



# Soil nitrogen oxide fluxes from lowland forests converted to smallholder rubber and oil palm plantations in Sumatra, Indonesia

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**Abstract.** Oil palm (*Elaeis guineensis*) and rubber (*Hevea brasiliensis*) plantations cover large areas of former rainforest in Sumatra, Indonesia, supplying the global demand for these crops. Although forest conversion is known to influence soil nitrous oxide (N<sub>2</sub>O) and nitric oxide (NO) fluxes, measurements from oil palm and rubber plantations are scarce (for N<sub>2</sub>O) or nonexistent (for NO). Our study aimed to (1) quantify changes in soil–atmosphere fluxes of N oxides with forest conversion to rubber and oil palm plantations and (2) determine their controlling factors. In Jambi, Sumatra, we selected two landscapes that mainly differed in texture but were both on heavily weathered soils: loam and clay Acrisol soils. Within each landscape, we investigated lowland forests, rubber trees interspersed in secondary forest (termed as “jungle rubber”), both as reference land uses and smallholder rubber and oil palm plantations as converted land uses. In the loam Acrisol landscape, we conducted a follow-on study in a large-scale oil palm plantation (called PTPN VI) for comparison of soil N<sub>2</sub>O fluxes with smallholder oil palm plantations. Land-use conversion to smallholder plantations had no effect on soil N-oxide fluxes ( $P = 0.58$  to  $0.76$ ) due to the generally low soil N availability in the reference land uses that further decreased with land-use conversion. Soil N<sub>2</sub>O fluxes from the large-scale oil palm plantation did not differ with those from smallholder plantations ( $P = 0.15$ ). Over 1-year measurements, the temporal patterns of soil N-oxide fluxes were influenced by soil mineral N and water contents. Across landscapes, annual soil N<sub>2</sub>O emissions were controlled by gross nitrification and sand content, which also suggest the influence of soil N and water availability. Soil N<sub>2</sub>O fluxes ( $\mu\text{g N m}^{-2} \text{h}^{-1}$ ) were  $7 \pm 2$  to

$14 \pm 7$  (reference land uses),  $6 \pm 3$  to  $9 \pm 2$  (rubber),  $12 \pm 3$  to  $12 \pm 6$  (smallholder oil palm) and  $42 \pm 24$  (large-scale oil palm). Soil NO fluxes ( $\mu\text{g N m}^{-2} \text{h}^{-1}$ ) were  $-0.6 \pm 0.7$  to  $5.7 \pm 5.8$  (reference land uses),  $-1.2 \pm 0.5$  to  $-1.0 \pm 0.2$  (rubber) and  $-0.2 \pm 1.2$  to  $0.7 \pm 0.7$  (smallholder oil palm). To improve the estimate of soil N-oxide fluxes from oil palm plantations in this region, studies should focus on large-scale plantations (which usually have 2 to 4 times higher N fertilization rates than smallholders) with frequent measurements following fertilizer application.

## 1 Introduction

Expansion of industrial forestry and agriculture has caused rapid deforestation in Sumatra, Indonesia, resulting in a total primary forest loss of 36 % between 1990 and 2010 (Margono et al., 2012). At present, most accessible lowland rainforests have been converted (Laumonier et al., 2010) into economically important crops, such as oil palm (*Elaeis guineensis*) and rubber (*Hevea brasiliensis*), with an area of 9.2 Mha (million hectare; BPS, 2016a). Indonesia is currently the principal oil palm producer and second largest rubber producer worldwide (FAO, 2016), and Sumatra is the most important contributor to the Indonesian production (BPS, 2016b). Despite the extent of land-use change in Sumatra, it is still uncertain how forest conversion will affect soil emissions of climate-relevant N-oxide gases, nitrous oxide (N<sub>2</sub>O) and nitric oxide (NO). Only a few studies so far have reported soil N<sub>2</sub>O fluxes from forest conversion to these rapidly increasing and economically important land uses, oil

palm and rubber, on lowland mineral soils in Southeast Asia (Aini et al., 2015; Ishizuka et al., 2002, 2005; Yashiro et al., 2008), and no study exists on soil NO fluxes.

Tropical forest soils are major sources of N<sub>2</sub>O and NO, emitting 1.3 Tg N<sub>2</sub>O-N yr<sup>-1</sup> (Werner et al., 2007) and 1.3 Tg NO-N yr<sup>-1</sup> (Davidson and Kinglerlee, 1997) into the atmosphere, whereby considerable amounts of NO are expected to get redirected in forest systems since NO is easily oxidized to NO<sub>2</sub> which, in turn, is absorbed by leaves (Jacob and Bakwin, 1991; Sparks et al., 2001). N<sub>2</sub>O is a potent greenhouse gas (IPCC, 2013) and is projected to be the single most important ozone-depleting substance throughout the 21st century (Ravishankara et al., 2009). NO plays an important role in the formation of tropospheric ozone, which in itself is an important greenhouse gas (Lammel and Graßl, 1995). N<sub>2</sub>O and NO are produced in soil by the microbial processes of nitrification and denitrification. The conceptual hole-in-the-pipe (HIP) model, which had been validated by studies in the tropics (Davidson et al., 2000), suggests that production and consumption of these gases in soils are influenced by two levels of control: first, the amount of soil available N, and, second, the soil water content. HIP suggests that the higher the soil N availability is, the higher the soil N-oxide fluxes are and that well-aerated soil conditions (low moisture contents) favor for nitrification with NO as the main gaseous product, while with increasing water content denitrification with increasing proportion of N<sub>2</sub>O prevails (Davidson et al., 2000). Although there are other factors affecting soil N<sub>2</sub>O and NO fluxes through their influence on nitrification and denitrification (e.g., soil pH, temperature, bioavailable carbon; Firestone and Davidson, 1989; Heinen, 2006; Skiba and Smith, 2000), landscape-scale investigations in tropical areas show the dominant role of soil N availability and water content (Corre et al., 2014; Koehler et al., 2009; Müller et al., 2015).

Conversion of tropical forests to agricultural land uses generally alters soil N-oxide fluxes through their effects on soil N availability and aeration as a consequence of management practices (e.g., fertilization, harvest, cultivation), which can add and export nutrients as well as compact or loosen the soil (Keller and Reiners, 1994; Veldkamp et al., 2008). In particular, the application of N-containing fertilizers can increase N-oxide emissions (Matson et al., 1996; Veldkamp et al., 1998), whereas agricultural land uses without fertilizer application lead to long-term reductions of soil N-oxide fluxes or to comparably low-level fluxes as those from previous forests (Ishizuka et al., 2005; Keller and Reiners, 1994; Verchot et al., 1999). In tropical regions, it has been shown that soil NO and N<sub>2</sub>O emissions can be very high following fertilizer application, constituting 6.4–8.6 % of applied N fertilizer especially at high fertilizer application rates (Veldkamp and Keller, 1997; Veldkamp et al., 1998).

For lowland forests on highly weathered soils in Sumatra, Indonesia, where our present study was conducted, it has been shown that soil N availability (with gross rates of

ammonium, NH<sub>4</sub><sup>+</sup>, transformations as indices) is higher in the clay than in the loam Acrisol soils (Allen et al., 2015), suggesting that soil texture controls soil fertility, which in turn affects plant productivity, soil water holding capacity, decomposition and ultimately soil N cycling (Allen et al., 2015). Conversion of lowland forest and jungle rubber to oil palm and rubber on these Acrisol soils showed intermediate soil N availability in oil palm plantations due to abatement of soil fertility decline by low to moderate applications of fertilizers and lime, whereas the unfertilized rubber plantations displayed the lowest soil N availability and fertility in general (Allen et al., 2015).

Our present study focuses on soil N<sub>2</sub>O and NO fluxes from a region in Jambi, Sumatra, where increased deforestation for rubber and oil palm production has occurred in the last two decades. We covered four land uses within two landscapes on highly weathered soils that mainly differed in soil texture (clay and loam Acrisols): forest, rubber trees interspersed in secondary forest (hereafter, termed as jungle rubber) as the reference land uses, and smallholder rubber and oil palm plantations as the converted land uses. In addition, we conducted a follow-on study to evaluate the effect of N input rate on soil N<sub>2</sub>O fluxes by comparing a large-scale plantation (with 2–4 times higher fertilization rate) and smallholder plantations within the same landscape of the loam Acrisol soil. Based on the above-mentioned findings on soil N availability, we formulated two hypotheses: (H1) soil N<sub>2</sub>O and NO fluxes from the reference land uses will be higher in the clay than the loam Acrisol landscape; and (H2) forest and jungle rubber will have the highest soil N<sub>2</sub>O and NO fluxes, followed by the smallholder oil palm plantations (fertilized at low to moderate rates), with the lowest fluxes from the unfertilized rubber plantations. Our study aimed to (1) quantify changes in soil–atmosphere fluxes of N oxides with forest conversion to smallholder oil palm and rubber plantations, (2) determine the temporal controls of soil N-oxide fluxes measured within 1 year and (3) assess landscape-scale controlling factors of annual soil N<sub>2</sub>O fluxes from converted lowland landscapes in Sumatra, Indonesia. Our study contributes to the much needed information on soil N-oxide fluxes from these economically and globally relevant tropical land uses.

## 2 Material and methods

### 2.1 Study area, experimental design and management practices

The study region is situated in Jambi province, Sumatra, Indonesia (2°0′57″ S, 103°15′33″ E; elevation of 73 ± 3 m above sea level), where conversion of forest to rubber and oil palm plantations is widespread. The area has a mean annual temperature of 26.7 ± 0.1 °C and a mean annual precipitation of 2235 ± 381 mm (1991–2011; data from a climatological

station at the Jambi Sultan Thaha Airport). During our study year (2013), annual rainfall in the study region was 3418–3475 mm (data from climatological stations at the Harapan Rainforest, Sarolangun and Lubuk Kepayang, approximately 10–20 km from our sites), which was higher than the long-term average. Total dissolved N deposition via rainfall was between  $12.9 \pm 0.1$  and  $16.4 \pm 2.6$  kg N ha<sup>-1</sup> yr<sup>-1</sup>, measured at two locations in the study region during 2013 (Kurniawan, 2016).

We delineated the study region in two landscapes, which had the same highly weathered soil group but mainly differed in soil texture: clay and loam Acrisol soils. The clay Acrisol soil had a larger pH ( $4.5 \pm 0.0$ ), base saturation ( $23 \pm 6$  %) and Bray-extractable P ( $1.4 \pm 0.1$  g P m<sup>-2</sup>), and lower Al saturation ( $61 \pm 3$  %) in the top 10 cm depth compared to the loam Acrisol soil ( $4.3 \pm 0.0$  pH,  $11 \pm 1$  % base saturation,  $0.5 \pm 0.1$  g P m<sup>-2</sup> and  $80 \pm 1$  % Al saturation; all  $P \leq 0.05$ ; Allen et al., 2015). In the first part of our study, we investigated four land-use types within each landscape: lowland forest, jungle rubber, both as the reference land uses, and smallholder monoculture plantations of rubber and oil palm, as the converted land uses. Each land use within each landscape had four sites as replicates, and we laid out a 50 m × 50 m plot in each replicate site; in total we had 32 plots. Within each plot, a 10 × 10 grid was established and we randomly selected four subplots (5 m × 5 m each) per plot, each with one permanently installed chamber base for measurements of soil N-oxide fluxes. All measurements (see Sect. 2.2) were conducted in 2013 (Appendix Table A1). A more detailed description of the study sites and plot design was reported earlier by Allen et al. (2015) and Hassler et al. (2015).

The second part was a follow-on study, wherein we conducted additional measurements in a large-scale oil palm plantation (called PTPN VI) in the loam Acrisol landscape from 2014 to 2015 in order to compare with the smallholder oil palm plantations within the same landscape (Appendix Table A1). In the PTPN VI site, we selected four replicates at a distance of 50 m apart. At each replicate, we installed three permanent chamber bases at 0.8, 2.8 and 4.8 m from the tree base in order to characterize possible spatial variation caused by management practices within each replicate.

Based on our interviews with the smallholders, the monoculture plantations were established after clearing and burning of either forest or jungle rubber, and hence these land uses served as the reference land uses with which the converted plantations were compared. Additionally, the comparability of initial soil conditions between the reference and converted land uses was tested based on a land-use-independent soil characteristic, i.e., clay content at a 0.5–2 m depth, which did not statistically differ among land uses within each landscape (Allen et al., 2015; Hassler et al., 2015). Thus, changes in soil N-oxide fluxes can be attributed to land-use change with its associated management practices. The plantations' ages ranged between 7 and 17 years, and tree density, tree height, basal area and tree species abundance were higher in

the reference land uses than the monoculture plantations (all reported by Allen et al., 2015; Hassler et al., 2015; Kotowska et al., 2015).

Management practices in the plantations included manual harvest, weeding and fertilizer application (details reported by Hassler et al., 2015). In 2013, fertilization in the smallholder oil palm plantations was conducted one to two times per year, and fertilization rates ranged between 48–88 kg N ha<sup>-1</sup> yr<sup>-1</sup> (except two smallholders who applied 138 kg N ha<sup>-1</sup> yr<sup>-1</sup>), 21–38 kg P ha<sup>-1</sup> yr<sup>-1</sup> and 40–157 kg K ha<sup>-1</sup> yr<sup>-1</sup>, with the lower range in the clay Acrisol and the upper range in the loam Acrisol. The fertilizer sources were NPK complete, urea and KCl. One of the smallholders in the loam Acrisol landscape applied 200 kg dolomite ha<sup>-1</sup> yr<sup>-1</sup>. Fertilizers were applied around each palm tree at about 0.8–1 m from the stem base (Hassler et al., 2015). Rubber plantations were not fertilized. In the large-scale oil palm plantation, fertilizer application rates were typically higher than those in smallholder plantations; fertilizers were applied once in 2014 at the rates of 196–36–206 kg N, P and K ha<sup>-1</sup> yr<sup>-1</sup>, with also 602 kg dolomite ha<sup>-1</sup> yr<sup>-1</sup>, and once before the end of our measurements in July 2015 at the rates of 96–23–96 kg N, P and K ha<sup>-1</sup> yr<sup>-1</sup>. The fertilizer forms were NPK complete, urea, triple superphosphate and KCl. Application in this large-scale plantation was done partly manually by applying the fertilizers at a 1 m distance to the tree base and partly mechanically by broadcasting the fertilizer within a 1–3 m distance from the palm rows. In 2015, fertilizers were mainly mechanically broadcasted within these inter-rows.

## 2.2 Soil N-oxide fluxes and supporting soil factors

In the first part of our study, soil N<sub>2</sub>O fluxes were measured in all land uses (32 plots) at monthly intervals from December 2012 to December 2013, whereas soil NO fluxes were measured four times between March and September 2013 (Appendix Table A1). Two forest sites and one jungle rubber site in the clay Acrisol landscape were not measured for soil NO fluxes due to difficulty in accessing these sites, which did not allow us to stabilize the NO detector during transport in the field (i.e., using motorcycles on very rugged trails). Soil NO fluxes were not measured as frequently as N<sub>2</sub>O fluxes because these fluxes were always very low at all sites and we decided to stop this measurement in September 2013. In the follow-on study, soil N<sub>2</sub>O fluxes were measured more frequently (biweekly from July 2014 to July 2015; Appendix Table A1) in a large-scale oil palm plantation (in congruence with its high fertilizer application rate) to compare with the smallholder oil palm plantations within the same landscape of the loam Acrisol soil.

For the first part of our study, we used randomly installed chamber bases (inserted to ~0.03 m depth with distances to the tree base between 1.8 and 5 m; see Sect. 2.1) with monthly measurements, which may have missed the

N-fertilizer-induced pulse of soil N-oxide emissions in the smallholder oil palm plantations (Veldkamp and Keller, 1997; Veldkamp et al., 1998). Therefore, we conducted more intensive measurements of soil N<sub>2</sub>O fluxes during the 3 to 8.5 weeks (with 6 to 11 sampling days) following fertilizer application at three of the smallholder oil palm plantations within each landscape. These measurements served to characterize the short-term, N-fertilizer-induced contribution (e.g., Koehler et al., 2009) to total N<sub>2</sub>O fluxes. Soil NO fluxes were also measured during 6 to 8.5 weeks (with 9 to 10 sampling days) following fertilizer application at one of the smallholder oil palm plantations within each landscape. Measurements in the three smallholder oil palm plantations at each landscape were conducted during October–December 2013, January–March 2014 and February–April 2014 (Appendix Table A1). We applied the same fertilizer forms, rates and methods as used by the smallholders. Three oil palm trees were selected in each of the six sites. In the clay Acrisol landscape, 2 kg of complete NPK fertilizer (equivalent to 0.32 kg N tree<sup>-1</sup>) was applied to each tree, whereas in the loam Acrisol, 2 kg of combined complete NPK, ammonium sulfate and KCl fertilizers (equivalent to 0.26 kg N tree<sup>-1</sup>) was applied to each tree. The fertilizer was applied within a 0.8–1 m distance from the tree base. We installed three permanent chamber bases at various distances from the tree base: 0.3 m from the tree base (F1 is the chamber location with incidental fertilization), 0.8 m from the tree base that was on the fertilized area (F2 is the fertilized chamber location) and 4–4.5 m from the tree base that was in the middle of the inter-rows and served as the reference chamber without fertilizer application (NF is the non-fertilized chamber location).

Soil N<sub>2</sub>O fluxes were measured using the same methods employed in our earlier studies (e.g., Corre et al., 2014; Koehler et al., 2009). During gas sampling, the permanently installed chamber bases were covered with vented static, polyethylene hoods (chamber area of 0.05 m<sup>2</sup> and total volume of 12 L), and four gas samples (30 mL each) were taken at 1, 11, 21 and 31 min after chamber closure by connecting a syringe with a Luer lock to the chamber sampling port. Gas samples were immediately injected into pre-evacuated 12 mL Labco exetainers sealed with rubber septa (Labco Limited, Lampeter, UK), maintaining an overpressure; these exetainers have been tested by our group to be leak proof during extended period of storage (e.g., up to 6 months; Hassler et al., 2015). Within 3–4 months the gas samples were transported by airfreight to Germany and were analyzed upon arrival using a gas chromatograph with an electron capture detector (GC 6000 Vega Series 2, Carlo Erba Instruments, Milan, Italy). For the measurements from March to July 2015 in the large-scale oil palm plantation, the gas samples were analyzed with another gas chromatograph (SRI 8610C, SRI Instruments Europe GmbH, Bad Honnef, Germany), which had been previously cross calibrated using the same standards. For calibration, three standard gases were used with concen-

trations of 360, 1000 and 1600 ppb N<sub>2</sub>O (Deuste Steininger GmbH, Mühlhausen, Germany).

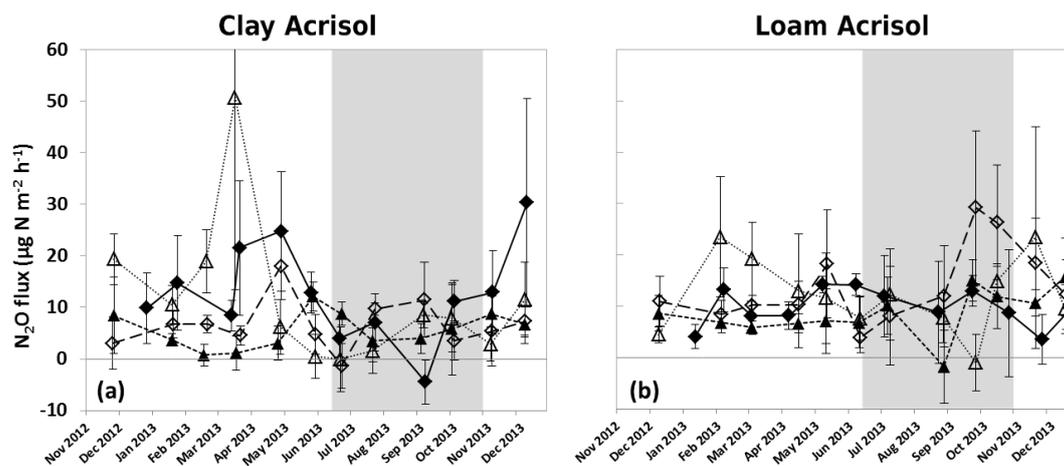
Soil NO fluxes were measured (described in detail in our earlier works, e.g., Corre et al., 2014; Koehler et al., 2009) using the same chamber bases described above. During measurements, the chamber bases were covered with vented dynamic, polyethylene hoods (total volume of 12 L), and NO concentrations were measured in situ during 5–7 min following chamber closure using a Scintrex LMA-3 chemiluminescence detector (Scintrex, Ontario, Canada) in which NO is oxidized to NO<sub>2</sub> by a CrO<sub>3</sub> catalyst, after which it reacts with a luminol solution. Calibration of the NO detector was carried out at each site prior to and after measurements using a two-point calibration of a standard gas with 3000 ppb NO (Deuste Steininger GmbH, Mühlhausen, Germany) which was diluted using dried ambient air. NO measurements were recorded every 5 s using a data logger (CR510, Campbell Scientific, Logan, USA).

Soil N<sub>2</sub>O and NO fluxes were calculated from the linear increase of concentration over time of chamber closure and adjusted for air temperature and atmospheric pressure, measured at each site on each sampling day. Annual soil N<sub>2</sub>O fluxes from the monthly sampling at each site were estimated using the trapezoidal rule, which is an interpolation between measured fluxes and the interval between sampling days. Interpolated fluxes were summed for the entire year (e.g., Hassler et al., 2015). Annual NO fluxes were not calculated, since we only conducted four measurement periods for each plot as explained above. To calculate the N-fertilizer-induced pulse of soil N-oxide fluxes, we also used the trapezoidal rule on day intervals between measured flux rates to estimate the total flux during the entire period following fertilizer application, covering the pre-fertilizer level, the peak and the return to background levels of soil N-oxide fluxes. We calculated the percentage of combined soil NO and N<sub>2</sub>O emissions from the applied N-fertilizer rate at each site as follows:

$$\text{The percentage (\%)} \frac{\text{NO-N} + \text{N}_2\text{O-N}}{\text{applied}} \text{ of N} = \frac{(\text{NO-N} + \text{N}_2\text{O-N}) \times \text{frequency of fertilization}}{\text{F1 and F2 chambers} - \text{NO-N} + \text{N}_2\text{O-N} \text{ fluxes from NF chamber} \times \text{fertilized area (m}^2 \text{ ha}^{-1}) / \text{N fertilization rate (kg N ha}^{-1} \text{ yr}^{-1} \times 10^9 \text{ } \mu\text{g kg}^{-1})} \times 100,$$

where NO-N + N<sub>2</sub>O-N is expressed in  $\mu\text{g N m}^{-2}$  for the entire period of the fertilizer effect. In this calculation, we included fluxes from chamber location F1 in order to include any incidental fertilizer application to this area (possibly from previous applications by the smallholders and possible redistribution of applied nutrients within the soil), since N-oxide fluxes from chamber location F1 were often higher than those from NF chambers (see Sect. 3.2).

Soil factors known to control soil N-oxide fluxes, i.e., temperature, water-filled pore space (WFPS), and extractable NH<sub>4</sub><sup>+</sup> and nitrate (NO<sub>3</sub><sup>-</sup>), were measured within the top 0.05 m depth during each soil N-oxide flux measurement at



**Figure 1.** Mean ( $\pm$  SE,  $n = 4$  sites) soil  $\text{N}_2\text{O}$  fluxes from forest ( $\blacklozenge$ ), jungle rubber ( $\diamond$ ), rubber ( $\blacktriangle$ ) and oil palm ( $\triangle$ ), located within the clay (a) and loam Acrisol (b) landscapes in Jambi, Indonesia. Measurements were carried out monthly from December 2012 to December 2013; gray shadings mark the dry season.

all 32 sites and at the 6 sites of smallholder oil palm plantations following fertilization. Soil temperature was measured close to each chamber base using a digital thermometer. Soil samples were taken at 1 m distance from the four chambers, pooled, mixed thoroughly and subsampled for immediate extraction of mineral N in the field, using prepared extraction bottles containing 150 mL 0.5 M  $\text{K}_2\text{SO}_4$ . Upon arrival at the field station, extraction bottles were shaken for 1 h and filtered, and extracts were frozen immediately. The remaining soil sample was used to determine the gravimetric moisture content (by oven-drying for at least 1 day at  $105^\circ\text{C}$ ), whereby WFPS was calculated using a particle density of  $2.65\text{ g cm}^{-3}$  for mineral soil and the measured soil bulk density at our study sites (Allen et al., 2015). Concurrent to the measurements following the fertilizer applications, soil was sampled close to each of the chamber locations, F1, F2 and NF (described above), and was processed separately for mineral N extraction and WFPS determination. Frozen extracts were transported by airfreight to Germany and analyzed for  $\text{NH}_4^+$  and  $\text{NO}_3^-$  concentrations using continuous flow injection colorimetry (SEAL Analytical AA3, SEAL Analytical GmbH, Norderstedt, Germany), as described in detail by Hassler et al. (2015).

In addition, soil physical and biochemical parameters within the top 0.1 m were measured once in 2013 at all 32 plots (i.e., soil N-cycling processes, including gross nitrification as one of the indices of N availability in the soil, microbial biomass, total organic C, total N, exchangeable cations, pH, soil texture and soil bulk density), reported by Allen et al. (2015). We used these soil parameters to analyze their relationships (see Sect. 2.3) with annual soil  $\text{N}_2\text{O}$  fluxes and reported the parameters that showed significant relationships with annual soil  $\text{N}_2\text{O}$  fluxes in Appendix Table A2.

### 2.3 Statistical analysis

We first tested each parameter for normal distribution (Shapiro–Wilk’s test) and equality of variance (Levene’s test), and a logarithmic transformation was applied when these assumptions were not met. Linear mixed-effect (LME) models (Crawley, 2007) were used to assess differences in N-oxide fluxes between landscapes for the reference land uses (testing H1) or to assess differences in N-oxide fluxes among land uses within each landscape (testing H2). Furthermore, an LME model was applied to assess differences in soil  $\text{N}_2\text{O}$  fluxes between the smallholder and large-scale oil palm plantations (as a follow-on study) within the loam Acrisol landscape. The LME models were also used to assess fertilization effects (i.e., as represented by the chamber locations F1, F2 and NF) on soil N-oxide fluxes from smallholder oil palm plantations and to test differences in N-oxide fluxes between landscapes following fertilization for chamber locations F1 and F2. The detailed descriptions of the LME models are provided in Appendix A. Significant differences were based on the analysis of variance with Fisher’s least significant difference (LSD) test for multiple comparisons. We set the statistical significance at  $P \leq 0.05$ , and, only for a few specified parameters, we also considered marginal significance at  $P \leq 0.09$  because our experimental design encompassed the inherently high spatial variability in our study area (e.g., Hassler et al., 2015).

To assess the temporal relationships between soil N-oxide fluxes and soil factors (temperature, WFPS,  $\text{NO}_3^-$  and  $\text{NH}_4^+$ ), we used the means of the replicate plots per land use on each of the 12 monthly measurements and conducted Pearson’s correlation test separately for the reference land uses (forest and jungle rubber,  $n = 48$  ( $\text{N}_2\text{O}$ ),  $n = 16$  (NO)) and the converted land uses (rubber and oil palm,  $n = 48$  ( $\text{N}_2\text{O}$ ),  $n = 16$  (NO)) across landscapes for the whole year. Similarly, for

**Table 1.** Mean ( $\pm$  SE,  $n = 4$  sites) soil N<sub>2</sub>O (with 12 monthly measurements) and NO fluxes (with four monthly to bimonthly measurements) as well as annual soil N<sub>2</sub>O fluxes from different land uses within each landscape in Jambi, Indonesia. Means followed by different lowercase letters indicate significant differences among land uses within each landscape and different capital letters indicate significant differences between landscapes within each land use (linear mixed-effect models with Fisher's LSD test at  $P \leq 0.09$ ). For soil NO fluxes in the clay Acrisol, forest was excluded in the comparison among land uses because measurements were only carried out in two sites. Annual soil N<sub>2</sub>O fluxes are calculated from the monthly fluxes using the trapezoidal rule. For smallholder oil palm plantations, values in italics were the fertilizer-induced annual soil N<sub>2</sub>O fluxes (see Sect. 2.2). In the loam Acrisol landscape, soil N<sub>2</sub>O fluxes were additionally measured in a large-scale oil palm plantation (mean  $\pm$  SE,  $n = 4$  replicates); these fluxes did not differ from those of smallholder plantations within the same landscape (linear mixed-effect models with Fisher's LSD test;  $P = 0.15$ ).

Land-use type	N <sub>2</sub> O fluxes ( $\mu\text{g N m}^{-2} \text{h}^{-1}$ )	NO fluxes ( $\mu\text{g N m}^{-2} \text{h}^{-1}$ )	Annual N <sub>2</sub> O fluxes ( $\text{kg N ha}^{-1} \text{year}^{-1}$ )
Clay Acrisol landscape			
Forest	12.8 $\pm$ 5.6 <sup>a,A</sup>	(1.7 $\pm$ 0.3)	1.0 $\pm$ 0.4
Jungle rubber	6.7 $\pm$ 1.5 <sup>a,A</sup>	-0.6 $\pm$ 0.7 <sup>a,A</sup>	0.6 $\pm$ 0.1
Rubber	5.6 $\pm$ 2.5 <sup>a,A</sup>	-1.0 $\pm$ 0.2 <sup>a,A</sup>	0.5 $\pm$ 0.2
Oil palm (smallholder plantation)	11.5 $\pm$ 2.9 <sup>a,A</sup>	-0.2 $\pm$ 1.2 <sup>a,A</sup>	1.0 $\pm$ 0.3 0.2 $\pm$ 0.0
Loam Acrisol landscape			
Forest	9.8 $\pm$ 1.5 <sup>a,A</sup>	1.9 $\pm$ 1.3 <sup>ab</sup>	0.9 $\pm$ 0.2
Jungle rubber	14.0 $\pm$ 6.7 <sup>a,A</sup>	5.7 $\pm$ 5.8 <sup>a,A</sup>	1.2 $\pm$ 0.6
Rubber	8.6 $\pm$ 2.0 <sup>a,A</sup>	-1.2 $\pm$ 0.5 <sup>b,A</sup>	0.7 $\pm$ 0.2
Oil palm (smallholder plantation)	12.2 $\pm$ 6.1 <sup>a,A</sup>	0.7 $\pm$ 0.7 <sup>ab,A</sup>	1.1 $\pm$ 0.5 0.1 $\pm$ 0.0
Oil palm (large-scale plantation)	42.3 $\pm$ 24.2	–	3.3 $\pm$ 1.7

soil N<sub>2</sub>O and NO fluxes following fertilizer application from smallholder oil palm plantations, we used the means of the three replicate trees per chamber location on each sampling day and conducted Pearson's correlation test for each site across the entire measurement period of fertilization effects ( $n = 6$ –11). To assess the spatial controls of soil biochemical characteristics (Appendix Table A2) on annual soil N<sub>2</sub>O fluxes, we used the annual flux of each replicate plot and conducted Spearman's rank correlation test separately for the reference land uses and converted land uses across landscapes ( $n = 16$ ) and within each landscape ( $n = 8$ ). We did not assess the spatial control of soil biochemical characteristics on annual soil NO fluxes since we did not calculate annual flux from the four measurement periods (as explained in Sect. 2.2). Correlations were considered statistically significant at  $P \leq 0.05$  and marginally significant at  $P \leq 0.09$ . All statistical analyses were conducted using R 3.2.2 (R Development Core Team, 2015).

### 3 Results

#### 3.1 Soil N-oxide fluxes

In the reference land uses (forest and jungle rubber), N<sub>2</sub>O was the dominant N oxide emitted from soils. In the clay Acrisol landscape, there was a net NO consumption in the

soil of the jungle rubber (Table 1). Soil N<sub>2</sub>O and NO fluxes from reference land uses were comparable between the two landscapes ( $P = 0.54$ – $0.74$ ; Table 1; Fig. 1a, b). These fluxes also exemplified high inherent spatial and temporal variations as indicated by their large standard errors.

In the converted land uses (smallholder rubber and oil palm plantations), soil N<sub>2</sub>O fluxes were similar to the fluxes of reference land uses ( $P = 0.58$ – $0.76$ ; Table 1; Fig. 1a, b) within each landscape. However, in the loam Acrisol landscape, the large-scale oil palm plantation had on average 3.5 times higher soil N<sub>2</sub>O fluxes than those from the smallholder plantations (Table 1), although this trend was not statistically different ( $P = 0.15$ ) because of the large variation among replicate plots (as indicated by the large standard error) in this large-scale plantation. Soil NO fluxes were not different either among land uses in the clay Acrisol landscape ( $P = 0.73$ ; Table 1). However, in the loam Acrisol landscape, soil NO fluxes were marginally lower ( $P = 0.07$ ) in rubber plantations (with net NO consumption in the soil) than in jungle rubber (with net NO emission), whereas they were intermediary in forests and oil palm plantations (Table 1).

#### 3.2 Fertilization effects on soil N-oxide fluxes from smallholder oil palm plantations

In comparison to the unfertilized area (chamber location NF at 4–4.5 m from the tree base), soil N<sub>2</sub>O fluxes were

**Table 2.** Mean ( $\pm$  SE,  $n = 3$  oil palm trees) soil  $\text{N}_2\text{O}$  and NO fluxes from three chamber locations during a fertilization in three (for  $\text{N}_2\text{O}$ ) or one (for NO) smallholder oil palm plantations within each landscape, measured 6 to 11 times during the 3–8.5 weeks following fertilization. Means followed by different letters indicate significant differences among chamber locations within each site (linear mixed-effect models with Fisher's LSD test at  $P \leq 0.05$ ). Chamber F1, F2 and NF were placed at 0.3 m (with incidental fertilization), 0.8 m (fertilized area) and 4–4.5 m (non-fertilized area, serving as the reference chamber), respectively, from the stem base. A total of  $0.32 \text{ kg N tree}^{-1}$  was applied in the clay Acrisol and  $0.26 \text{ kg N tree}^{-1}$  in the loam Acrisol in accordance to the smallholders' practices.

Oil palm site	Chamber location	$\text{N}_2\text{O}$ fluxes ( $\mu\text{g N m}^{-2} \text{ h}^{-1}$ )	NO fluxes ( $\mu\text{g N m}^{-2} \text{ h}^{-1}$ )
Clay Acrisol landscape			
1	F1	$156.7 \pm 86.8^b$	–
	F2	$910.1 \pm 410.0^a$	–
	NF	$6.9 \pm 3.3^c$	–
2	F1	$130.6 \pm 34.6^b$	–
	F2	$692.7 \pm 144.1^a$	–
	NF	$9.9 \pm 3.0^c$	–
3	F1	$45.5 \pm 3.7^b$	$4.7 \pm 1.7^b$
	F2	$1281.0 \pm 486.7^a$	$535.3 \pm 194.5^a$
	NF	$1.1 \pm 1.6^c$	$1.5 \pm 1.5^b$
Loam Acrisol landscape			
1	F1	$33.5 \pm 9.8^b$	–
	F2	$133.4 \pm 34.9^a$	–
	NF	$11.8 \pm 6.1^b$	–
2	F1	$129.7 \pm 46.2^a$	$46.2 \pm 19.6^b$
	F2	$205.3 \pm 24.2^a$	$157.1 \pm 35.7^a$
	NF	$7.9 \pm 4.8^b$	$0.7 \pm 0.3^b$
3	F1	$5.2 \pm 1.0^b$	–
	F2	$104.5 \pm 81.9^a$	–
	NF	$3.7 \pm 1.7^b$	–

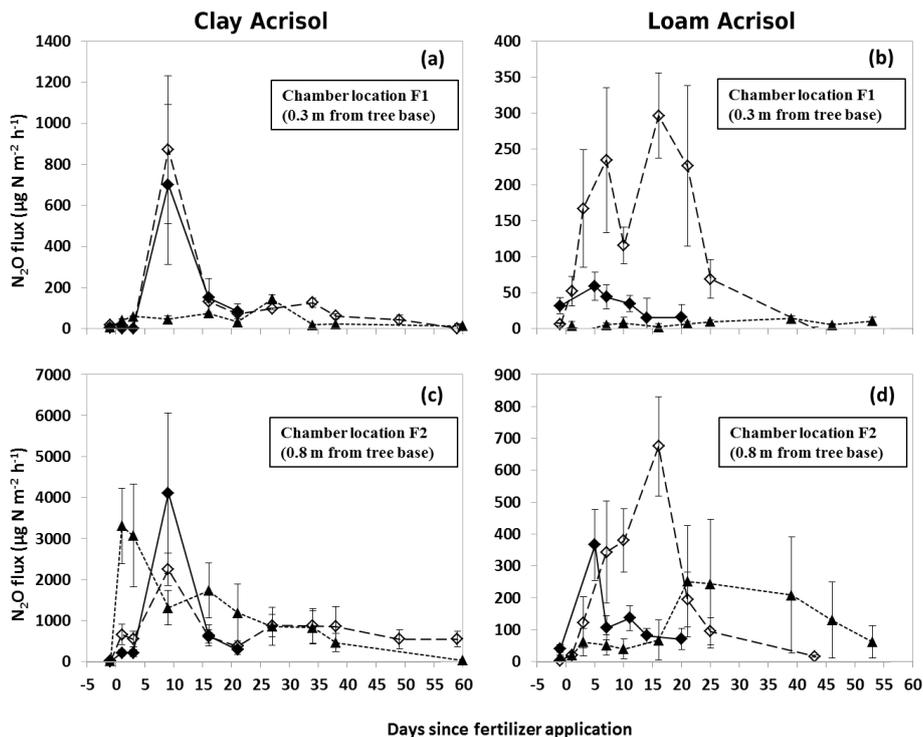
on average 442 times (clay Acrisol) and 22 times (loam Acrisol) higher within the small fertilized areas around the oil palms (chamber location F2 at 0.8–1 m from the tree base that received  $0.32$  and  $0.26 \text{ kg N tree}^{-1}$  in the clay and loam Acrisols, respectively) during the 3 to 8.5 weeks following fertilizer applications (all  $P < 0.01$ – $0.03$ ; Table 2; Fig. 2c, d). In the chamber location closest to the tree (chamber location F1 at 0.3 m from the tree base), soil  $\text{N}_2\text{O}$  emissions were also 25 times higher compared to the reference chamber location NF in the clay Acrisol landscape (all  $P < 0.01$ ; Table 2; Fig. 2a). In the loam Acrisol landscape, we only detected such an effect in site 2, which displayed 16 times higher soil  $\text{N}_2\text{O}$  emissions in chamber location F1 compared to the reference chamber location NF ( $P = 0.03$ ; Table 2; Fig. 2b).

In the clay Acrisol landscape, soil  $\text{N}_2\text{O}$  emissions in chamber location F2 increased immediately after fertilizer application, reached a peak within 9 days following fertilizer application and stayed elevated for at most 2 months (Fig. 2c). In the loam Acrisol landscape,  $\text{N}_2\text{O}$  fluxes in chamber loca-

tion F2 increased within the first 5 days, reached maximum fluxes within 5–21 days and remained elevated for at most 6.5 weeks (Fig. 2d). Soil  $\text{N}_2\text{O}$  fluxes in chamber location F1 displayed a similar but less pronounced pattern to those of chamber location F2 in both landscapes (Fig. 2a, b).

The average contributions of the fertilizer-induced  $\text{N}_2\text{O}$  emissions to the annual fluxes were 21 % in the clay Acrisol landscape and only 6 % in the loam Acrisol landscape (Table 1). To calculate this contribution (see Sect. 2.2), we considered the area coverage (4 % of a hectare, based on the number of palms  $\text{ha}^{-1}$ ) and time span of fertilizer-induced  $\text{N}_2\text{O}$  emissions.

Compared to the unfertilized area (chamber location NF), soil NO fluxes from the fertilized area (chamber location F2) had on average 357 times (clay Acrisol) and 238 times (loam Acrisol) higher fluxes (both  $P < 0.01$ ) during 6 to 8.5 weeks of measurements following fertilizer application (Table 2; Fig. 3c, d). No differences in soil NO fluxes were detected between chamber locations F1 and NF ( $P = 0.10$ – $0.12$ ; Table 2; Fig. 3a, b). Soil NO fluxes in chamber location F2



**Figure 2.** Mean ( $\pm$  SE,  $n = 3$  oil palm trees) soil  $\text{N}_2\text{O}$  fluxes during a fertilization in smallholder oil palm plantations 1 ( $\blacklozenge$ ), 2 ( $\diamond$ ) and 3 ( $\blacktriangle$ ) in the clay (a, c) and loam Acrisol (b, d) landscapes. Smallholders fertilized around the base of each tree at about 0.8–1 m from the tree base. Fluxes were measured at F1 = 0.3 m from the tree base (a, b) and at F2 = 0.8 m from the tree base on the fertilized location (c, d) with  $0.32 \text{ kg N tree}^{-1}$  in the clay Acrisol and  $0.26 \text{ kg N tree}^{-1}$  in the loam Acrisol in accordance to the smallholders' practices.

peaked after 10 days in the loam Acrisol and after 3 weeks in the clay Acrisol landscape (Fig. 3c, d) and returned to the background fluxes after 6–8.5 weeks, with a drastic drop after 3–5 weeks (Fig. 3c, d). In chamber location F1, soil  $\text{NO}$  fluxes increased quickly and decreased to the background fluxes within at most 16 days following fertilizer application (Fig. 3a, b). As was the case for the monthly sampling, soil  $\text{N}_2\text{O}$  fluxes from chamber locations F1 and F2 were larger than soil  $\text{NO}$  fluxes for both landscapes (Table 2; Figs. 2a–d and 3a–d). Comparing between landscapes, soil  $\text{N}_2\text{O}$  fluxes from chamber location F2 were higher in the clay than in the loam Acrisol soils ( $P = 0.09$ ; Table 2; Fig. 2c, d) but were comparable for chamber location F1 ( $P = 0.41$ ; Table 2; Fig. 2a, b) and for soil  $\text{NO}$  fluxes of both chamber locations ( $P = 0.45$ – $0.78$ ; Table 2; Fig. 3a–d).

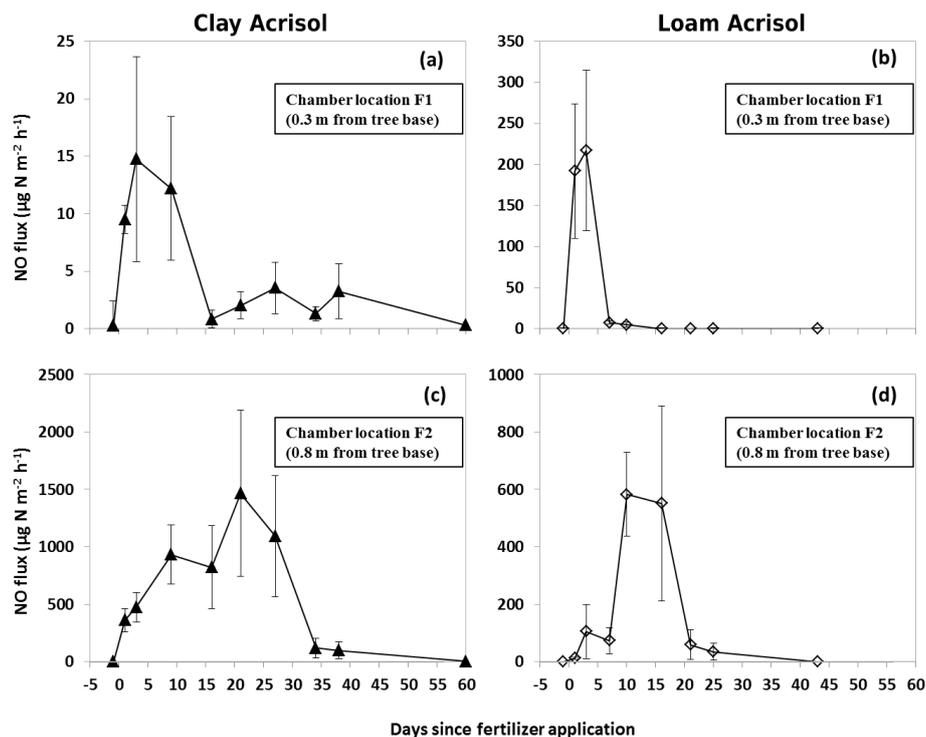
Fertilizer-induced soil  $\text{NO}$  fluxes in the loam Acrisol landscape were  $0.07 \pm 0.02 \text{ kg NO-N ha}^{-1} \text{ yr}^{-1}$ , which was roughly the same as our extrapolated annual value of  $0.06 \pm 0.06 \text{ kg NO-N ha}^{-1} \text{ yr}^{-1}$  from the four measurement periods (Table 1). In the clay Acrisol landscape, fertilizer-induced soil  $\text{NO}$  fluxes were  $0.12 \pm 0.04 \text{ kg NO-N ha}^{-1} \text{ yr}^{-1}$ , which was a net emission compared to our extrapolated annual value with a net sink of  $-0.02 \pm 0.11 \text{ kg NO-N ha}^{-1} \text{ yr}^{-1}$ , based on the four measurement periods (Table 1). The percentages of combined soil  $\text{N}_2\text{O}$  and  $\text{NO}$  fluxes

to the applied N-fertilizer rate were on average  $0.73 \% \text{ yr}^{-1}$  in the clay Acrisol landscape and  $0.20 \% \text{ yr}^{-1}$  in the loam Acrisol landscape.

### 3.3 Temporal controls of soil N-oxide fluxes

In the reference land uses, soil  $\text{N}_2\text{O}$  and  $\text{NO}$  fluxes were both positively correlated with soil  $\text{NO}_3^-$  contents, while soil  $\text{NO}$  fluxes were also negatively correlated with WFPS and soil  $\text{NH}_4^+$  contents (Table 3). In the converted land uses, soil  $\text{N}_2\text{O}$  fluxes were positively correlated with soil  $\text{NO}_3^-$  contents (Table 3). There were no significant correlations observed between soil  $\text{NO}$  fluxes and soil factors in the converted land uses due to the very low  $\text{NO}$  emissions and even net  $\text{NO}$  uptake.

From the fertilizer application experiment in the smallholder oil palm plantations, the location directly receiving fertilizer (chamber location F2) showed positive correlations of soil  $\text{N}_2\text{O}$  fluxes with soil  $\text{NH}_4^+$  and/or  $\text{NO}_3^-$  contents in three of the six sites (Table 4). Here, soil  $\text{NO}$  fluxes also correlated positively with soil  $\text{NO}_3^-$  contents in the loam Acrisol but not in the clay Acrisol (Table 4). In chamber location F1, positive correlations of soil  $\text{N}_2\text{O}$  fluxes with soil  $\text{NH}_4^+$  and/or  $\text{NO}_3^-$  contents were observed in four of the six sites (Table 4). The correlations of soil  $\text{N}_2\text{O}$  fluxes with mineral N for



**Figure 3.** Mean ( $\pm$  SE,  $n = 3$  oil palm trees) soil NO fluxes during a fertilization in a smallholder oil palm plantation in the clay (a, c) and loam Acrisol (b, d) landscapes. Smallholders fertilized around the base of each tree at about 0.8–1 m from the tree base. Fluxes were measured at F1 = 0.3 m from the tree base (a, b) and at F2 = 0.8 m from the tree base on the fertilized location (c, d) with  $0.32 \text{ kg N tree}^{-1}$  in the clay Acrisol and  $0.26 \text{ kg N tree}^{-1}$  in the loam Acrisol in accordance to the smallholders' practices.

**Table 3.** Pearson correlation coefficients between soil  $\text{N}_2\text{O}$  flux ( $n = 48$ ;  $\mu\text{g N m}^{-2} \text{ h}^{-1}$ ), soil NO flux ( $n = 16$ ;  $\mu\text{g N m}^{-2} \text{ h}^{-1}$ ), water-filled pore space (WFPS; %, top 0.05 m depth), soil temperature ( $^{\circ}\text{C}$ , top 0.05 m depth) and extractable mineral N ( $\text{mg N kg}^{-1}$ , top 0.05 m depth) across landscapes for the reference and converted land uses. The correlation was conducted using the means of the four replicate plots per land use on each of the 12 monthly measurements (for soil  $\text{N}_2\text{O}$  fluxes) and four monthly to bimonthly measurements (for soil NO fluxes).

Land-use type	Variable	WFPS	Soil temp.	$\text{NH}_4^+$	$\text{NO}_3^-$
Reference land uses (forest and jungle rubber)	Soil $\text{N}_2\text{O}$ flux	-0.21	-0.09	-0.23	0.38 <sup>b</sup>
	Soil NO flux	-0.74 <sup>b</sup>	-0.15	-0.48 <sup>a</sup>	0.69 <sup>b</sup>
Converted land uses (rubber and oil palm)	Soil $\text{N}_2\text{O}$ flux	0.11	0.15	0.23	0.37 <sup>b</sup>
	Soil NO flux	-0.05	0.09	-0.05	0.23

<sup>a</sup>  $P \leq 0.09$ , <sup>b</sup>  $P \leq 0.01$ .

chamber location F1 in site 2 of the clay Acrisol landscape were caused by one measurement period with very high flux, and exclusion of this observation resulted in a non-significant correlation. For soil NO fluxes from chamber location F1, we did not detect any significant correlation with soil factors (Table 4). A positive correlation of soil  $\text{N}_2\text{O}$  fluxes with WFPS was observed for chamber locations F1 and F2 in site 1 of the loam Acrisol landscape, whereas this correlation was negative for chamber location F1 in site 3 of the same landscape (Table 4). We also detected a negative correlation between soil NO fluxes and WFPS for chamber location F2 in site 3 of the clay Acrisol, whereas in the same site soil NO fluxes and

WFPS were positively correlated for the unfertilized chamber location NF (Table 4); however, the latter correlation was caused by only one sampling time with a high flux and high WFPS.

### 3.4 Spatial controls of annual soil $\text{N}_2\text{O}$ fluxes

The soil physical and biochemical characteristics (reported earlier by Allen et al., 2015) that showed significant correlations with annual soil  $\text{N}_2\text{O}$  fluxes are reported in Appendix Table A2. For the reference land uses, annual  $\text{N}_2\text{O}$  fluxes were positively correlated with gross nitrification rates

**Table 4.** Pearson correlation coefficients ( $n = 6$ – $11$  measurements following fertilization) between N-oxide fluxes ( $\mu\text{g N m}^{-2} \text{h}^{-1}$ ), water-filled pore space (WFPS; %, top 0.05 m depth) and extractable mineral N ( $\text{mg N kg}^{-1}$ , top 0.05 m depth), measured at different chamber locations (F1, F2 and NF were at 0.3 m, with incidental fertilization; 0.8 m, fertilized area; and 4–4.5 m, non-fertilized area; respectively, from the stem base). The correlation was conducted using the means of the three replicate trees per chamber location on each sampling day following fertilization.

Oil palm plantation site	Chamber location	Variable	WFPS	$\text{NH}_4^+$	$\text{NO}_3^-$
Clay Acrisol landscape					
1 ( $n = 6$ measurements)	F1	Soil $\text{N}_2\text{O}$ flux	0.55	0.88 <sup>b</sup>	0.46
	F2		0.57	−0.22	−0.31
	NF		0.37	−0.64	−0.44
2 ( $n = 11$ measurements)	F1	Soil $\text{N}_2\text{O}$ flux	0.11	0.93 <sup>c</sup>	0.95 <sup>c</sup>
	F2		0.08	0.05	−0.06
	NF		0.09	−0.44	−0.45
3 ( $n = 10$ measurements)	F1	Soil $\text{N}_2\text{O}$ flux	−0.19	0.10	0.09
	F2		0.05	0.86 <sup>c</sup>	0.85 <sup>c</sup>
	NF		−0.32	0.06	−0.44
3 ( $n = 10$ measurements)	F1	Soil NO flux	−0.34	0.44	0.48
	F2		−0.61 <sup>a</sup>	0.10	−0.04
	NF		0.59 <sup>a</sup>	−0.14	−0.13
Loam Acrisol landscape					
1 ( $n = 6$ measurements)	F1	Soil $\text{N}_2\text{O}$ flux	0.96 <sup>c</sup>	−0.18	0.03
	F2		0.78 <sup>a</sup>	0.61	−0.40
	NF		−0.06	−0.29	< 0.01
2 ( $n = 9$ measurements)	F1	Soil $\text{N}_2\text{O}$ flux	−0.55	0.71 <sup>b</sup>	−0.03
	F2		0.35	−0.20	0.89 <sup>c</sup>
	NF		0.34	< 0.01	−0.35
3 ( $n = 11$ measurements)	F1	Soil $\text{N}_2\text{O}$ flux	−0.68 <sup>b</sup>	0.67 <sup>b</sup>	0.62 <sup>b</sup>
	F2		−0.27	−0.20	0.57 <sup>a</sup>
	NF		0.36	0.19	0.06
2 ( $n = 9$ measurements)	F1	Soil NO flux	−0.07	0.18	−0.27
	F2		0.07	−0.11	0.96 <sup>c</sup>
	NF		−0.16	0.12	−0.23

<sup>a</sup>  $P \leq 0.09$ , <sup>b</sup>  $P \leq 0.05$ , <sup>c</sup>  $P \leq 0.01$ .

across landscapes (Spearman's  $\rho = 0.57$ ,  $P = 0.02$ ,  $n = 16$ ). Within each landscape, annual soil  $\text{N}_2\text{O}$  fluxes from the reference land uses correlated negatively with soil C:N ratio ( $\rho = -0.69$ ,  $P = 0.07$ ,  $n = 8$ ) in the clay Acrisol, whereas in the loam Acrisol annual soil  $\text{N}_2\text{O}$  fluxes correlated positively with microbial C ( $\rho = 0.69$ ,  $P = 0.07$ ,  $n = 8$ ). For the converted land uses, annual  $\text{N}_2\text{O}$  fluxes correlated negatively with sand content across landscapes ( $\rho = -0.57$ ,  $P = 0.06$ ,  $n = 12$ ). There were no other correlations detected with any other soil biochemical parameters.

## 4 Discussion

### 4.1 Soil $\text{N}_2\text{O}$ and NO fluxes from the reference land uses

The  $\text{N}_2\text{O}$  fluxes from our forest soils (Table 1) fell at the lower end of those reported for humid tropical forests ( $10$ – $85 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$ ; summarized by Castaldi et al., 2013). Compared to soil  $\text{N}_2\text{O}$  fluxes measured in Indonesia, our values were comparable to those reported for montane forests on Cambisol soil with similar sampling frequency and spatial replication ( $13 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$ ; Purbopuspito et al., 2006) and to five lowland forest stands on Acrisol soil measured once ( $12 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$ ; Ishizuka et al., 2005). However, soil  $\text{N}_2\text{O}$  fluxes from our forests were lower

than those reported for montane forests on Cambisol soils with six monthly measurements and comparable replication ( $25 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$ ; Veldkamp et al., 2008) and from a lowland forest on Ferralsol soil with 13 measurements at monthly intervals ( $20 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$ ; Aini et al., 2015). In contrast, our values were higher than those reported for two lowland forests on Ferralsol soil with nine measurements at monthly intervals ( $3 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$ ; Ishizuka et al., 2002). Since the studies from the montane forests were conducted on fertile, less weathered Cambisol soils and the studies within the same region (Jambi province) by Ishizuka et al. (2002, 2005) and Aini et al. (2015) have less sampling frequency or spatial replication, their values should be carefully related to our measured fluxes.

Soil NO fluxes from Southeast Asian lowland forests are not reported so far. Our measured NO fluxes from the forest soils (Table 1) tended to be lower than those reported for lowland forests in Latin America, with soils ranging from less weathered Cambisols to highly weathered Acrisols and Ferralsols (from  $3\text{--}90 \mu\text{g NO-N m}^{-2} \text{h}^{-1}$ ; Corre et al., 2014; Davidson et al., 2004; Keller et al., 2005; Verchot et al., 1999). There are only two studies conducted in Indonesia that reported soil NO fluxes from montane forests on Cambisol soils (Purbopuspito et al., 2006; Veldkamp et al., 2008). Our measured soil NO fluxes were comparable to the values reported for montane forests at  $\geq 1800 \text{ m}$  elevation ( $2 \mu\text{g NO-N m}^{-2} \text{h}^{-1}$ ; Purbopuspito et al., 2006) but lower than those reported for (pre)montane forests ( $6\text{--}12 \mu\text{g NO-N m}^{-2} \text{h}^{-1}$ ; Purbopuspito et al., 2006; Veldkamp et al., 2008). Although it is known that tropical forest soils are the largest natural source of  $\text{N}_2\text{O}$  and produce considerable amounts of NO, our measurements from these lowland forests in Jambi, Indonesia, on highly weathered Acrisol soils showed generally low soil N-oxide fluxes.

In contrast to our first hypothesis, soil N-oxide fluxes from the reference land uses were comparable between loam and clay Acrisol landscapes. This is possibly due to the generally low soil N availability in these sites, as indicated by their lower gross N mineralization rates (Allen et al., 2015) compared, for example, to the less weathered Cambisol and Nitisol soils in a lowland forest of Panama (Corre et al., 2010). Soil N-oxide fluxes are largely controlled, first, by the magnitude of soil N availability, as depicted in the HIP conceptual model (Davidson et al., 2000). This influence of soil N availability on N-oxide fluxes was illustrated by the positive correlations of soil N-oxide fluxes with soil  $\text{NO}_3^-$  contents (Table 3). Across landscapes, this first level of control was also corroborated by the positive correlations of annual soil  $\text{N}_2\text{O}$  fluxes with gross nitrification rates and within each landscape by the negative correlation with the soil C:N ratio (clay Acrisol landscape) and by the positive correlation with microbial C (loam Acrisol landscape; see Sect. 3.4). Our findings were consistent with those from other tropical soils, illustrating that soil N-oxide fluxes across or within sites are controlled by soil N availability as expressed in various in-

dexes such as soil  $\text{NO}_3^-$  contents (Keller and Reiners, 1994; Müller et al., 2015), nitrification rates (Davidson et al., 2000) and the soil C:N ratio (Breuer et al., 2000).

Moreover, we attributed the low soil NO fluxes and the dominance of  $\text{N}_2\text{O}$  (Table 1) in our sites to the second level of control of N-oxide fluxes – soil aeration status (HIP model; Davidson et al., 2000). The ratio of  $\text{N}_2\text{O}$  to NO is expected to increase when WFPS exceeds 60 % as low soil aeration favors  $\text{N}_2\text{O}$  production by denitrification and nitrification processes (Davidson et al., 2000). WFPS in the reference land uses were  $\geq 60 \%$  (Appendix Table A3, except in jungle rubber of the loam Acrisol with 54 % WFPS). Hence, it was not surprising that our measured soil NO fluxes were close to zero or showed net consumption (Table 1); the high WFPS may have led to NO reduction to  $\text{N}_2\text{O}$  (Conrad, 1996; Pilegaard, 2013). This was supported by the negative correlation between soil NO fluxes and WFPS (Table 3). Furthermore, increased concentrations of NO in the atmosphere due to biomass burning in this region (Field et al., 2009; Levine, 1999), which also occurred in 2013 (Gaveau et al., 2014), may have resulted in a net NO consumption (not only in the reference land uses but also in the converted land uses; Table 1) since increased ambient NO concentration could have enhanced soil NO uptake (Conrad, 1994). In summary, soil NO fluxes from the reference land uses were of minor importance compared to soil  $\text{N}_2\text{O}$  fluxes. However, if droughts were to occur more frequently or extremely in this region (Lestari et al., 2014), soil NO fluxes might become important.

#### 4.2 Land-use change effects on soil $\text{N}_2\text{O}$ and NO fluxes

Soil  $\text{N}_2\text{O}$  fluxes from our unfertilized rubber plantations (Table 1) were comparable to a rubber plantation on Ferralsol soil in Malaysia with eight measurements during a 1.5-year period ( $8 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$ , fertilized with  $9 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ ; Yashiro et al., 2008) and slightly higher than fluxes reported from a rubber plantation on a lateritic soil in China with only two months of measurement ( $4 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$ , fertilized with  $55 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ ; Werner et al., 2006). Studies from the same region (Jambi, Indonesia) report either lower soil  $\text{N}_2\text{O}$  fluxes from a rubber plantation on Ferralsol soil with 9 sampling days at monthly intervals ( $1 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$ ; Ishizuka et al., 2002) or higher fluxes from five rubber plantations on Acrisol soils with only a one-time measurement ( $21 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$ ; Ishizuka et al., 2005) and from one rubber plantation on Ferralsol soil with 13 sampling days at monthly intervals ( $12 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$ ; Aini et al., 2015). The rubber plantations in these latter three studies were all unfertilized. Soil  $\text{N}_2\text{O}$  fluxes from our oil palm plantations (Table 1), which had fertilization of  $48\text{--}88 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ , were in the same order of magnitude as those reported from three fertilized oil palm plantations on Acrisol soils in Jambi, Indonesia, with only a one-time measurement ( $15 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$ ;

Ishizuka et al., 2005) and from one unfertilized oil palm plantation on Cambisol soil in Jambi, Indonesia, with 13 monthly measurements ( $12 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$ ; Aini et al., 2015). However, soil  $\text{N}_2\text{O}$  fluxes from our oil palm sites were higher compared to one oil palm plantation on Ferralsol soil in Malaysia with eight measurements during a 1.5-year period ( $-0.1 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$ , fertilized with  $25 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ ; Yashiro et al., 2008). Soil NO fluxes have never been reported from rubber or oil palm plantations.

In contrast to our second hypothesis, soil N-oxide fluxes were comparable among land uses (except for soil NO fluxes between rubber and jungle rubber in the loam Acrisol landscape as discussed below), even with the observed decreases in soil mineral N levels among land uses (i.e., generally lower  $\text{NH}_4^+$  and  $\text{NO}_3^-$  levels in rubber plantations than in the reference land uses at both landscapes; Appendix Table A3). In the same study sites, Allen et al. (2015) found differences in other indices of soil N availability with land-use change, particularly in the clay Acrisol landscape: microbial C and N, gross N mineralization and  $\text{NH}_4^+$  immobilization rates decrease with conversion of forest to rubber or oil palm plantations. N-oxide emissions generally account for only a small fraction of soil available N (e.g.,  $\text{N}_2\text{O} + \text{NO}$  emissions comprise 0.03 % of gross N mineralization rates in a lowland forest on Cambisol and Nitisols soils in Panama; Corre et al., 2014). In our present study, the reference land uses on highly weathered Acrisol soils have low soil N availability, and their conversion to these plantations further decreases the soil N-cycling rates (Allen et al., 2015). Hence, we reason that we did not detect differences in N-oxide fluxes with land-use conversion to rubber and oil palm plantations because we started with low soil N availability and low N-oxide emissions and any changes were probably too small to detect statistically. The temporal pattern of soil  $\text{N}_2\text{O}$  fluxes in the converted land uses were also controlled by soil  $\text{NO}_3^-$  contents (Table 3), emphasizing the first level of control of soil N availability on soil  $\text{N}_2\text{O}$  fluxes (HIP model; Davidson et al., 2000). Across landscapes, the correlations of annual soil  $\text{N}_2\text{O}$  fluxes from these converted land uses with sand contents (see Sect. 3.4) also suggested the indirect influence of soil texture on water holding capacity, or conversely soil aeration status, which is the second level of control on soil  $\text{N}_2\text{O}$  fluxes (HIP model). Consequently, the soil N-oxide emission footprint of smallholder oil palm and rubber plantations was similar to the original land uses (Table 1). This finding was in contrast to a study by Hewitt et al. (2009) conducted in Sabah, Malaysian Borneo, wherein they showed that oil palm plantations emit more N oxides than rainforests, which may be explained by their higher fertilization rate ( $500 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ ) compared to our smallholder oil palm plantations ( $48\text{--}88 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ ). Thus, an increase in fertilizer usage, e.g., in large-scale plantations in our study region, might change this soil N-oxide emission footprint drawn mainly from smallholder plantations (see Sect. 4.3).

The lower soil NO fluxes in rubber compared to jungle rubber in the loam Acrisol (Table 1) partly supports our second hypothesis. These differences might be related to the high soil  $\text{NO}_3^-$  contents and low WFPS in jungle rubber (Appendix Table A3), which could favor its relatively high soil NO emissions; this was also supported by the opposing correlations of soil NO flux with soil  $\text{NO}_3^-$  and WFPS (Table 3). Additionally, the low soil NO fluxes from rubber plantations could be the result of the effect of monoterpenes, produced by rubber trees, which reduce nitrification in soil (Wang et al., 2007; White, 1991). This is supported by low gross nitrification rates (measured in the same plots by Allen et al., 2015), low soil  $\text{NO}_3^-$  contents (Appendix Table A3) and consequently low soil NO fluxes in rubber plantations (Table 1).

#### 4.3 Soil management effects on soil $\text{N}_2\text{O}$ and NO fluxes from oil palm plantations

N-fertilizer application, a commonly employed soil management in oil palm plantations (e.g., Allen et al., 2015; Hassler et al., 2015), increases N-oxide emission for a relatively short period (e.g., Koehler et al., 2009). Our findings show that these fertilizer-induced N-oxide emissions were mainly limited to the small area around the palm base where fertilizer was commonly applied (4 % of the area in a hectare) and that N-oxide emissions peaked within 3 weeks (Figs. 2 and 3). These N-fertilizer-induced  $\text{N}_2\text{O}$  fluxes of 6–21 % of the annual soil  $\text{N}_2\text{O}$  fluxes were similar in magnitude to the standard errors of the annual fluxes (estimated from the monthly measurements; Table 1). Thus, inclusion of these N-induced emissions in our annual estimates did not result in statistically significant effects of land-use change.

The percentages of soil  $\text{N}_2\text{O}$  and NO fluxes to the applied N-fertilizer rate were smaller than those reported from other agricultural land uses in humid tropical regions (6.4–8.6 %; Veldkamp and Keller, 1997; Veldkamp et al., 1998). Usually the percentage of soil N-oxide emissions to applied N-fertilizer rate increases with increasing N fertilization rates (Hoben et al., 2011; Pennock and Corre, 2001). Since the fertilization rates in our studied smallholder oil palm plantations ( $48\text{--}88 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ ) were lower compared to the fertilization rates in these other studies ( $300\text{--}360 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ ; Veldkamp and Keller, 1997; Veldkamp et al., 1998), our quantified N-oxide loss from the N fertilizer were also low. The relatively high soil  $\text{N}_2\text{O}$  fluxes from the large-scale oil palm plantation, although not statistically different from the smallholder plantations (Table 1), could be attributed to its high N fertilization rate ( $196 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ ). Summing the fertilizer-induced N-oxide fluxes and the annual soil N-oxide emissions based on the monthly measurements (Table 1), these values from the smallholder plantations were low relative to the annual flux from the large-scale plantation (Table 1). Based on our finding that soil  $\text{N}_2\text{O}$  fluxes following fertilizer application (chamber location F2) were higher in the clay than in the loam Acrisol landscapes (most likely

due to higher WFPS in the clay,  $61 \pm 8\%$ , than in the loam Acrisol,  $27 \pm 3\%$ , during this measurement period), soil N<sub>2</sub>O fluxes from large-scale plantations on clay soils could be even higher than what we measured here from a large-scale plantation on a loam soil. Our findings reinforced the need to quantify these climate-relevant N-oxide gases in large-scale plantations, which constitute  $\sim 50\%$  of the land area under oil palm plantation in all of Sumatra (BPS, 2014).

Temporal patterns of soil N-oxide fluxes following fertilizer application were also controlled by soil N availability, as reflected by their positive correlations with soil  $\text{NH}_4^+$  and/or  $\text{NO}_3^-$  contents (Table 4). The application of N fertilizer provides a temporary surplus of mineral N that was lost via gaseous emission and leaching (Kurniawan, 2016), and such effect diminished with time as the mineral N is incorporated into the soil N-cycling processes (Allen et al., 2015). The positive correlation between soil N<sub>2</sub>O fluxes and WFPS (i.e., chamber locations F1 and F2 in site 1 of the loam Acrisol; Table 4) and the negative correlation between soil NO fluxes and WFPS (i.e., chamber location F2 in site 3 of the clay Acrisol landscape; Table 4) again attested that when the first level of control (soil N availability) was favorable (i.e., high soil mineral N contents in these fertilized chamber locations), the control of soil moisture on aeration status was enhanced, as such correlation was not seen in the unfertilized area (chamber location NF) or in the monthly measured fluxes (Tables 3 and 4). These correlations indicated that following fertilizer application soil NO fluxes decreased, whereas soil N<sub>2</sub>O fluxes increased with an increase in WFPS. In site 3 of the loam Acrisol, the seemingly contradicting negative correlation of soil N<sub>2</sub>O fluxes with WFPS (Table 4) was due to a decreasing WFPS following fertilizer application with concurrently increasing soil mineral N contents, with the latter dominantly driving the increases in soil N<sub>2</sub>O fluxes (i.e., positive correlations with  $\text{NH}_4^+$  and  $\text{NO}_3^-$ ; Table 4). In summary, the short-term effect of fertilization also depicted the two levels of controls on soil N-oxide fluxes as exemplified in the HIP model.

## 5 Conclusions

Our study provides the first spatially replicated study with a full year of measurements (at monthly interval) of soil N<sub>2</sub>O fluxes and the first reported soil NO fluxes from this region of hotspots of land-use conversion for globally important tree cash crops. In contrast to our first hypothesis, soil

texture, through its role on soil fertility, did not directly affect soil N-oxide fluxes (as shown by the comparable fluxes between landscapes with soil textural differences) but indirectly influenced the landscape-scale pattern of annual soil N<sub>2</sub>O fluxes in the converted land uses (i.e., negative correlation between annual N<sub>2</sub>O fluxes and sand content), most likely through its role on soil moisture availability. The generally low soil N-oxide fluxes from the reference land uses were due to the low soil N availability in these highly weathered Acrisol soils (Allen et al., 2015). Forest or jungle rubber conversion to rubber and oil palm by smallholders also did not show significant changes in soil N-oxide fluxes, except for the decrease in soil NO fluxes in rubber plantations and for the short-term pulse of soil N-oxide fluxes following fertilizer application in oil palm plantations. These partly support our second hypothesis. Using a conservative estimate of N-oxide (N<sub>2</sub>O + NO) loss from the applied N fertilizer in oil palm plantations (average of 0.5% from the loam and clay Acrisol landscapes) and a conservative average N fertilization rate across smallholder and large-scale plantations of  $100 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ , with a total land area of oil palm in Jambi province of 721 000 ha (BPS, 2014), we estimated an annual soil N-oxide emission from N fertilization of  $361 \text{ t N yr}^{-1}$ . The N fertilization rates in our smallholder oil palm plantations were only about one-fourth to one-half of what is commonly practiced in large-scale industrial plantations (e.g.,  $130\text{--}260 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  in Jambi, Indonesia; Pahan, 2010), and our measurements from a large-scale oil palm plantation showed relatively high soil N-oxide fluxes. To improve the estimate of soil N-oxide fluxes at the regional level, future studies should focus on large-scale plantations (which constitute 38% of oil palm land area in Jambi province; BPS, 2014), with frequent measurements during the 2 months following the fertilizer application and particularly during the wet season for N<sub>2</sub>O flux measurements and during the dry season for NO flux measurements.

*Data availability.* The underlying research data of this study are deposited at the EFForTS-IS data repository (<https://efforts-is.uni-goettingen.de>), an internal data exchange-platform, which is accessible to all members of the Collaborative Research Center (CRC) 990 (see Acknowledgements). Based on the data sharing agreement within the CRC 990, these data are currently not publicly accessible but will be made available through a written request to the senior authors.

### Appendix A: Detailed description of the linear mixed-effect models application

For analysis of differences in N-oxide fluxes among land uses or between soil landscapes, we used the means of the four chambers representing each replicate plot on a sampling day. Linear mixed-effect (LME) models (Crawley, 2007) were used to assess differences between landscapes for the reference land uses (testing H1) or differences among land uses within each landscape (testing H2). In the LME models, either landscape or land use was considered as a fixed effect, whereas replicate plots and sampling days were considered as random effects. For comparison of soil N<sub>2</sub>O fluxes between the large-scale (PTPN VI) and smallholder oil palm plantations within the loam Acrisol landscape, we also used the means of the three chambers per replicate plot on each sampling day in the PTPN VI site, as there were no significant differences between these chamber locations (based on LME models with chamber location as a fixed effect and replicates as well as sampling days as random effects;  $P = 0.70$ ). We then used the LME model with plantation ty-

pes (i.e., large scale vs. smallholder) as a fixed effect and replicates and sampling days as random effects. For analysis of fertilization (i.e., as represented by the chamber locations F1, F2 and NF) on soil N-oxide fluxes from smallholder oil palm plantations, this was conducted for each site with oil palm trees as replicates. In the LME model for this experiment, chamber location was the fixed effect, whereas replicate palm trees and sampling days were the random effects. To assess differences in N-oxide fluxes between landscapes following fertilization for chamber locations F1 and F2, we also used LME models with landscape as a fixed effect and with replicate plots (for N<sub>2</sub>O) or replicate palm trees (for NO) and sampling days as random effects. In all LME models, we included (1) a variance function that allows different variances of the fixed effect and/or (2) a first-order temporal autoregressive function to account for decreasing correlation between sampling days with increasing time difference, if these functions improved the relative goodness of the model fit based on the Akaike information criterion.

**Table A1.** Location and year of measurement.

Measurement	Sampling location	N-oxide determined	Measurement year
Clay Acrisol landscape			
Four land uses (forest, jungle rubber, rubber, oil palm)	all 16 replicate plots	N <sub>2</sub> O and NO	2013
Intensive measurements following fertilization (oil palm)	three oil palm replicate plots	N <sub>2</sub> O	2013–2014
Intensive measurements following fertilization (oil palm)	one oil palm replicate plot	NO	2013
Loam Acrisol landscape			
Four land uses (forest, jungle rubber, rubber, oil palm)	all 16 replicate plots	N <sub>2</sub> O and NO	2013
Intensive measurements following fertilization (oil palm)	three oil palm replicate plots	N <sub>2</sub> O	2013–2014
Intensive measurements following fertilization (oil palm)	one oil palm replicate plot	NO	2013
Large-scale oil palm plantation	PTPN VI	N <sub>2</sub> O	2014–2015

**Table A2.** Mean ( $\pm$  SE,  $n = 4$  sites) soil physical and biochemical characteristics in the top 0.10 m depth (except sand content with  $n = 3$  sites) from different land uses within each landscape in Jambi, Sumatra, Indonesia. These soil factors and the gross nitrification rates were reported by Allen et al. (2015).

Soil characteristics	Land-use type			
	Forest	Jungle rubber	Rubber	Oil palm
Clay Acrisol landscape				
Sand (%)	36 $\pm$ 11	27 $\pm$ 20	35 $\pm$ 7	11 $\pm$ 2
Soil C : N ratio	13.1 $\pm$ 1.3	13.0 $\pm$ 0.3	14.3 $\pm$ 0.6	13.5 $\pm$ 0.2
Microbial C (mg C kg <sup>-1</sup> )	1048 $\pm$ 20	922 $\pm$ 223	561 $\pm$ 61	617 $\pm$ 112
Gross nitrification rate (mg N kg <sup>-1</sup> day <sup>-1</sup> )	0.9 $\pm$ 0.3	1.0 $\pm$ 0.2	0.7 $\pm$ 0.2	2.0 $\pm$ 0.8
Loam Acrisol landscape				
Sand (%)	39 $\pm$ 8	42 $\pm$ 19	26 $\pm$ 13	43 $\pm$ 14
Soil C : N ratio	14.3 $\pm$ 0.2	13.7 $\pm$ 0.8	11.7 $\pm$ 0.7	12.5 $\pm$ 0.5
Microbial C (mg C kg <sup>-1</sup> )	514 $\pm$ 48	578 $\pm$ 45	461 $\pm$ 58	403 $\pm$ 24
Gross nitrification rate (mg N kg <sup>-1</sup> day <sup>-1</sup> )	1.9 $\pm$ 0.4	0.9 $\pm$ 0.2	0.9 $\pm$ 0.2	1.2 $\pm$ 0.5

**Table A3.** Mean ( $\pm$  SE,  $n = 4$  sites) soil water-filled pore space (WFPS) and extractable mineral N in the top 0.05 m depth for different land uses within each landscape in Jambi, Sumatra, Indonesia. Means followed by different lowercase letters indicate significant differences among land uses within each landscape and different capital letters indicate significant differences between landscapes within each land use (linear mixed-effect models with Fisher's LSD test at  $P \leq 0.05$ ). These soil factors were reported by Hassler et al. (2015).

Land-use type	WFPS (%)	NH <sub>4</sub> <sup>+</sup> (mg N kg <sup>-1</sup> )	NO <sub>3</sub> <sup>-</sup> (mg N kg <sup>-1</sup> )
Clay Acrisol landscape			
Forest	73.0 $\pm$ 12.3 <sup>a,A</sup>	7.0 $\pm$ 1.0 <sup>a,A</sup>	2.2 $\pm$ 0.4 <sup>a,A</sup>
Jungle rubber	86.7 $\pm$ 5.9 <sup>a,A</sup>	7.3 $\pm$ 0.2 <sup>a,A</sup>	0.2 $\pm$ 0.1 <sup>b,B</sup>
Rubber	61.5 $\pm$ 7.4 <sup>a,A</sup>	4.3 $\pm$ 0.2 <sup>b,A</sup>	0.1 $\pm$ 0.0 <sup>b,B</sup>
Oil palm	74.0 $\pm$ 7.3 <sup>a,A</sup>	5.8 $\pm$ 0.6 <sup>a,A</sup>	0.8 $\pm$ 0.5 <sup>b,A</sup>
Loam Acrisol landscape			
Forest	64.0 $\pm$ 3.3 <sup>a,A</sup>	5.9 $\pm$ 0.4 <sup>a,A</sup>	0.6 $\pm$ 0.2 <sup>ab,B</sup>
Jungle rubber	53.9 $\pm$ 3.7 <sup>a,B</sup>	5.6 $\pm$ 0.3 <sup>a,B</sup>	1.3 $\pm$ 0.6 <sup>a,A</sup>
Rubber	72.6 $\pm$ 5.7 <sup>a,A</sup>	4.1 $\pm$ 0.6 <sup>b,A</sup>	0.1 $\pm$ 0.0 <sup>b,A</sup>
Oil palm	59.0 $\pm$ 6.7 <sup>a,A</sup>	4.2 $\pm$ 1.1 <sup>b,B</sup>	0.6 $\pm$ 0.4 <sup>ab,A</sup>

*Competing interests.* The authors declare that they have no conflict of interest.

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