Sensitivity and resistance of soil fertility indicators to land-use changes: New concept and examples from conversion of Indonesian rainforest to plantations

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ABSTRACT

Tropical forest conversion to agricultural land leads to a strong decrease of soil organic carbon (SOC) stocks. While the decrease of the soil C sequestration function is easy to measure, the impacts of SOC losses on soil fertility remain unclear. Especially the assessment of the sensitivity of other fertility indicators as related to ecosystem services suffers from a lack of clear methodology. We developed a new approach to assess the sensitivity of soil fertility indicators and tested it on biological and chemical soil properties affected by rainforest conversion to plantations. The approach is based on (non-)linear regressions between SOC losses and fertility indicators normalized to their level in a natural ecosystem. Biotic indicators (basal respiration, microbial biomass, acid phosphatase), labile SOC pools (dissolved organic carbon and light fraction) and nutrients (total N and available P) were measured in Ah horizons from rainforests, jungle rubber, rubber (*Hevea brasiliensis*) and oil palm (*Elaeis guineensis*) plantations located on Sumatra. The negative impact of land-use changes on all measured indicators increased in the following sequence: forest < jungle rubber < rubber < oil palm. The basal respiration, microbial biomass and nutrients were resistant to SOC losses, whereas the light fraction was lost stronger than SOC. Microbial C use efficiency was independent on land use. The resistance of C availability for microorganisms to SOC losses suggests that a decrease of SOC quality was partly compensated by litter input and a relative enrichment by nutrients. However, the relationship between the basal respiration and SOC was non-linear; i.e. negative impact on microbial activity strongly increased with SOC losses. Therefore, a small decrease of C content under oil palm compared to rubber plantations yielded a strong drop in microbial activity. Consequently, management practices mitigating SOC losses in oil palm plantations would strongly increase soil fertility and ecosystem stability. We conclude that the new approach enables quantitatively assessing the sensitivity and resistance of diverse soil functions to land-use changes and can thus be used to assess resilience of agroecosystems with various use intensities.

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1. Introduction

The increase of agricultural land area in the tropics is ongoing mainly at the expense of primary and secondary forests (Gibbs et al., 2010). While tropical deforestation rates are tending to stabilize or to decrease in regions like Brazil, they are still increasing in Indonesia, driven by the international demand for wood-derived products as well as for agricultural land for oil palm and rubber plantations (Abood et al., 2015; Margono et al., 2014). Forest

conversion in general and especially to oil palm and rubber plantations strongly changes ecosystem functioning (Barnes et al., 2014). This results in losses of biodiversity (Barlow et al., 2007), ecosystem services such as water supply (Bruijnzeel, 2004) and C sequestration in the plant biomass and in the soil (Don et al., 2011; Kotowska et al., 2015). Guillaume et al. (2015) observed up to 70% soil organic carbon (SOC) losses in the topsoil under oil palm and rubber plantations in Indonesia compared to rainforest. Further, SOC losses depended on land-use intensity. Tropical forest conversion to agricultural land also leads to a decrease of biological and chemical indicators of soil fertility (Joergensen, 2010; Kaschuk et al., 2010). Nevertheless, only few studies have included rubber and oil palm plantations, despite the large-scale extension of these land-use types in the last decades (Gatto et al., 2015). In a recent review on the impact of land-use changes on microorganisms in the tropics (Joergensen, 2010), only six studies on rubber and oil palm plantations encompassing two continents were included, and only three of them used forest sites as a baseline to evaluate the plantation's impact.

The decrease of C sequestrated in soils is a major concern because it represents the biggest terrestrial C pool and is in exchange with the biological C cycle and atmospheric CO_2. The loss of the C sequestrating function of soils after forest conversion to plantations is measured straightforwardly by comparing SOC stocks among undisturbed (e.g. forest) and agricultural ecosystems. SOC losses are also associated with a decrease of soil quality and fertility and thus, with a soil's capacity to provide sustainable ecosystem services (Bastida et al., 2008; Lal, 2010, 2006). SOC is considered as an "umbrella" property of soil fertility because SOC decrease is associated with the decrease of most soil properties and functions related to fertility. This includes bulk density, nutrient availability, water penetration and holding capacity, erodibility, faunal and microbial activity (Lal, 2006). For instance, SOC and crop yield are positively correlated in various agricultural systems (Bauer and Black, 1994; Ganzhara, 1998). Nevertheless, the effects of SOC losses due to mineralization or erosion on soil fertility remain unclear because it is difficult to quantify relationships between soil properties and soil functions (Letey et al., 2003).

Soil fertility cannot be measured directly because the commonly used crop yield reflects only one of many soil functions and services. Therefore, soil fertility is classically assessed by selecting and interpreting changes of properties or processes recognized as important for fertility, i.e. using them as indicators of soil fertility (Askari and Holden, 2014). Maximal or optimal levels of biological, chemical or physical soil properties are specific for each natural or agricultural system. Consequently, in order to evaluate the impact of land-use changes, indicators must be compared to a baseline level from undisturbed environments or from specific sustainable management practices (Gil-Sotres et al., 2005). Moreover, various soil properties and functions are not similarly affected by land-use changes. This calls for determining the sensitivity or the resistance of fertility indicators to land-use changes in order to identify which functions are at risk and to target appropriate management practices. For this purpose, determining the sensitivity of indicators to SOC losses is especially appropriate because SOC is (i) correlated with most soil fertility indicators, (ii) easily measurable and (iii) directly affected by management practices.

Biological soil properties and SOC labile pools are in general more sensitive to land-use or management changes than physical or chemical soil properties (Bastida et al., 2008; Raiesi and Beheshti, 2015; Sharma et al., 2011). For instance, microbial biomass, basal respiration, extracellular enzymes activities, SOC light fraction or dissolved organic carbon (DOC) decreased generally faster after land-use changes than the total SOC (Bolinder et al., 1999; Kandeler et al., 1999; Powlson et al., 1987; Sparling, 1992). Microbial activity is a main indicators reflecting soil fertility because microorganisms

favors plant growth by driving all C and nutrient cycles and depends strongly on C content (Anderson and Domsch, 1989). Microbial activity, however, depends not only on the total amount of SOC but also on its availability for microorganisms, e.g. the proportion of labile SOC pools (von Lützow et al., 2006) or the nutrient content (Cleveland et al., 2006). For instance, microbial activities measured based on basal respiration during incubation of free particulate organic matter, the light fraction or the water- or K_2SO_4-soluble C were higher than the basal respiration of the bulk soil (Alvarez et al., 1998; Haile-Mariam et al., 2008; Mueller et al., 2014; Wagai et al., 2013; Wang et al., 2003). Thus, the basal respiration reported per unit of SOC is an indicator of C availability. Using ratios of single indicators, further indices were developed reflecting microbial community functioning or SOC functions in the soil (Anderson, 2003). Among them, the metabolic quotient (qCO_2) (basal respiration to microbial biomass ratio) is one of the most widely used and reflects the carbon-use efficiency of microbial communities (Anderson and Domsch, 1990). The microbial quotient (microbial biomass to soil SOC ratio) was suggested to reflect the soil function of supporting microbial growth (Insam and Domsch, 1988).

Sun-ray plots or radar plots provide quick overviews of the sensitivity of all indicators (Bloem et al., 2006; Schloter et al., 2003), but do not quantitatively assess differences in their sensitivity. Changes after site conversion of indices based on the ratios of two soil properties reflect differences in the sensitivity of these two properties, i.e. one variable change more or less than the other. However, because comparisons are made between groups (land-use types) and not along a continuous and quantitative variable, it is not possible to determine the type of relationship between these properties. Linear and non-linear relationships among soil properties or functions have completely different ecological meaning and implications for management practices. On the one hand, a linear relationship between the decrease of SOC and of a soil property or function implies that SOC losses have the same effect at any C content whenever the property or function is sensitive, resistant or proportionally decreases with SOC losses (Fig. 1). On the other hand, a non-linear relationship implies that the effect of SOC losses depends on the C content. The same absolute SOC loss has a higher negative impact at low C than at high C content for indicators being resistant, or vice versa for indicators being sensitive.

We hypothesized that (1) SOC losses in plantations are associated with a strong decrease of soil fertility indicators. Furthermore, (2) the indicators do not necessarily decrease proportionally with SOC losses but could be more resistance or more sensitive than SOC to land-use change (Fig. 1). Finally, (3) the indicators' sensitivity varies depending on the SOC loss intensity. Therefore, the study objectives were to (1) quantify the changes in soil fertility indicators following SOC losses after forest conversion to oil palm and rubber plantations, (2) relate C availability with biological and chemical indicators of soil fertility and (3) provide a comprehensive approach to assess the sensitivity of these (and other) fertility indicators to SOC losses.

2. Materials and methods

2.1. Study sites

Study sites were located in Jambi Province (Sumatra, Indonesia) under a humid tropical climate (27 °C; 2400 mm y^{-1}; 112–259 mm month^{-1}) with a drier season lasting from May to September. A space-for-time substitution approach was used to assess the impact of rainforest conversion on soil fertility indicators. The experimental design includes natural lowland tropical rainforest as reference site and three land-use types dominating on Sumatra: (1) jungle rubber, (2) rubber plantation and (3) oil

Soil Organic Carbon
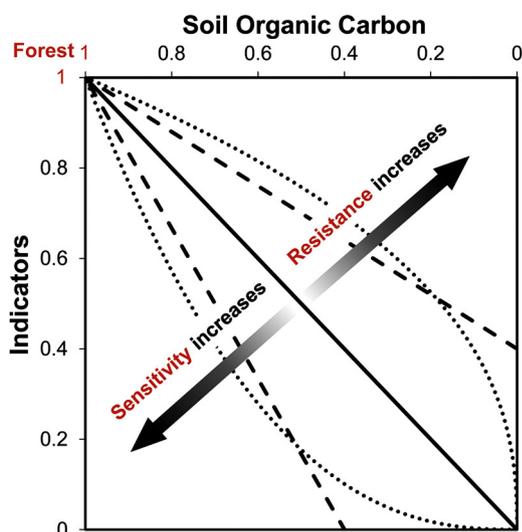
Fig. 1. Concept of sensitivity of soil fertility indicators to SOC losses (or other main variables) by land-use changes. Indicators can decrease proportionally with the decrease of C content (solid line), or be resistant or sensitive to it. In the latter case, the indicator sensitivity or resistance is either independent of SOC loss intensity (linear relationships; dashed lines) or dependent on SOC loss intensity (non-linear relationships; dotted lines). All indicators were normalized to adjust all values measured in different scales and units to a common scale ranging from 1 to 0. Thus the maximum of normalized values (1.0) corresponds to that measured in soil under rainforest. Every indicator was normalized to its value under rainforest by calculating the ratio between the values measured under plantations (I_p) and rainforest (I_f): I_p/I_f.

palm plantation. The sites were very carefully selected based on climatic conditions, vegetation (for forest sites), plantation age and soil texture, and being located on similar landscape positions. Soils were Acrisols with loamy texture. Forest sites were located in Harapan Rainforest, an old-growth forest that was subject to minor logging until 2003, when it became a conservation and restoration area. Jungle rubber corresponds to an agroforest, in which rubber trees are extensively planted in partially logged forest. Rubber and oil palm plantations were smallholding intensive monocultures of similar average age (14 years), ranging from 12 to 17 years. Four replicate sites for each land-use type were selected for a total of 16 field sites. Site altitudes varied between 50 and 100 m a.s.l. Ah horizons of loamy Acrisols were collected in soil pits. A detailed description of sites, sampling and soil parameters was presented earlier (Guillaume et al., 2015). Further information on study sites and land-use history in the study region are available in Allen et al. (2015), Barnes et al. (2014) and Gatto et al. (2015).

2.2. Chemical analyses

Total C and N contents in soil were measured using an Elemental Analyser (Eurovector). Available P was defined as the sum of P by a two-step extraction method (Hedley et al., 1982). First, the labile inorganic P that is directly exchangeable with the soil solution was extracted using deionized water. Then, the labile inorganic and organic P sorbed onto mineral surfaces were extracted using 0.5 M NaHCO₃ at pH 8.5. Phosphate concentrations in soil extracts were determined by molybdate colorimetry (Murphy and Riley, 1962) using a calibrated spectrophotometer (Specord 40).

2.3. Incubation experiment

Soil from Ah horizons from the 16 sites were incubated in the dark at room temperature (23 °C) during 70 days. Six subsamples from each site were incubated. Twenty grams of air-dried and sieved soil were rewetted to 60% of their water holding capacity

and incubated in 250 ml bottles. To determine respiration rates, CO_2 was continuously trapped within 2 ml of 1.0 M NaOH. Trapped-CO_2 was then back-titrated using 0.1 M HCl against phenolphthalein, after $BaCl_2$ addition to precipitate carbonates.

A two-pool mixed-model was used to describe SOC mineralization kinetics, thereby estimating the basal respiration (Bonde and Lindberg, 1988). The first pool follows a first-order decomposition kinetics, while the second follows a zero-order kinetics, i.e. the decomposition rate is constant over time:

$$\text{Cmin} = C_l(1 - \exp^{-tk_l}) + BRt \tag{1}$$

where t is the time, Cmin is the cumulative C mineralized to time t. C_l, k_l, and BR are the estimated parameters of the model. C_l corresponds to the size of the labile C pool mineralized during the first weeks. This pool originates mostly from sample preparation and re-wetting. k_l is the decomposition constant of this labile pool. BR corresponds to the constant respiration rate over time observed after the exhaustion of the initial labile pool, i.e. the basal respiration.

2.4. Microbial biomass and DOC

Microbial biomass (Cmic) was measured by the fumigation–extraction method (Vance et al., 1987). Briefly, 7 g of incubated samples were fumigated with ethanol-free $CHCl_3$ for 24 h in a desiccator. After $CHCl_3$ removal, soluble C from fumigated and non-fumigated samples was extracted with 30 ml of 0.5 M K_2SO_4 by shaking for 1 h on an orbital shaker (120 rpm). Extracts were filtered and soluble C was measured using a Multi N/C 2100s (Analytik Jena, Germany). The DOC corresponded to the soluble C extracted by K_2SO_4 in the non-fumigated extract. The difference in soluble C between fumigated and non-fumigated samples was converted to Cmic using a factor of 0.45. This factor was chosen in order to compare our data with other studies because it is the most widely used (Joergensen, 2010).

2.5. Enzyme activities

Extracellular enzyme activity (EEA) of acid phosphatase was measured by fluorimetric microplate assay using fluorogenic methylumbelliferone-based (MU) substrates (Marx et al., 2001). Briefly, 0.5 g of incubated soil was shaken for 30 min with 50 ml of sterile water and then dispersed by an ultrasonic disaggregator (50 J s⁻¹ for 120 s). For each sample, three 50 μl aliquots of the stirred suspension were mixed in a 96-well microplate (Brand pureGrade, black) with 50 μl buffer (MES) and 100 μl of substrate solution of increasing concentrations (0, 20, 40, 60, 80, 100, 200 and 400 μmol substrate). Plates were measured directly after substrate addition and 1 h later with an automated fluorometric plate-reader (Wallac 1420, Perkin Elmer, Turku, Finland). The phosphatase activity corresponded to the maximal reaction rate (V_{max}) estimated by fitting a Michaelis–Menten kinetics function to the reaction rate measured at the increasing substrate concentrations. Further details on the method can be found in Loeppmann et al. (2016).

2.6. Density fractionation

The density fractionation was a simplification of the method described by John et al. (2005). Four grams of incubated soil were placed in a centrifuge tube with 5 glass beads of 5 mm diameter and 20 ml of sodium polytungstate solution (SPT; 1.6 g cm⁻³). The tube was shaken 16 h on an orbital shaker (120 rpm) to disperse the free particulate organic matter and the one occluded in macroaggregates. After dispersion, the suspension was centrifuged for 1 h at 4700 rpm. The supernatant composed of free and occluded particulate organic matter was then filtered (0.45 μm) using vacuum and washed twice with 100 ml deionized water. The C content of the

light fraction, composed of free and occluded particulate organic matter, were measured using a CN elemental analyser (Vario EL cube, Elementar Analysensysteme GmbH, Germany). The value is expressed in milligrams of C per gram of soil.

2.7. Sensitivity of soil fertility indicators to SOC losses

To compare the sensitivity of soil properties to SOC losses, each variable was normalized to its mean value under rainforest. Thus, values ranging from 0 to <1 indicate that the values of an indicator decreased after forest conversions to plantation. If an indicator decreases proportionally with the C content (e.g. a decrease of 50% of C content is associated with a decrease of 50% of a soil property), then the regression between both variables has a slope of 1 and an intercept of 0 (Fig. 1). The data normalization imposes the conditions that $f(1) = 1$; therefore the sensitivity or resistance of the variables can be assessed by linear or power regressions for which only one parameter has to be estimated. The linear regression slope was estimated by the following equation:

$$y = ax + 1 - a \tag{2}$$

where y is the predicted normalized value of a variable at a C content of x, and a the slope of the linear regression, corresponding to the sensitivity of the variable. The intercept (b) can be calculated from the slope ($b = 1 - a$). According to the hypothesis that the relation between the decreases of variables and C content might be non-linear, power function regressions were fitted with the following equation:

$$y = x^a \tag{3}$$

where y is the predicted normalized value of a variable at a C content of x, and a the exponent of the non-linear regression. Eq. (3) satisfies the condition $f(1) = 1$ independently of a. However, it also imposes the condition that $f(0) = 0$, i.e. that the variable must reach 0 in the absence of SOC.

The proportionality of the decrease between two variables is assessed if confidence intervals of the estimated slope (Eq. (2)) or exponent (Eq. (3)) of the models include 1. If 1 is excluded, then the indicator is either resistant to SOC losses (slope or exponent <1) or sensitive to SOC losses (slope or exponent >1). Finally, the linearity or non-linearity of a variable decrease was assessed by choosing the model with the highest R^2, by plotting the residuals to fitted values of model and by the physical meaning of the relationship. For instance, if the microbial activity is resistant to SOC losses, the relationship cannot be linear because this model would mean that the microorganisms would be still active when the C content reaches zero.

2.8. Response of indices to land-use changes

Three classical indices of microbial activity based on the ratio between two measured soil parameters were calculated: (1) the metabolic quotient; ratio between the basal respiration (μg C-CO_2 g^{-1} soil d^{-1}) and microbial biomass (μg C-mic g^{-1} soil), (2) the microbial quotient; ratio between the microbial biomass (μg C-mic g^{-1} soil) and the C content (mg C g^{-1} soil), and (3) the specific basal respiration; ratio between the basal respiration (μg C-CO_2 g^{-1} soil d^{-1}) and the C content (mg C g^{-1} soil). Because indices under plantations may be either higher or lower compared to forest, the response to land-use change was calculated with the following equation:

$$R_i = \frac{I_p - I_f}{I_f} \times 100 \tag{4}$$

where R_i is the index response, I_p is the index value in a plantation site and I_f is the mean index value under forest. Thus, the forest
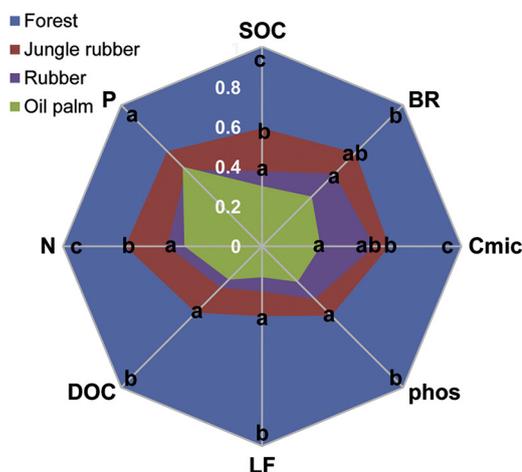
Fig. 2. Decrease of soil fertility indicators per land-use type. Carbon content (SOC), basal respiration (BR), microbial biomass (Cmic), acid phosphatase (phos), light fraction (LF), K_2SO_4-soluble C, N content (N) and available P (P). The values are normalized to the respective rainforest mean (=1). Different letters represent significant differences of the indicator between land uses ($n = 4$, except for P $n = 3$; ANOVA; $p < 0.05$). Letter a was not repeated if land-use types with lower values were not significantly different.

average is 0 and positive values indicate an increase of the index under plantations, and vice versa.

2.9. Statistics

All statistical analyses were performed using the open source software R version 3.2.0. Land-use type effect on indicators or indices was tested by analysis of variance (ANOVA) with forest, jungle rubber, rubber and oil palm as fixed factors. For each factor, four independent field sites were used as replicates. Normality of residuals and variance homogeneity were tested with Shapiro–Wilk and a Bartlett test, respectively. Subsequently, a *post hoc* Tukey HSD test was performed to assess differences between factors. Linear and non-linear regressions were fitted using the function *nls* (*nls2* package). Residuals normality was tested by a Shapiro–Wilk test. The C mineralization kinetic model was fitted for each field replicate using the data from the 6 laboratory replicates. Data are presented as mean of four replicates $\pm$ standard error (SE). If not specified, discussed differences are significant at a p-value <0.05.

3. Results

3.1. SOC mineralization kinetics

Soil re-wetting led to high respiration rates that stabilized three weeks after water addition. After a time-lag of maximum 3 days, labile organics released by sample preparation and soil re-wetting followed first-order decays in all land-use types. The half-life of the labile pools ranged from 4.5 ± 0.2 for forest to 8.6 ± 0.8 days for rubber plantations (Table 1). After the consumption of the initial labile pool, respiration rates stabilized in all land-use types to a constant basal respiration. Therefore, the mineralization of the SOC pools sustaining the basal respiration had to be fitted with a zero-order kinetics. This indicates that the mineralization rates were very low compared to pool size. The basal respiration reached $18.7 \pm 1.4 \, \mu g$ C-CO_2 g^{-1} soil d^{-1} under forest, but was strongly reduced under plantations; up to $65 \pm 8\%$ less under oil palm and $48 \pm 10\%$ less under rubber plantations (Fig. 2). The basal respiration under jungle rubber was $33 \pm 10\%$ lower than under forest. Considering a carbon use efficiency of 50%, the proportion of the SOC processed by microorganisms during 70 days ranged from

Table 1
Soil properties and processes under forest, extensive rubber plantations (jungle rubber), rubber and oil palm monocultures.

	C content ($mg\,C\,g^{-1}$)	N content ($mg\,N\,g^{-1}$)	P available ($\mu g\,P\,g^{-1}$)	CN	LF ($mg\,C\,g^{-1}$)	DOC ($\mu g\,C\,g^{-1}$)	Cmic ($\mu g\,C\,g^{-1}$)	Basal respiration ($\mu g\,C\text{-}CO_2\,g^{-1}\,d^{-1}$)	Half-life[a] (days)	Acid phosphatase ($nM\,g^{-1}\,h^{-1}$)
Rainforest	68 ± 8	4.3 ± 0.4	25.5 ± 4.4	15.7 ± 0.4	18.5 ± 2.9	256 ± 26	576 ± 35	18.7 ± 1.4	4.5 ± 0.2	189 ± 24
Jungle rubber	40 ± 7	3.0 ± 0.4	17.3 ± 1.6	13.5 ± 0.4	6.5 ± 1.3	121 ± 25	367 ± 38	12.4 ± 1.8	5.9 ± 0.6	93 ± 23
Rubber	26 ± 3	2.0 ± 0.1	14.0 ± 1.8	12.4 ± 0.8	4.2 ± 0.7	76 ± 11	327 ± 32	9.7 ± 1.8	8.6 ± 0.8	71 ± 15
Oil palm	21 ± 3	1.7 ± 0.3	14.5 ± 1.8	12.2 ± 0.3	2.9 ± 0.8	61 ± 5	169 ± 45	6.6 ± 1.5	8.0 ± 0.3	48 ± 11

[a] Half-life of the labile pool mineralized during the initial CO_2-flush from soil incubation.
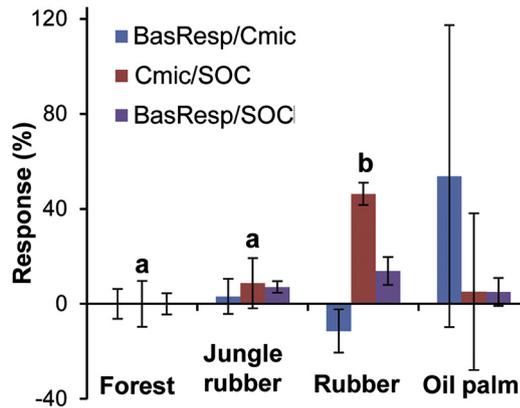
Fig. 3. Response of microbial activity indices by land-use type. Indices were calculated as ratios between (BasResp) basal respiration, (Cmic) microbial biomass or (SOC) soil organic carbon. The response represents the percentage of increase (positive values) or decrease (negative values) of the indices values compared to the values under forest. Different lower case letters indicate significant differences (ANOVA, $n = 4$). Oil palms were not included in the test because of the high variability between sites.

Fig. 4. Logarithmic relationship between basal respiration and C content (solid line) fitted with the 16 sites (empty symbols). The basal respiration is resistant at high C content but strongly decreases at low C content. Land-use types' averages (filled symbols; mean ± SE; $n = 4$) were not used for the regression. The relationship for forest plots (dashed-line) showed that the basal respiration under natural conditions does not increase proportionally with an increased amount of C sequestrated in soil.

6% under forest to 9% under rubber plantations. This corresponds to 20% of the remaining light fraction under forest and 55% under rubber, indicating that most of the light fraction in the soil under all land-use types remained after the incubation.

3.2. Effect of land-use on soil fertility parameters

All measured biological and chemical indicators of soil fertility decreased in plantations compared to tropical rainforest (Fig. 2). Similarly to the SOC, the highest values were found under rainforest, and decreased in the following order: rainforest > jungle rubber > rubber > oil palm. Land-use effect was significant for all indicators except for the available P ($p = 0.09$). All other indicators were significantly lower under the three plantation types compared to forest (except the basal respiration under jungle rubber, $p = 0.08$). While the SOC labile pools (LF and DOC) and acid phosphatases showed no difference among plantations, the plantation type had an effect on the N content, microbial biomass and basal respiration. Compared to forest, the basal respiration was significantly reduced only under monocultures. However, the microbial biomass was significantly lower under oil palm compared to jungle rubber.

The response of indices reflecting microbial ecological strategies or C availability (BasResp/Cmic, BasResp/SOC, Cmic/SOC) showed no clear trends among land-use types (Fig. 3). The variability of indices was high within land use, reducing considerably the power of analysis of variance. Especially the microbial community under oil palm showed the lowest and the highest BasResp/Cmic and Cmic/SOC ratios measured in any land-use type. By excluding oil palm from the analysis, Cmic/SOC was the only index showing a significant effect of land use. Rubber plantations had higher Cmic/SOC ratios compared to jungle rubber and forest sites, indicating an increase of the C availability and, consequently, better conditions for microbial growth under rubber plantations.

3.3. Sensitivity of soil fertility indicators to SOC losses

To demonstrate the sensitivity or resistance of soil fertility indicators, they were related to SOC losses according to the suggested concept (Fig. 1). The basal respiration showed a strong ($R^2 = 0.91$) and positive relationship with the C content (Fig. 4), better explained by a logarithmic than by a linear model. The linear model explains 1% less of the variability compared to the non-linear model (Table 2). Furthermore, positive intercept of the linear model assumes active microorganisms in absence of SOC, what is impossible. The non-linear relationship between the basal respiration and the C content indicates a strong negative effect of SOC losses on C availability at a low C content, but only a weak negative effect at high C content. The regression slope estimated only for forest sites (Fig. 4, dashed-line) showed that the basal respiration decreased proportionally 30% less than the C content. Thus, soils under natural conditions had higher specific basal respiration (BasResp/SOC) at lower C content. Because of the logarithmic relationship, the specific basal respiration of soils under plantations also increased until the C content reached 2.7%; i.e. when the tangent of the non-linear regression line crossed the axes' origin. Below 2.7% C content, the basal respiration decreased faster than the C content, indicating a strong decrease of C availability at low C content. This limit was similar to the average C content under rubber plantations and above the average under oil palm plantations. Accordingly, the difference in basal respiration between oil palm plantations and rubber plantations was higher than the difference in C content.
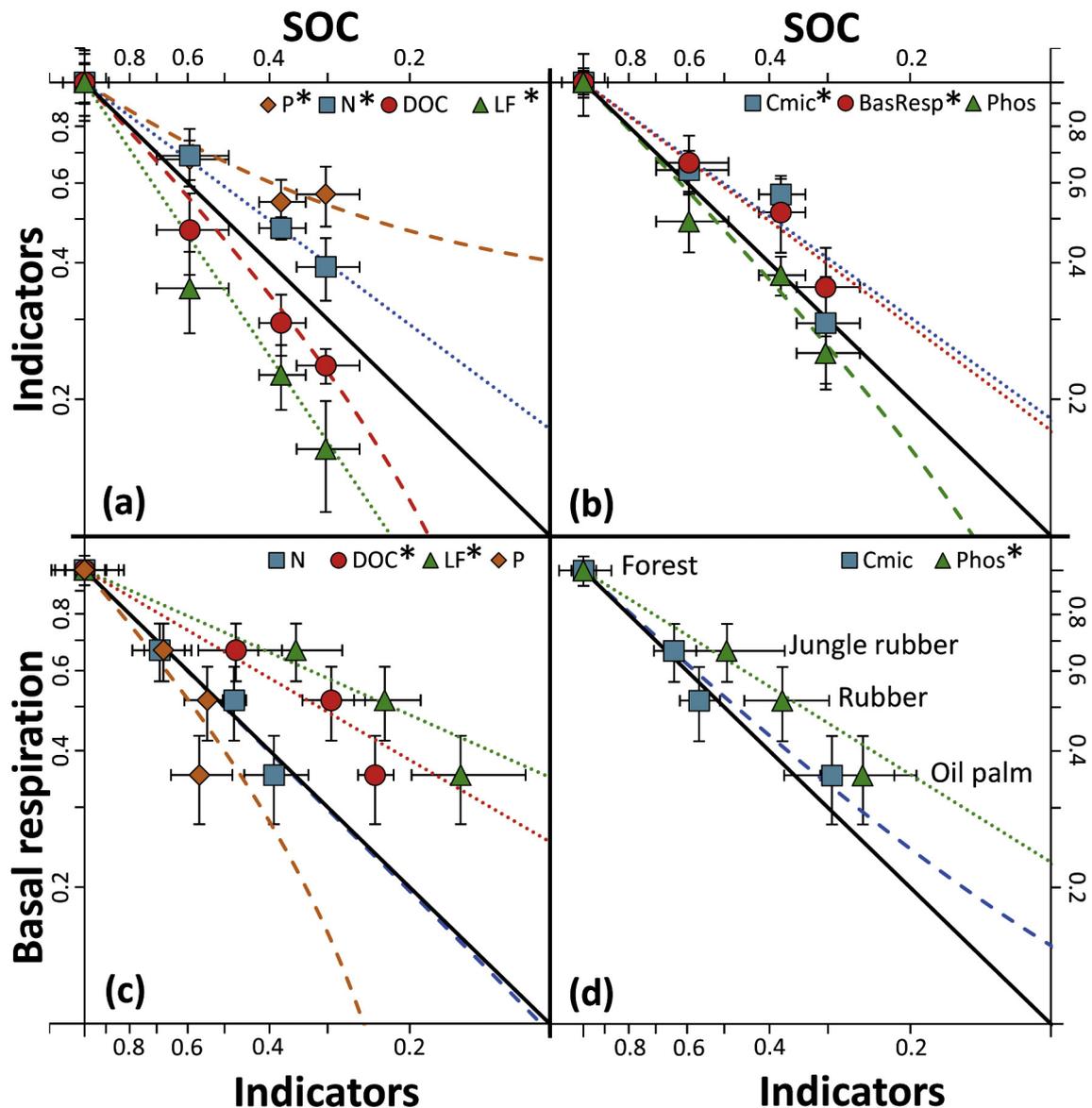
Fig. 5. Sensitivity of soil fertility indicators to SOC losses (a, b) and the coupling of indictors with basal respiration (c, d). Indicators: (P) available P, (N) N content, (DOC) K_2SO_4-soluble C, (LF) light fraction, (Cmic) microbial biomass, (BasResp) basal respiration and (phos) acid phosphatase. Indicators with non-proportional decrease are indicated with a star in the legend. Linear relationships (dashed lines) and non-linear relationships (dotted lines) were fitted on 16 sites. Note the logarithmic scale of the axes. Because of the logarithmic axis scale, the linear relationships are represented by curves (dashed lines) and non-linear relationships by straight lines (dotted lines).

The C content was strongly correlated with all measured parameters independently of the land-use type ($R^2 > 0.72$; Table 2). Therefore, to assess the sensitivity of microbial activities, SOC pools and nutrients to SOC losses, all indicators were normalized to the forest mean. Then, linear and non-linear regressions were fitted using the C content as independent variable (Fig. 5a, b). The decrease of all variables, except DOC and phosphatase activity, was not proportional to the C content decrease: the slope of the linear regression (Eq. (2)) and the exponent of the non-linear regression (Eq. (3)) were significantly different from 1 (Table 2). The light fraction was sensitive to SOC losses as indicated by a slope and an exponent greater than 1. In contrast, N and available P were resistant to SOC losses as indicated by a slope and an exponent lower than 1, resulting in a relative nutrient enrichment under plantations. While the power of the ANOVA was too low to reveal significant land-use effects on available P, regressions showed a decrease of this soil parameter with C content and thereby an effect of land-use changes. Similar to the basal respiration and the

nutrients, the microbial biomass decrease was resistant to SOC losses. The linear model had a higher R^2 for nutrient contents (N and P). For all other indicators, the variability explained by the exponential model (R^2 ranged from 0.73 to 0.91) was slightly higher. Nonetheless, exponential models explain only around 1% more of the variability (Table 2).

The same analysis was repeated with the basal respiration as a dependent variable to observe its coupling to the decrease of nutrients, labile pools and microbial activity (Fig. 5c, d). The basal respiration decreased proportionally with the microbial biomass and N decrease, but was resistant to the decrease of SOC, LFC, DOC and phosphatase activity. This indicates that the microbial activity was not directly dependent on these soil parameters. The available P had a slope of 1.2 but was not significantly different from 1 because of a large confidence interval (high variability between the plots). For variables decreasing non-proportionally with the basal respiration, the exponential models (R^2 ranged from 0.80 to 0.88) explained 1–6% more variability than the linear models (Table 2).

Table 2
Linear and non-linear regressions between indicators and SOC as independent variable, and between the basal respiration and indicators as independent variables.

	Regression type[a]	a[b]	CI down	CI up	R^2
Indicator versus SOC					
Basal respiration*[c]	l	0.86	0.77	0.94	0.90
	nl	0.77	0.66	0.88	0.91
Microbial biomass*	l	0.84	0.70	0.98	0.72
	nl	0.74	0.56	0.92	0.73
Acid phosphatase	l	1.05	0.92	1.19	0.82
	nl	1.08	0.83	1.33	0.82
DOC	l	1.10	0.98	1.22	0.84
	nl	1.19	0.94	1.44	0.84
Light fraction*	l	1.24	1.09	1.39	0.82
	nl	1.52	1.14	1.89	0.83
N content*	l	0.85	0.81	0.88	0.98
	nl	0.76	0.72	0.81	0.98
P available*	l	0.66	0.54	0.79	0.75
	nl	0.54	0.40	0.68	0.73
Basal respiration versus indicator					
Microbial biomass	l	0.95	0.79	1.10	0.75
	nl	0.98	0.72	1.24	0.74
Acid phosphatase*	l	0.78	0.69	0.87	0.86
	nl	0.64	0.53	0.75	0.88
DOC*	l	0.74	0.63	0.85	0.79
	nl	0.60	0.47	0.73	0.80
Light fraction*	l	0.65	0.55	0.75	0.77
	nl	0.46	0.36	0.55	0.83
N content	l	1.00	0.90	1.11	0.89
	nl	0.99	0.83	1.15	0.89
P available	l	1.20	0.97	1.44	0.78
	nl	1.20	0.84	1.55	0.75

[a] l: linear regression; nl: non-linear regression.
[b] Estimated parameter of the linear ($y = ax + 1 - a$) and non-linear ($y = x^a$) regressions.
[c] Stars indicate a non-proportional decrease between variables.

In summary, soil fertility indicators decreased under plantations compared to forest, but not all indicators were equally affected by forest conversion. While classical indices built on the ratio of two single indicators yielded very variable results, regressions between indicators highlighted clear differences in the indicators sensitivity and resistance to land-use changes.

4. Discussion

The results confirmed the hypothesis that rainforest conversion to oil palm and rubber plantations negatively affects soil fertility, reflected in the decrease of all measured biological and chemical indicators. The basal respiration and microbial biomass decrease under rubber plantations (−48 and −43%, respectively) were surprisingly similar to the decreases reported for rubber plantations in India (−56 and −36% respectively; Dinesh et al., 2004), despite differences in climate, soil type and microbial biomass between both studies. The measured microbial biomass (169 µg C g^{-1} soil) and the microbial quotient (0.9%) fell into the low range of microbial biomass (80–390 µg C g^{-1} soil) and microbial quotient (0.5–2.4%) measured in Malaysian plantations (Adachi et al., 2006; Haron et al., 1998).

All measured parameters were highly correlated with SOC, confirming the usefulness of SOC as an indicator and umbrella property of soil fertility, i.e. the conservation of SOC has a positive effect on most soil properties important for soil fertility. Differences in the indicators' sensitivity, however, show that quantifying SOC losses alone is insufficient to assess the impact of land-use change on soil fertility. Indeed, the microbial biomass and activity were resistant to SOC losses, whereas the measured labile pools showed the same pattern (DOC) or were sensitive (LF) to SOC losses. A stronger response of labile pools to SOC losses was expected because of their sensitivity to land-use changes by being preferentially mineralized

(Bolinder et al., 1999). Nonetheless, the resistance of basal respiration and microbial biomass to those losses contradicts the general view that microbiological indicators are also sensitive indicators of land-use changes and decrease in SOC quality (e.g. Mganga and Kuzyakov, 2014).

The metabolic quotient was not affected by land-use changes, as reflected by a proportional decrease between basal respiration and microbial biomass. Therefore, the highest specific basal respiration under plantations resulted not from a lower C use efficiency of the microbial community but rather from a relative increase of the available organics to support microbial activity. C availability, however, should decrease faster than total SOC losses. This is because SOC labile pools are mineralized first, resulting in a relative accumulation of refractory SOC having a lower availability (Six et al., 2002). This explains that the light fraction under plantations decreased more than the total SOC. Nevertheless, the decoupling between basal respiration or microbial biomass, which were resistant, and labile SOC pools, which were sensitive, indicates that the microbial activity was not limited by the amount of labile SOC pools. Furthermore, SOC mineralization rates were very low compared to the pool's size, and basal respiration did not decrease over two months after the initial CO_2-flush, resulting in zero-order kinetics. This type of kinetics characterizes reactions that are not limited by the substrate concentration but by other factors such as the catalyst amount, e.g. exoenzyme production (Paul and Clark, 1996). The strong decrease of labile pools, the resistance of basal respiration to SOC losses and the SOC mineralization kinetics strongly suggest that SOC mineralization rate did not depend on SOC quantity or quality. Interestingly, higher or similar specific basal respiration was also observed in subsoil compared to topsoil (Agnelli et al., 2004; Salomé et al., 2010), even though subsoil SOC is considered more recalcitrant than topsoil SOC (Rumpel and Kögel-Knabner, 2011). Input of fresh C was shown to control the decomposition of recalcitrant SOC in the subsoil by stimulating microorganisms (Fontaine et al., 2007). The input of leaf and root residues as well as of root exudates to soil could therefore stimulate microbial activity under plantations, although little of the fresh input remained stabilized in the SOC. Accordingly, the stronger decrease of basal respiration under oil palm compared to rubber plantations reflects the highly reduced leaf litter input in oil palm plantations (Kotowska et al., 2015). Based on the δ^{13}C values of SOC in the Ah horizon, Guillaume et al. (2015) already hypothesized slower decomposition rates under oil palm and that the absence of ^{13}C enrichment with depth indicated that the fresh C input was not stabilized in the SOC.

SOC losses resulted in a relative enrichment of N and available P under plantations. Since no fertilizers are applied in jungle rubber and only minimal amounts near the trees in oil palm and occasionally in rubber plantations, the relative enrichment in these nutrients mainly arose from SOC losses through the mineralization process. Therefore, relative nutrient availability increases. Phosphorus is generally the most limiting nutrient in heavily-weathered tropical soils, while N is in relative excess (Cleveland et al., 2006, 2003; Vitousek, 1984). The fact that basal respiration decreased more strongly than the phosphorus decrease indicates that phosphorus was not the main limiting factor of microbial activity under plantations. Phosphatase activity reflects microorganisms demand for P, which increases with increasing P-limitations (Allison et al., 2011; Weintraub et al., 2012). Phosphatase activity decreased more strongly than the microbial biomass, indicating also of lower microbial P demand under plantations because of a relative enrichment in P. The proportional decreases of N, microbial biomass and basal respiration suggest that N content was a limiting factor for microbial activity and for their ability to mineralize SOC. Therefore, C availability and microbial activity are resistant to SOC losses not because the C availability decreased, but because C was lost faster than N.

Fontaine et al. (2003) already suggested that, at the community level, microorganisms can shift their C sources to more recalcitrant SOC pools, if nutrients are not sequestered by r-strategist microorganisms feeding on the more labile SOC.

Normalizing soil property values or process intensities to the reference (here undisturbed rainforest sites), and using Eqs. (2) and (3), provided a simple and efficient method to discriminate between proportional and non-proportional decreases of two variables. Consequently, the sensitivity of indicators to SOC losses, and thereby to land-use changes, can be assessed straightforwardly by the confidence interval of the estimated parameter alone. The discrimination between exponential or linear relationships between two variables should also be straightforward using the model with the highest R^2. Nonetheless, the differences in the variability explained by both models were not higher than 7%. Because the values predicted by the models differ the most at low C content (Fig. 1), the determination of the variables' responses would be improved by adding to the analysis sites with lower C content (even more strongly degraded). Moreover, including sites with lower C content would enable testing whether the relationships reach zero for both variables or not; i.e. following models such as $y = a^*\log(x) + b$ or $a^* e^{(x^*b)}$. Nevertheless, the trends in the distribution of residuals and the physical meaning of the model, when SOC reaches zero, allow a clear preference of the non-linear compared to the linear models.

Non-linear relationships between variables challenged the use of indices (ratios of two indicators) to assess the sensitivity of soil properties. First, sites with the lowest C content do not necessarily show the strongest change in indices compared to the reference sites. Consequently, the intensity of the indices change is not related with the intensity of soil degradation. Indices changes in the case of non-linear relationships should therefore be evaluated according to the C content level. Second, the derivative of a non-linear model varies with the C content. This makes single indicators and indices variabilities within land-use type inconsistent among land-use types having different average C content, but similar C content variability. This leads to difficulties in reaching the condition of variance homogeneity when testing land-use effects with ANOVA.

5. Conclusions

SOC losses after tropical forest conversion to oil palm or rubber plantations were associated with a strong decrease of chemical and biological components of soil fertility. The new approach based on (non-)linear regressions of normalized values allowed a simple discrimination between sensitive and resistant indicators to SOC losses and, thus, to land-use changes. The resistance of microbial activity and biomass to the decrease of SOC and labile SOC pools highlighted that lower nutrients-to-SOC ratios under plantations maintain microbial activity in tropical soils. Nevertheless, microbial activity sustained SOC losses up to a turning point. Further SOC losses, due to a strong reduction of the fresh C input from the vegetation, led to a drop in microbial activity. Management practices that slightly reduce SOC losses in intensive plantations could therefore significantly mitigate the decrease of microbial activity and potentially of soil fertility. Spreading the residues of oil palm fronds in the plantation instead of stacking them to piles could increase SOC and therefore microbial activity by increasing C input and decreasing SOC losses by soil erosion. In conclusion, the suggested and tested new approach allowed the dynamic assessment of sensitive and resistant soil fertility indicators. It enables the identification of thresholds in the response to land-use changes of a wide range of indicators of various ecosystem functions and to adapt management practices accordingly. This is an important step forward in evaluating the effects of natural ecosystem conversion to intensive plantations and can be useful for estimating ecosystem service changes.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2016.02.039.

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