	23.74 \pm 2.19 ^c	12.78 \pm 0.20 ^{ab}	7.80 \pm 0.53 ^a	14.36 \pm 0.68 ^b	0.0001***
Soil organic carbon (g kg ⁻¹ soil)	15.19 \pm 0.89 ^b	10.57 \pm 1.25 ^a	8.60 \pm 0.80 ^a	7.50 \pm 0.05 ^a	0.0011**
Total nitrogen (g kg ⁻¹ soil)	1.35 \pm 0.09 ^b	0.91 \pm 0.09 ^a	0.85 \pm 0.08 ^a	0.72 \pm 0.01 ^a	0.0027**
Carbon nitrogen ratio	11.04 \pm 0.14 ^{bc}	11.31 \pm 0.06 ^c	10.13 \pm 0.08 ^a	10.35 \pm 0.28 ^{ab}	0.0033**
Soil organic matter (g kg ⁻¹ soil)	25.82 \pm 1.52 ^b	17.97 \pm 2.13 ^a	14.62 \pm 1.37 ^a	12.75 \pm 0.09 ^a	0.0011**
Potential of hydrogen-water	4.75 \pm 0.03 ^a	4.61 \pm 0.04 ^a	6.08 \pm 0.06 ^b	6.17 \pm 0.13 ^b	0.0001***

CS clay sandy, CL clay, SC sandy clay, SA sandy, biological parameters $N = 120$, physico-chemical parameters $N = 72$, One-way ANOVA test

** $P < 0.01$, *** $P < 0.001$; different superscript lowercase letters indicate significant variations between the soil textures (Tukey's HSD test)

Table 7. Change in soil physico-chemical and biological (mean \pm standard error) characteristics across the soil textures of the site of La Mé

Soil characteristics	Soil textures		P value
	CS	SA	
Total density (10 ³ ind m ⁻²)	3.02 \pm 1.27 ^a	0.79 \pm 0.46 ^a	0.1616
Species richness	2.10 \pm 0.45 ^a	1.05 \pm 0.57 ^a	0.1926
Bulk density (g cm ⁻³)	0.99 \pm 0.02 ^a	1.17 \pm 0.01 ^b	0.0024**
Water content (%)	13.85 \pm 0.76 ^a	12.29 \pm 0.53 ^a	0.1683
Soil organic carbon (g kg ⁻¹ soil)	17.47 \pm 1.27 ^a	16.06 \pm 0.12 ^a	0.3303
Total nitrogen (g kg ⁻¹ soil)	1.50 \pm 0.10 ^a	1.36 \pm 0.10 ^a	0.3996
Carbon nitrogen ratio	11.99 \pm 0.03 ^a	13.67 \pm 0.91 ^a	0.1413
Soil organic matter (g kg ⁻¹ soil)	29.71 \pm 2.16 ^a	27.30 \pm 0.22 ^a	0.3303
Potential of hydrogen-water	5.21 \pm 0.09 ^a	5.42 \pm 0.19 ^a	0.3712

CS clay sandy, SA sandy, biological parameters $N = 120$, physico-chemical parameters $N = 72$, t-test of Student. ** $P < 0.01$; different superscript lowercase letters indicate significant variations between the soil textures



The soil water content ($23.74 \pm 2.19\%$), and the amounts of organic carbon ($15.19 \pm 0.89 \text{ g kg}^{-1}$ soil), total nitrogen ($1.35 \pm 0.09 \text{ g kg}^{-1}$ soil) and soil organic matter ($25.82 \pm 1.52 \text{ g kg}^{-1}$ soil) were higher in the clay sandy soils than the other textures of the site 1. Soils with clay sandy ($\text{pH} = 4.75 \pm 0.03$) and clay ($\text{pH} = 4.61 \pm 0.04$) textures were more acids compared to the sandy clay ($\text{pH} = 6.08 \pm 0.06$) and sandy ($\text{pH} = 6.17 \pm 0.13$) textures. On the site of La Mé (site 2), only the soil bulk density was significantly higher (t-test, $p < 0.0100$) in the sandy soils ($1.17 \pm 0.01 \text{ g cm}^{-3}$) than in the clay sandy soils ($0.99 \pm 0.02 \text{ g cm}^{-3}$). The other soil physico-chemical and biological properties were slightly high in the clay sandy soils than in the sandy soils, but did not vary significantly (Table 7).

Response of soil Oribatid mite abundance and species richness to the establishment of rubber and oil palm plantations

The response of Oribatid mites to the transformation of secondary forests into agrosystems varied according to community groups. The abundance of Desmonomata (+0.50, moderate stimulation) and Brachypylina (+0.12, mild stimulation) was positively impacted, and respectively, after the conversion of secondary forests into rubber and oil palm plantations (Table 8). The abundances from other groups were negatively affected by the establishment of plantations, and where a moderate inhibition was observed with the Mixonomata (rubber plantations: -0.42 ; oil palm plantations: -0.38) and total Oribatid mites (oil palm plantations: -0.55). The species richness of Desmonomata (+0.50, moderate stimulation; +0.66, moderate stimulation), Brachypylina (+0.04, mild stimulation; +0.08, mild stimulation) and Mixonomata (+0.14, mild stimulation) were positively affected by the transformation of forest landscapes into rubber and oil palm plantations. The species richness from other groups were negatively impacted (mild inhibition) after the plantations establishment.

Table 8. Impact of rubber and oil palm plantations on Oribatid mite major groups with reference to data listed in Appendix 1

Major groups	Indice V			
	Abundance		Species richness	
	RBP	OPP	RBP	OPP
Mixonomata	-0.42	-0.38	-0.23	+0.14
Desmonomata	+0.50	-0.13	+0.50	+0.66
Brachypylina	-0.15	+0.12	+0.04	+0.08
Poronota	-0.16	-0.25	+0.00	-0.21
Total Oribatida	-0.17	-0.55	-0.17	-0.26

RBP rubber plantations of 7-25 years, OPP oil palm plantations of 13-39 years

Index V ranges from -1 to +1 and is increasingly negative or positive as the group under consideration is increasingly decreased or increased in rubber or oil palm plantations compared to secondary forest

Relationships between Oribatid mite communities, soil physico-chemical parameters and land use types.

Canonical correspondence analysis indicated that the eigenvalues of Axes 1 (0.604) and 2 (0.308) explained 85% of the variance in the data (56% for the first and 29% for the second). The Anderson-Darling test with Monte Carlo p-value showed that the *Oppia* sp.6 ($F = 0.58$, $p = 0.0445$), *Oppia* sp.13 ($F = 0.57$, $p = 0.0437$), *Oppia* sp.15 ($F = 0.57$, $p = 0.0435$) and the Schelorbitatidae sp.3 ($F = 0.82$, $p = 0.0001$) were significantly distributed along Axis 1, whilst the *Javacarus* sp.1 ($F = 0.82$, $p = 0.0001$), Belbidae sp.1 ($F = 0.58$, $p = 0.0411$), *Galumna* sp.3 ($F = 0.82$, $p = 0.0001$), Oppiidae sp.2 ($F = 0.58$, $p = 0.0412$) and *Oppia* sp.10 ($F = 0.82$, $p = 0.0001$) were significantly distributed along Axis 2 (Fig. 4). The Axis 1 shared the rubber and oil palm plantations 'monospecific agrosystem', characterized by a high human interference, with the secondary forests of Grand Lahou and La Mé 'plurispecific system', representing the reference system with low interference. The Axis 2 shared the site of Grand Lahou (forests converted to rubber plantations) with the site of La Mé (forests converted to oil palm plantations). The emerging patterns of individual species were as follows. Quadrant I contained abundant individuals of *Javacarus* sp.1, Damaeidae sp.1, Haplozetidae sp.1, Mycobatidae sp.2, *Oppia* sp.1 and *Oppia* sp.10 associated with the rubber plantations. The soil under the rubber plantations was influenced by the bulk density. The Pearson correlation coefficients indicated positive and significant correlations of abundance of *Javacarus* sp.1 with Haplozetidae sp.1 ($r = 0.98$, $p = 0.0188$), Damaeidae sp.1 ($r = 0.97$, $p = 0.0262$) and *Oppia* sp.10 ($r = 0.99$, $p = 0.0001$); abundance of Damaeidae sp.1 with *Oppia* sp.10 ($r = 0.97$, $p = 0.0262$) and Haplozetidae sp.1 ($r = 0.99$, $p = 0.0013$); abundance of Haplozetidae sp.1 with *Oppia* sp.10 ($r = 0.98$, $p = 0.0188$), and abundance of Mycobatidae sp.2 with *Oppia* sp.1 ($r = 0.96$, $p = 0.0328$). Quadrant II contained abundant individuals of Schelorbitatidae sp.3, Oppiidae sp.4 and *Oppia* sp.6 associated with the oil palm plantations. The soil in the

oil palm plantations may be controlled by the pH. The abundance of Scheloribatidae sp.3 was significantly and positively correlated with the Oppiidae sp.4 ($r = 0.95$, $p = 0.0460$) and *Oppia* sp.6 ($r = 0.98$, $p = 0.0135$).

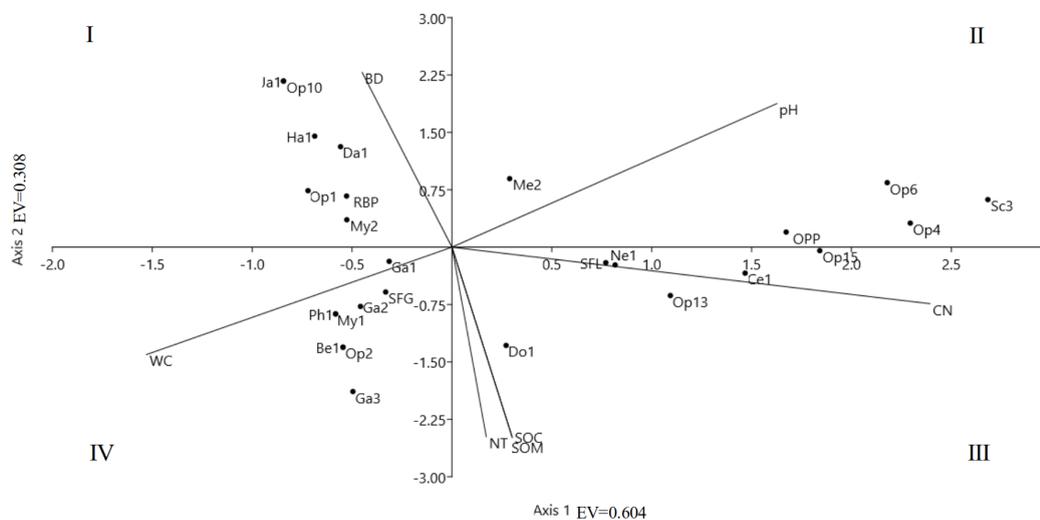


Figure 4. Biplot of CCA result indicating an ordination of most Oribatid morphospecies abundances, land use types and soil physico-chemical parameters. *SFG* secondary forests of Grand Lahou, *RBP* rubber plantations of 7-25 years, *SFL* secondary forests of La Mé, *OPP* oil palm plantations of 13-39 years, *Ja1* *Javacarus* sp.1, *Me2* *Meristacarus* sp.2, *Ph1* *Phthiracarus* sp.1, *Do1* *Dolicheremaeus* sp.1, *Da1* *Damaeidae* sp.1, *Be1* *Belbidae* sp.1, *Ne1* *Neoliodes* sp.1, *Op1* *Oppia* sp.1, *Op6* *Oppia* sp.6, *Op10* *Oppia* sp.10, *Op13* *Oppia* sp.13, *Op15* *Oppia* sp.15, *Op2* *Oppiidae* sp.2, *Op4* *Oppiidae* sp.4, *Ce1* *Ceratozetidae* sp.1, *Ga1* *Galumna* sp.1, *Ga2* *Galumna* sp.2, *Ga3* *Galumna* sp.3, *My1* *Mycobatidae* sp.1, *My2* *Mycobatidae* sp.2, *Sc3* *Schelorbitidae* sp.3, *Ha1* *Haplozetidae* sp.1, *BD* bulk density, *WC* water content, *NT* total nitrogen, *SOC* soil organic carbon, *SOM* soil organic matter, *pH* potential of hydrogen, *CN* carbon nitrogen ratio, *EV* eigenvalues.

Quadrant III contained abundant individuals of *Dolicheremaeus* sp.1, *Neoliodes* sp.1, *Ceratozetidae* sp.1, *Oppia* sp.13 and *Oppia* sp.15 associated with the secondary forests of La Mé. In these forests, soils may be controlled by the organic carbon, organic matter, total nitrogen and the carbon nitrogen ratio. The abundance of *Neoliodes* sp.1 was significantly and positively correlated with the *Oppia* sp.13 ($r = 0.96$, $p = 0.0377$); identically for the amount of total nitrogen with soil organic carbon ($r = 0.99$, $p = 0.0072$), soil organic matter ($r = 0.99$, $p = 0.0072$) and the abundance of *Dolicheremaeus* sp.1 ($r = 0.95$, $p = 0.0490$). Quadrant IV contained abundant individuals of *Phthiracarus* sp.1, *Belbidae* sp.1, *Oppiidae* sp.2, *Galumna* sp.1, *Galumna* sp.2, *Galumna* sp.3 and *Mycobatidae* sp.1 associated with the secondary forests of Grand Lahou. The soil under these forests was impacted by the water content. Indeed, the abundance of *Phthiracarus* sp.1 ($r = 0.99$, $p = 0.0097$), *Belbidae* sp.1 ($r = 0.99$, $p = 0.0067$), *Oppiidae* sp.2 ($r = 0.99$, $p = 0.0067$), *Galumna* sp.2 ($r = 0.97$, $p = 0.0268$), *Galumna* sp.3 ($r = 0.96$, $p = 0.0317$) and *Mycobatidae* sp.1 ($r = 0.99$, $p = 0.0097$) was positively and significantly correlated with the soil water content. Similarly, a positive and significant correlation was recorded in the abundance between (i) the *Phthiracarus* sp.1 and the *Belbidae* sp.1, *Oppiidae* sp.2, *Galumna* sp.2 and *Mycobatidae* sp.1, (ii) the *Belbidae* sp.1 and the *Oppiidae* sp.2, *Galumna* sp.2, *Galumna* sp.3 and *Mycobatidae* sp.1, (iii) the *Oppiidae* sp.2 and the *Galumna* sp.2, *Galumna* sp.3 and *Mycobatidae* sp.1, and (iv) the *Mycobatidae* sp.1 and *Galumna* sp.2.

Discussion

Response of soil Oribatid mite's communities to secondary forests transformation into agrosystems

Soil organisms play a key role in the ecosystem functioning, including fragmentation, decomposition, mineralization of organic matter and nutrient cycling (Lisafitri *et al.*, 2015; Haq, 2016; Sulistyorini *et al.*, 2018; Mandal *et al.*, 2019). Due to their low mobility (Berthet, 1964), most of these organisms are likely to be sensitive to environmental changes (Dervash *et al.*, 2018; Sulistyorini *et al.*, 2018). Several research studies have highlighted the drastic decline in the density and diversity of soil organisms after the conversion of forests into agrosystems, and particularly in monocultural system (Lisafitri *et al.*, 2015; Beckendorff, 2016; Drescher *et al.*, 2016; Dervash *et al.*, 2018; Mandal *et al.*, 2019; Singh *et al.*, 2019; Hemati *et al.*, 2020; Krause, 2020; Yéo *et al.*, 2020).

These observations are in line with the results of the present investigation. Indeed, the data indicated a decrease in density (-29% and -71%), species richness (-29% and -42%) and Shannon index (-29% and

–59%), respectively, in the rubber and oil palm plantations, after the conversion of secondary forests. This trend could be explained by the fact that the forest is a complex, self-regenerating system, encompassing soil, water, microclimate, energy, and a wide variety of plants and animals in mutual relation (Swarnalatha, 2010). It provides more diverse shelter and food for animals (Singh *et al.*, 2021). Vertically, a forest comprises multi-story vegetation in different strata owing to the distribution of understory grasses and shrubs and over story trees of varying heights (Singh *et al.*, 2021). The conversion of forests to rubber plantations is clearly viewed as an acute threat to plant diversity, which was also lower in rubber plantations than in forests (Drescher *et al.*, 2016; Singh *et al.*, 2021). In fact, the forest had almost six times as many species, especially in vascular plant as the monocultures (Drescher *et al.*, 2016). With the decline in plant diversity, oribatid mite diversity also declines along the transformation gradient (Beckendorff, 2016). Substrate is one of the main factors which indirectly regulates oribatid mite density by generating the presence of soil decomposers (Beckendorff, 2016). Furthermore, the soil mesofauna influence plant productivity and microbial biomass and are key organisms which control ecosystem production, especially in nutrient-limited ecosystems (Dervash *et al.*, 2018). In this way, plant diversity, soil properties and soil fauna have a strong relationship with each other (Hemati *et al.*, 2020).

Soil mesofauna are able to use the existing pore space in soil. They constitute important reservoirs of biodiversity and are reflectors of ecosystem metabolism (Dervash *et al.*, 2018). Unfortunately, the clearance of forests and the subsequent tillage practices affect the soil porosity by compacting the upper layers (Demessie *et al.*, 2013). Soil temperature perceived as one of the soil physics factors that determine the presence and density of soil organisms was higher in monocultural plantation and lower in primary forest, probably due to the reduction of living tree density by regular land clearance and understory vegetation removal in the first one (Sulistiyorini *et al.*, 2018; Singh *et al.*, 2021). According to authors, high soil temperatures will affect the water content in the soil. A rainfall range between 100–200 mm was optimal condition for Oribatid mites' development so their abundance and diversity increased (Lisafitri *et al.*, 2015). This is due to the fact that during rainy periods, the soil moisture content gradually increases by reducing the temperature of the soil (Hemati *et al.*, 2020).

Contrary to our data, an increasing Oribatid mite density following the conversion of forest into rubber (Sulistiyorini *et al.*, 2018) and oil palm (Beckendorff, 2016) plantation was observed. According to authors, the lack of decline in oribatid mite density from rainforest to monocultural plantation could also be due to a decline in predators. A recent study made by Mumme *et al.* (2015) indicated that the density of winged predators such as predatory beetles was reduced in oil palm with only 12% remaining. However, the diversity of oribatid mites was significantly affected by transformation system; the mean number of species was by far higher in rainforest than in oil palm, indicating that fewer species are responsible for the non-altered oribatid mite density (Beckendorff, 2016; Sulistiyorini *et al.*, 2018). At the reproduction level, most oribatid mite species in the forest site are sexual species, as they often seem to depend on a thick litter layer and are therefore not present in oil palm, because reduced by 84% (Beckendorff, 2016).

Whatever the land use types, the sampling rate of Oribatid species represented 72–96% of the expected species. The asymptote has not been reached, but indicating an acceptable sampling rate which is consistent with the results provided by Minor and Cianciolo (2007). At the landscape scale, 80 Oribatid species classified in five cohorts or infraorders (Palaeosomata, Mixonomata, Desmonomata, Brachypylina and Poronota) were recorded. This investigation reveals that the Poronota and Brachypylina represent the major groups from the two study sites. They respond differently through the land use types with a significant variation observed in the Palaeosomata, Mixonomata and Poronota. The reaction of the soil Oribatida consecutive to disturbance varies according to taxa and species (Maraun *et al.*, 2003). The high sensibility of Poronota to mechanic disturbances was noticed in a forest in Göttingen, Germany (Maraun *et al.*, 2003). Admittedly, the agricultural soils derived from secondary forests have recorded a decline in the abundance and species richness of Oribatida, nevertheless, a few major groups react favorably after the conversion of these forests. Indeed, the Desmonomata (+0.50) and Brachypylina (+0.12) respond positively in abundance, and respectively, after transformation of the secondary forests into rubber and oil palm plantations. Likewise, the species richness of Desmonomata (+0.50; +0.66), Brachypylina (+0.04; +0.08) and Mixonomata (+0.14) are positively affected by the forest transition to rubber and oil palm plantations.

In the structure and functions of the terrestrial ecosystems, the mite species from the highest classes of dominance and constancy are the most important in populations structure and in decomposer process (Honciuc and Manu, 2010). The structure study showed that the dominant-accidental Oribatid mite (*Acaridida* sp.1) was specialist (only observed on the site of La Mé) with a small ecological niche, having preferences strictly on the organical level of woody origin and can be explained by the diversity and the provenience of the primary producers from these site. The subdominant-subconstant Oribatid mite (*Haplozetidae* sp.1) was generalist, considered redundant along the two study sites with a large ecological niche. The presence of a higher number of residents-accessory (10 species) and subresident-accidental

(60 species) reflects the modifications on the trophic source of Oribatid mites, due to the biotical and abiotical factors (Honciuc and Manu, 2010).

Soil quality following the secondary forests conversion

Forests and soils play an important role in the carbon storing and mitigating of climate change (Rossi *et al.*, 2015). The Forests provide fundamental protection to the soil and its resources (Miura *et al.*, 2015) by influencing the nutrient cycle (Allen, 2015). The soil considered as a biological entity with complex biochemical reactions is a regenerative ecosystem where energy and matter are transformed and transported (Swarnalatha, 2010). Plant diversity affects soil properties, which in turn, affects plant productivity. Several properties of the soil such as carbon, nitrogen, and soil fauna are highly driven by plant community and diversity (Hemati *et al.*, 2020). However, human activity generates the largest disturbances to the soil system (Allen, 2015). In fact, agricultural developments derived from forest soils are characterized by an alteration of soil physical and chemical properties (Demessie *et al.*, 2013; Chiti *et al.*, 2014; Allen *et al.*, 2015; Drescher *et al.*, 2016; Hemati *et al.*, 2020; Krause, 2020; Nguyen *et al.*, 2020). Thus, the monocultural plantations affect soil quality with feedback in the decline of timber yield (Hemati *et al.*, 2020; Singh *et al.*, 2021). This trend is consistent with the results of our study, where the bulk density increases (+28% and +21%), whilst organic carbon (-56% and -17%), total nitrogen (-55% and -12%) and the soil organic matter (-56% and -17%) decrease respectively, after conversion of secondary forests into rubber and oil palm plantations. High soil compaction in agrosystems highlights the low porosity of soils and therefore the low water retention (Demessie *et al.*, 2013; Krashevskaya *et al.*, 2015; Nguyen *et al.*, 2020). The investigations of Allen *et al.* (2015) in Indonesia indicate an increase in soil bulk density (+10% and +20%), respectively, in rubber and oil palm plantations derived from forests. These results are in line with the works made by Demessie *et al.* (2013) which showed an increase in the bulk density in agroforestry and agricultural farms after conversion of forests in southern Ethiopia. According to authors, the higher bulk density in the upper layer of agroforestry and agricultural farms as compared to natural forest may be attributed to lower SOC content and soil compaction caused by cultivation practices.

The highest SOC losses in the 0–30 cm layer were caused by the conversion of primary forests to tree plantations: cocoa -61% of the original SOC stock, coconut -55%, rubber -35% and oil palm -28% (Chiti *et al.*, 2014). These observations were supported by the research of Guillaume *et al.* (2015) which showed a decline in organic carbon and total nitrogen up to 70% in the oil palm and 62% in the rubber plantations. The high amount of soil organic carbon, total nitrogen and organic matter in secondary forests may be explained by the regular input of litter from diverse plant communities as compared to monocultural system (Demessie *et al.*, 2013). Moreover, forest clearing and tillage practices could (i) affect the soil capacity of carbon absorption by decreasing the litter input to compensate the decomposition, (ii) reduce ability of the soil to physically protect SOC from the decomposition due to the destruction of soil aggregates and the loss of particulate organic carbon through runoff and erosion (DeBlécourt *et al.*, 2013; Guillaume *et al.*, 2015) which in turnover influence soil biota and food web due to differences in soil clay content (Demessie *et al.*, 2013). Whatever the site, our results showed that the clay sandy and clay textures stabilize the soil physico-chemical and biological properties more than the sandy clay and sandy textures. Furthermore, the former presented a soil more acid than the latter. The most important factor affecting soil N availability is soil texture and clay is assumed to protect organic matter against decomposition (Demessie *et al.*, 2013). The same trend was confirmed by several publications, where soil biochemical characteristics, nutrient stocks, gross soil-N cycling rates and water holding capacity in the reference land uses were higher in the clay soil compared to the loam acrisol and sandy soil (Silver *et al.*, 2000; Sotta *et al.*, 2008; Allen, 2015). The low organic matter and the dryness recorded in the sandy soil could be perceived as disturbance factors for the mite's dynamics (Honciuc and Manu, 2010). An increase soil pH following the transition of natural vegetation into agrosystem was in line with the works of Krashevskaya *et al.* (2016) conducted in southeast Sumatra in Indonesia and where a pH = 4.3 and 4.5 have been measured respectively in rubber and oil palm plantations, after the forest conversion (pH = 3.8).

Previous studies demonstrated that the conversion of natural forests into monocultural plantations is associated with soil disturbance and changes in vegetation structure, leading to changes in soil properties (Conti, 2015; Vrignon-Brenas *et al.*, 2019; Hemati *et al.*, 2020; Nguyen *et al.*, 2020). However, it is possible to maintain or improve soil conditions on a site by maintaining or increasing organic matter, nutrients and soil organism diversity (Conti, 2015; Vrignon-Brenas *et al.*, 2019; Hemati *et al.*, 2020; Nguyen *et al.*, 2020). Indeed, the incorporation of woody trees with an understory of smaller trees during the early establishment periods of plantations can create a sustainable agroforestry system with improved land functionality (Nguyen *et al.*, 2020; Singh *et al.*, 2021). The use of nitrogen-fixing legume species as a cover crop is by far the best soil management technique with respect to nutrient management during the immature phase because it allows to avoid soil degradation and loss (Vrignon-Brenas *et al.*, 2019). This will help regulate physical properties and processes of the soil, and further support C and nutrient cycles (Tongkaemkaew *et al.*, 2018).

Conclusion

Our findings showed a decrease in Oribatid density (–29% and –71%), species richness (–29% and –42%), diversity (–29% and –59%), soil organic carbon (–56% and –17%), total nitrogen (–55% and –12%) and soil organic matter (–56% and –17%), and an increase in bulk density (+28% and +21%), respectively after transformation of the secondary forests into rubber and oil palm plantations. In other word, the site of Grand Lahou (rubber landscapes) favors a high degradation of the soil physico-chemical properties, whereas the site of La Mé (oil palm landscapes) further deteriorates the soil Oribatid mites' communities. Whatever the study site, soil physico-chemical and biological properties were more stabilized in the clay and clay sandy textures compared to sandy clay and sandy soil textures. To offset the imbalance within agrosystems, a conservation agriculture related to management of the natural understory vegetation would be beneficial for the maintenance of soil quality.

Conflicts of Interest

The authors have no conflict of interest to declare.

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Appendix 1. Abundance (secondary forests: individuals per 15 soil cores / plantations: individuals per 45 soil cores) of the species recorded among the land use types.

Oribatida	Land use types				Landscape			
	SFG	RBP	SFL	OPP	% of total Oribatida	Dominance	% of occurrence	Frequency
Palaeosomata								
<i>Acaronychus</i> sp.2	0	3	0	0	0.56	subresident	2.50	accident
Mixonomata								
<i>Annectacarus</i> sp.1	1	1	1	0	0.56	subresident	2.50	accident
<i>Eulohmannia</i> sp.1	4	0	0	1	0.93	subresident	2.50	accident
<i>Euphthiracarus</i> sp.1	0	3	0	0	0.56	subresident	2.50	accident
<i>Epilohmannia</i> sp.1	2	0	0	0	0.37	subresident	0.83	accident
<i>Javacarus</i> sp.1	1	8	0	1	1.86	subresident	5.83	accessory
<i>Meristacarus</i> sp.1	1	0	0	0	0.19	subresident	0.83	accident
<i>Meristacarus</i> sp.2	0	5	1	1	1.30	subresident	5.00	accessory
<i>Meristacarus</i> sp.3	0	0	0	1	0.19	subresident	0.83	accident
<i>Haplacarus</i> sp.1	3	0	0	0	0.56	subresident	1.67	accident
<i>Phthiracarus</i> sp.1	4	4	1	0	1.67	subresident	6.67	accessory
<i>Torpacarus</i> sp.1	1	0	0	0	0.19	subresident	0.83	accident
Desmonomata								
<i>Afronothrus</i> sp.1	0	0	3	1	0.74	subresident	2.50	accident
<i>Nothrus</i> sp.2	0	5	0	1	1.11	subresident	3.33	accident
<i>Nothrus</i> sp.3	0	3	0	0	0.56	subresident	1.67	accident
<i>Nothrus</i> sp.4	0	0	0	1	0.19	subresident	0.83	accident
<i>Nothrus</i> sp.6	0	0	0	2	0.37	subresident	1.67	accident
<i>Nothrus</i> sp.7	0	0	0	1	0.19	subresident	0.83	accident



<i>Nanhermannia</i> sp.1	1	0	0	0	0.19	subresident	0.83	accident
<i>Malaconothrus</i> sp.1	0	0	0	1	0.19	subresident	0.83	accident
<i>Nothrus crassisetosus</i>	0	1	0	0	0.19	subresident	0.83	accident
Brachypylina								
<i>Lopheremaeus</i> sp.1	0	0	0	2	0.37	subresident	1.67	accident
<i>Dolicheremaeus</i> sp.1	2	4	1	3	1.86	subresident	5.83	accessory
<i>Paralopheremaeus</i> sp.1	0	0	0	1	0.19	subresident	0.83	accident
Damaeidae sp.1	1	15	2	4	4.08	resident	12.50	accessory
Damaeidae sp.2	2	0	0	0	0.37	subresident	1.67	accident
Damaeidae sp.3	0	0	0	2	0.37	subresident	1.67	accident
Belbidae sp.1	2	3	0	0	0.93	subresident	4.17	accident
Belbidae sp.2	0	1	0	0	0.19	subresident	0.83	accident
<i>Eremobelba</i> sp.1	0	0	1	0	0.19	subresident	0.83	accident
<i>Carabodes</i> sp.1	4	0	0	0	0.74	subresident	1.67	accident
Carabodidae sp.5	0	0	1	0	0.19	subresident	0.83	accident
<i>Neoliodes</i> sp.1	2	2	1	3	1.48	subresident	5.83	accessory
<i>Oppia</i> sp.1	2	12	0	11	4.64	resident	9.17	accessory
<i>Oppia</i> sp.2	0	1	0	0	0.19	subresident	0.83	accident
<i>Oppia</i> sp.6	0	5	1	8	2.60	subresident	7.50	accessory
<i>Oppia</i> sp.7	2	0	0	0	0.37	subresident	0.83	accident
<i>Oppia</i> sp.8	4	0	0	0	0.74	subresident	0.83	accident
<i>Oppia</i> sp.10	0	7	0	0	1.30	subresident	5.00	accessory
<i>Oppia</i> sp.11	0	1	0	0	0.19	subresident	0.83	accident
<i>Oppia</i> sp.13	2	0	0	19	3.90	resident	5.83	accessory
<i>Oppia</i> sp.15	0	0	5	8	2.41	subresident	5.83	accessory
<i>Oppia</i> sp.16	0	0	1	2	0.56	subresident	1.67	accident



<i>Oppia</i> sp.17	0	0	1	0	0.19	subresident	0.83	accident
<i>Oppia</i> sp.18	0	0	0	2	0.37	subresident	1.67	accident
Oppiidae sp.2	2	1	0	0	0.56	subresident	2.50	accident
Oppiidae sp.4	0	0	3	19	4.08	resident	12.50	accessory
Oppiidae sp.5	0	3	0	0	0.56	subresident	1.67	accident
Oppiidae sp.6	0	0	5	0	0.93	subresident	2.50	accident
Poronota								
Ceratozetidae sp.1	2	0	1	6	1.67	subresident	5.00	accessory
Ceratozetidae sp.3	0	0	0	3	0.56	subresident	2.50	accident
Ceratozetidae sp.5	0	0	0	1	0.19	subresident	0.83	accident
<i>Galumna</i> sp.1	6	11	1	1	3.53	resident	12.50	accessory
<i>Galumna</i> sp.2	10	12	1	1	4.45	resident	15.83	subconstant
<i>Galumna</i> sp.3	5	0	0	0	0.93	subresident	3.33	accident
<i>Galumna</i> sp.4	0	0	1	0	0.19	subresident	0.83	accident
<i>Galumna</i> sp.5	0	0	1	0	0.19	subresident	0.83	accident
<i>Galumna</i> sp.11	0	0	2	0	0.37	subresident	1.67	accident
<i>Galumna</i> sp.15	0	0	1	0	0.19	subresident	0.83	accident
<i>Galumna</i> sp.16	0	0	1	2	0.56	subresident	2.50	accident
<i>Galumnella</i> sp.1	0	0	1	0	0.19	subresident	0.83	accident
<i>Orthogalumna</i> sp.1	0	0	1	0	0.19	subresident	0.83	accident
Parakalummidae sp.1	2	1	0	0	0.56	subresident	2.50	accident
<i>Taeniogalumna</i> sp.1	0	0	1	0	0.19	subresident	0.83	accident
Mycobatidae sp.1	11	10	0	0	3.90	resident	10.83	accessory
Mycobatidae sp.2	3	12	1	1	3.15	resident	10.00	accessory
Mycobatidae sp.3	1	1	0	0	0.37	subresident	1.67	accident
Mycobatidae sp.4	0	3	0	0	0.56	subresident	0.83	accident



Schelorbitidae sp.1	1	3	0	0	0.74	subresident	2.50	accident
Schelorbitidae sp.2	0	3	0	0	0.56	subresident	2.50	accident
Schelorbitidae sp.3	0	0	1	10	2.04	subresident	5.00	accessory
Schelorbitidae sp.4	0	0	1	0	0.19	subresident	0.83	accident
Haplozetidae sp.1	2	37	0	2	7.61	subdominant	18.33	subconstant
<i>Rhizoglyphus</i> sp.1	0	0	0	1	0.19	subresident	0.83	accident
<i>Acaridida</i> sp.1	0	0	99	2	18.74	dominant	1.67	accident
Acaridae sp.2	0	1	0	0	0.19	subresident	0.83	accident
Oribatida sp.1	0	0	1	0	0.19	subresident	0.83	accident
Oribatida sp.2	0	1	0	0	0.19	subresident	0.83	accident
Oribatida sp.3	1	0	0	0	0.19	subresident	0.83	accident
Oribatida sp.6	0	1	0	0	0.19	subresident	0.83	accident

Total number of soil cores N = 120. Dominance and frequency were determined at the landscape scale. *SFG* secondary forests of Grand Lahou, *RBP* rubber plantations of 7-25 years, *SFL* secondary forests of La Mé, *OPP* oil palm plantations of 13-39 years

