



Reviews and syntheses: Soil N₂O and NO emissions from land use and land-use change in the tropics and subtropics: a meta-analysis

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Abstract. Deforestation and forest degradation in the tropics may substantially alter soil N-oxide emissions. It is particularly relevant to accurately quantify those changes to properly account for them in a REDD+ climate change mitigation scheme that provides financial incentives to reduce the emissions. With this study we provide updated land use (LU)-based emission rates (104 studies, 392 N₂O and 111 NO case studies), we determine the trend and magnitude of flux changes with land-use change (LUC) using a meta-analysis approach (44 studies, 135 N₂O and 37 NO cases) and evaluate biophysical drivers of N₂O and NO emissions and emission changes for the tropics.

The average N₂O and NO emissions in intact upland tropical forest amounted to 2.0 ± 0.2 ($n = 90$) and 1.7 ± 0.5 ($n = 36$) kg N ha⁻¹ yr⁻¹, respectively. In agricultural soils annual N₂O emissions were exponentially related to N fertilization rates and average water-filled pore space (WFPS) whereas in non-agricultural sites a Gaussian response to WFPS fit better with the observed NO and N₂O emissions. The sum of soil N₂O and NO fluxes and the ratio of N₂O to NO increased exponentially and significantly with increasing nitrogen availability (expressed as $\text{NO}_3^- / [\text{NO}_3^- + \text{NH}_4^+]$) and WFPS, respectively; following the conceptual Hole-In-the-Pipe model. Nitrous and nitric oxide fluxes did not increase significantly overall as a result of LUC (Hedges's d of 0.11 ± 0.11 and 0.16 ± 0.19 , respectively), however individual LUC trajectories or practices did. Nitrous oxide fluxes increased significantly after intact upland forest conversion to croplands (Hedges's $d = 0.78 \pm 0.24$) and NO increased significantly following the conversion of low forest cover (secondary forest younger than 30 years, woodlands, shrublands)

(Hedges's d of 0.44 ± 0.13). Forest conversion to fertilized systems significantly and highly raised both N₂O and NO emission rates (Hedges's d of 1.03 ± 0.23 and 0.52 ± 0.09 , respectively).

Changes in nitrogen availability and WFPS were the main factors explaining changes in N₂O emissions following LUC, therefore it is important that experimental designs monitor their spatio-temporal variation. Gaps in the literature on N oxide fluxes included geographical gaps (Africa, Oceania) and LU gaps (degraded forest, wetland (notably peat) forest, oil palm plantation and soy cultivation).

1 Introduction

Land use (LU) and land-use change (LUC) are important contributors to global greenhouse gas (GHG) emissions. The current contribution of LUC to total anthropogenic GHG emissions is estimated to be between 7 and 18 % (Houghton, 2003; Baumert et al., 2005; Baccini et al., 2012; Harris et al., 2012). This estimation heavily depends on biomass values and deforestation rates and is associated with high uncertainties, especially in the tropics (Houghton, 2005). Causes of LUC are a complex and interacting combination of economic, social and political factors (Lambin et al., 2001, 2003). However, population growth and agricultural export correlate well with forest conversion rates (DeFries et al., 2010). A recent comparative study showed commercial and subsistence agriculture to be the most prevalent deforestation driver in non-Annex I (i.e. developing) countries (Hosonuma et al., 2012). Between 1980 and 2000, 83 % of the new agri-

cultural land within the tropical region were converted from intact or disturbed forest (Gibbs et al., 2010). As the world population and food demand are expected to grow (respectively 34 and 70 % by 2050, FAO, 2009), further deforestation is likely in the near future.

By avoiding deforestation and forest degradation and through enhancing carbon (C) stocks in forests, reducing worldwide GHG emissions could be achieved with a reasonable level of cost-efficiency (Stern, 2008; Streck and Parker, 2012). However, for climate change mitigation schemes such as reducing emissions from deforestation and forest degradation (REDD+), where payments are based on performance, it is crucial to know how much emissions can be mitigated by preventing deforestation and reforestation. In addition to carbon dioxide (CO₂), several studies on LUC in the tropics reported high non-CO₂ GHG emissions, such as nitrous oxide (N₂O) (e.g. Ishizuka et al., 2005; Keller et al., 2005; Takakai et al., 2006; Verchot et al., 2006; Yashiro et al., 2008) and nitric oxide (NO) (e.g. Verchot et al., 1999; Erickson et al., 2002; Pérez et al., 2007; Davidson et al., 2008). Although the absolute mass of N₂O emissions might be small, the global warming potential for N₂O over a 100-year time horizon is 298 times greater than that of CO₂ (Myhre et al., 2013). In addition this trace gas also contributes to ozone depletion in the stratosphere (Crutzen, 1970). Nitric oxide, on the other hand, is a free radical that enhances ozone production in the troposphere (lower atmosphere) (Chameides et al., 1992); ozone in the troposphere is a GHG (Myhre et al., 2013). Although NO is in fact an indirect GHG, it is relevant to study its dynamic in combination with that of N₂O as they share the same processes of production (nitrification and denitrification) in the soil and are hypothesized to be interlinked (Firestone and Davidson, 1989).

Emissions factors in the IPCC guidelines for national GHG inventories (2006) have high uncertainties although some of these were slightly reduced in the 2013 wetlands supplement (Drösler et al., 2014). On the one hand, this high uncertainty can be explained by the high temporal and spatial variability of N₂O and NO emissions which are known to vary diurnally, seasonally (see e.g. Meixner et al., 1997; Chen and Huang, 2009; Lin et al., 2010), and locally due to micro site-specific soil variability (Dalal and Allen, 2008). On the other hand, the high uncertainty is partly due to the paucity of reliable estimates available in the peer-reviewed literature.

Sources of biogenic N₂O and NO fluxes from the soil can be a wide variety of microorganisms and processes (Anderson and Poth, 1989), but nitrification and denitrification are the main mechanisms (Davidson et al., 2000; Baggs and Philippot, 2010). Therefore, the magnitude of N₂O and NO fluxes depends on variables that enhance or inhibit nitrification and denitrification such as nitrogen (substrate) availability, soil water content (aeration status), soil temperature and pH (Skiba and Smith, 2000; Heinen, 2006; Dalal and Allen, 2008). Substrates for nitrification and denitrification are am-

monium and nitrate, respectively. Ammonium (NH₄⁺) is the result of microbial decomposition of soil organic matter and is converted to nitrate (NO₃⁻) by the nitrifying bacteria under aerobic conditions. In this process, N₂O and NO are produced and partly emitted to the atmosphere. NO₃⁻ in return is used under anaerobic conditions as a terminal electron acceptor for denitrifying bacteria that reduce NO₃⁻ to N₂. Along this reduction gradient N₂O and NO are also produced and partly emitted to the atmosphere (Anderson and Poth, 1989; Baggs and Philippot, 2010).

Both nitrification and denitrification produce N₂O and NO but are influenced differently by the same soil variables. Therefore, models predicting N₂O and NO fluxes need to consider both processes. Firestone and Davidson (1989) proposed a conceptual model – dubbed the “Hole-In-the-Pipe” (HIP) model – that uses two levels of control for N₂O and NO emissions in soils. The first level of control is nitrogen availability, symbolized as the amount of N flowing through the pipes. The second level of control is generally represented by the soil aeration status, explained as the size of the holes in the pipe through which N₂O and NO “leak” into the atmosphere. The HIP-model and its underlying assumptions were tested under distinct conditions, which showed that soil nitrogen availability could be expressed in different ways. Davidson et al. (2000) tested several indicators and found that the C/N ratio of litterfall and the ratio of NO₃⁻ to the sum of NO₃⁻ and NH₄⁺ were promising proxies of N cycling. Underlining the importance of rapid cycling N in N-oxide production, Purbopuspito et al. (2006) showed a good correlation between δ¹⁵N signatures of litter and soil and emissions of N₂O in Indonesia. Veldkamp et al. (1998) suggested that, in N-fertilized systems of Costa Rica, the major factor controlling N₂O emissions was the soil aeration status (second level of control), as N availability exceeded demand. The soil aeration status is commonly expressed by the water-filled pore space (WFPS) (Linn and Doran, 1984); with a high WFPS meaning a low aeration (Heinen, 2006). Nitric oxide is mainly produced when the WFPS is below field capacity, whereas N₂O is produced at higher WFPS, exceeding field capacity (Davidson et al., 1991, 1993; Dobbie et al., 1999; Davidson and Verchot, 2000; Bateman and Baggs, 2005). Depending on soil texture, the field capacity is at a WFPS of around 60 %; whenever the WFPS exceeds 80 %, most of the N is expected to be denitrified into N₂.

The goal of this study was to review how the emissions of N₂O and NO in the tropics were affected by LU and LUC and to examine their variation in relation to biophysical parameters. We used all studies published in the peer-reviewed literature up to 2013 to calculate emissions per LU type and evaluated relationships with environmental parameters. Next, the effect of LUC was assessed by using a quantitative meta-analysis statistical approach that allows for a comparison between independent studies, and weights studies according to their uncertainty (Hedges and Olkin, 1985). We used the

Hedges' *d* (Koricheva et al., 2013) metric to evaluate LUC effects. This is a standardized mean difference similar to the Hedges' *g* but adjusted for small sample sizes. Finally we ran a meta-analysis regression to express the changes in emission rates following LUC as a function of environmental and soil variables changes.

2 Material and methods

We followed three main steps to assess how soil N₂O and NO emissions were affected by LU and LUC in the tropics and subtropics: (i) compiling a database of all studies on soil N₂O and NO fluxes, selecting those integrating seasonal variation in their experimental design and categorizing LU types; (ii) estimating average emission rate per LU category and exploring biophysical factors affecting them; and (iii) characterizing the magnitude of emission change due to LUC using a meta-analysis approach and evaluating how this change could be expressed as a function of the change in biophysical factors through a meta-analysis regression.

2.1 Data collection and calculation

The database of Stehfest and Bouwman (2006) (available at: www.mnp.nl/en/publications/2006) was used as a basis for our research. From this data set, we extracted the 102 studies located in the tropics and subtropics (hereafter collectively referred to as "tropics"), defined as climate types 3–6, using the climate classification defined by De Pauw et al. (1996). We then extended the database by including 279 additional peer-reviewed studies published between 1990 and 2013 on soil emissions of NO and/or N₂O in the tropics. A combination of the following keywords were used in the ISI Web of Science and ScienceDirect search engines: N₂O, nitrous oxide, NO, nitric oxide, emissions, fertilizers, forest, arable, grasslands, flux, nitrification, denitrification, land use, NO_x, nitrogen-oxide, tropics, subtropics. As N₂O and NO fluxes are known to vary seasonally (e.g. Meixner et al., 1997; Chen and Huang, 2009), we manually selected the studies that measured the fluxes during both dry and wet seasons. The 103 studies selected (Supplement S1), representing 392 N₂O and 111 NO LU case studies, were used to estimate annual mean N-oxides emission rates per LU category and to analyze their relationship with environmental proxies. Out of the 104 papers 44 measured N₂O and/or NO emissions synchronically in at least two different LUs, one of which was a forest. These 44 papers represented 135 N₂O and 37 NO LUC case studies which were analyzed using a meta-analysis statistical approach (Supplement S2).

We summarized the number of studies and assessed the representation of LU per continent categorizing them in five geographical areas: North-Central America, South America, Africa, South Asia and Oceania. Average annual emission rates were expressed in kg NO-N or N₂O-N ha⁻¹ yr⁻¹ us-

ing the estimates provided by the papers. Whenever annual fluxes were not provided by the authors, we calculated them. For studies covering year-round measurements, the annual flux was calculated by scaling up the units from hours or days to a year and cm² or m² to ha. Where possible reported fluxes were weighed according to their time interval. For instance, for studies covering measurements made during the dry and wet seasons, the annual flux was calculated as the sum of each seasonal flux weighted by the number of days per year corresponding to each season. The biophysical variables associated with N₂O and NO emissions from the publications were also expressed as annual averages. Soil variables (temperature, WFPS, bulk density, pH, C content, N content, NH₄⁺ and NO₃⁻) are from the soil top layer (0–10 cm). Nitrogen fertilization and litterfall are given as a mass of nitrogen per hectare per year. In some cases the water-filled pore space (WFPS, %) was manually calculated as a function of the gravimetric water content (m, g g⁻¹ d.w.), bulk density (yr_d, g cm⁻³) and particle density (yr_s, g cm⁻³) as $WFPS = 100 \times (m \times yr_d) / (1 - (yr_d/yr_s))$ (Linn and Doran, 1984). A yr_s default value of 2.65 g cm⁻³ was used for mineral soils (Hillel, 1980), whenever not provided by the studies. Nitrogen fixation was considered by using a dichotomous variable indicating the presence or absence of N₂ fixing species in the LU. Nitrogen fixation rates were barely reported and could not be included. For studies measuring N₂O and NO simultaneously, we calculated the ratio and sum of the two and tested their correlation with WFPS and soil N availability. The latter is expressed as the relative fraction of NO₃⁻ to total inorganic N ($NO_3^- / [NO_3^- + NH_4^+]$).

Three LU case studies from Takakai et al. (2006) and the celery plot in Xiong et al. (2006) were excluded from the analysis because the very high fertilizations rates were about three times higher than the International Fertilizer industry Association (IFA) recommended dose for the studied crops.

2.2 Land use and land-use change characterization

The LU were classified into nine main categories: (1) forest (primary forest and secondary forest older than 30 years), (2) wetland forest (swamp on peat, swamp on mineral soil and riparian forest), (3) low forest cover (low canopy closure: woodlands and shrublands, secondary forest younger than 30 years), (4) degraded forest (human-induced low forest cover after logging and burning or fallows), (5) agroforestry systems, (6) plantations (mono-specific plantations, e.g. *Acacia*, rubber, oil palm, cinnamon), (7) pastures (pastures and grasslands), (8) rice fields, and (9) croplands (annual and perennial crops). For agroforestry, plantation, pasture, rice and cropland both fertilized and unfertilized cases were combined and the effect of fertilization was tested separately. Only a few studies included age after conversion in a chronosequential sampling design; therefore we pulled together LU cases from different studies to evaluate the change in emission rates as a function of time since conversion.

The studies either focused on a specific LUC type (e.g. forest conversion to pasture), or considered several LUC types which were representative for the study region. In the latter case, when only one control (forest) site was available, we used the same control for all converted sites. Whenever several control sites were available in a study we averaged the fluxes from all control sites. When a study measured emissions for several years, each year was considered a separate case. The following LUC were analyzed: forest to degraded forest, agroforestry, plantation, pasture and cropland; wetland forest to degraded forest, plantation, pasture and rice; degraded forest to agroforestry; low forest cover to plantation, pasture and cropland. The effect of primary forest conversion to secondary forest is not included in this study as secondary forest (>30-years old) and primary forest were merged into a single category. The same holds for logging impacts in degraded forests.

2.3 Statistics

Statistical analysis was performed using the software IBM SPSS Statistics for Windows 21.0 (IBM Corp. 2012) and statistical significance was set at a maximum probability level of 5%. The normality of the flux distribution was tested using the test of Shapiro-Wilks. Neither NO and N₂O nor their log-transformed values were normally distributed hence a generalized linear model with a post-hoc pair-wise comparison was performed for comparing the fluxes between LU. Throughout the text averages are followed by standard errors (\pm SE).

Stepwise multiple linear regression was performed to identify the environmental variables that were significantly related to soil fluxes of N₂O and NO. Variables available in <10% of all study cases were excluded to obtain a sufficient sample size for the regression. In order to maximize the data availability we used pair-wise exclusion for dealing with missing values. We also excluded predictor variables that were collinear (multicollinearity test, VIF statistics) to other variables already included in the model. A non-linear Gaussian function was fit between N₂O, NO fluxes and WFPS using averages per 10% WFPS intervals.

Meta-analysis

A meta-analysis was used to quantify the effect of LUC on soil annual N₂O and NO fluxes. For this we used the software Comprehensive Meta-Analysis version 2.2.064 (Biostat Inc., New Jersey, USA) and MetaWin 2.0 (Sinauer Associates, Sunderland, Massachusetts). We defined N₂O or NO emissions after land-use change as being the treatment and N₂O or NO emissions before land-use change as being the control. Hedges' d (d) was used as metric to evaluate the effect size

of LUC on N₂O and NO fluxes. This metric is defined as:

$$d = \frac{(\bar{X}_T - \bar{X}_C)}{S} \times J \quad (1)$$

$$S = \sqrt{\frac{(N_C - 1)(SD_C)^2 + (N_T - 1)(SD_T)^2}{N_C + N_T - 2}} \quad (2)$$

$$J = 1 - \frac{3}{4(N_C + N_T - 2) - 1} \quad (3)$$

where \bar{X}_T and \bar{X}_C are the average N₂O or NO flux (in kg N ha⁻¹ yr⁻¹) of the treatment and control, respectively; S is the pooled standard deviation from the control and treatment flux standard deviations (SD_C and SD_T) and J is the correction factor calculated from the sample sizes (N_T and N_C). The effect size (d) for all LUC case studies combined, or that for a particular LUC type, was assessed using a random model which allows for a varying true effect size between studies (Gurevitch and Hedges, 1999; Borenstein et al., 2009). A d equal or smaller than 0.2 indicates a small effect size, a d around 0.5 a medium one and a $d > 0.8$ a large effect. Positive and negative d 's respectively imply an increase and decrease in N₂O or NO emission after LUC, respectively.

Calculation of d requires knowledge of the standard deviation and sample size associated with the average N₂O or NO flux rate. Whenever these were not available in the publication we contacted the authors, calculated it ourselves using the methodological description of the experimental design or measured it from the figures of the papers using PlotDigitizer 2.5.1 (Huwaldt, 2011).

Publication bias for studies with significant and/or high effect sizes was assessed using a normal quantile plot (Wang and Bushman, 1998). Deviation from linearity of the observed distribution suggests publication bias while gaps in the plotted scatter plot indicate that certain effect sizes are missing in the published literature (Borenstein, 2009).

Heterogeneity of effect sizes was assessed with the Q and I^2 statistics. A significant Q_{overall} means that the variance among LUC study cases is greater than that expected by sampling. In a heterogeneous data set, the $(1 - I^2)$ statistic quantifies the variation within case studies and I^2 the variation that could be explained by other variables (or "real variation"). I^2 of 25, 50, 75% are, respectively considered as low, moderate and high (Borenstein, 2009). An $I^2 > 0$ shows that a proportion of the observed variation is real; thus, subgroup division into LUC types and/or meta-analysis regression can be used (Gurevitch and Hedges, 1999). LUC effect sizes obtained from a low sample size are likely to be influenced by random deviations; hence their interpretation should be handled with caution.

Finally, we performed a meta-analysis regression (or "meta-regression") (Higgins and Green, 2011) to assess how the changes in environmental factors affected changes in soil N₂O or NO emission as a result of LUC. We looked at how

the standardized mean difference of an environmental parameter was affecting that of soil N₂O or NO emissions. A meta-analysis regression is considered robust when it includes ten case studies at least (Borenstein, 2009; Higgins and Green, 2011).

3 Results

3.1 Exploring the data set

The publication rate of peer-reviewed papers on LU and soil emissions of N₂O and NO in the tropics has more than doubled over the past decade (less than 2 publications yr⁻¹ before 2000, more than 5 yr⁻¹ afterwards), but remains low. The Americas (combining North-Central and South America) and South Asia represented the majority of the data set ($n = 229$ and $n = 137$), while Africa and Oceania were underrepresented ($n = 21$ and $n = 35$, respectively; Fig. 1).

LU types studied varied substantially across continents (Fig. 1). In South Asia 61 % of the LUs studied were croplands, rice fields or plantations, while these were only 13 % in South America. Some LUs were geographically well represented while others were clustered in one continent. For instance, agroforestry systems were spatially well represented, although few in numbers ($n = 8$), while rice paddies were mostly studied in Asia. Studies on wetland forest were underrepresented ($n = 7$) and restricted to South Asia (Fig. 1a).

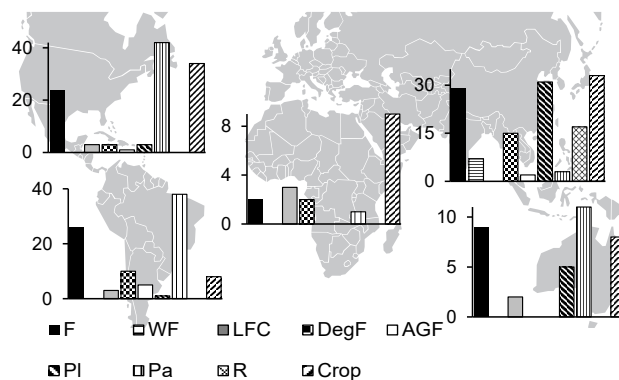
Ninety-four percent of the LU case studies on soil fluxes of NO were in North-Central and South America (respectively, $n = 62$ and $n = 36$). In Africa and South Asia, respectively, only five and eight LU case studies were found, while Oceania had no measurements at all.

3.2 Average land-use emissions and environmental parameter values

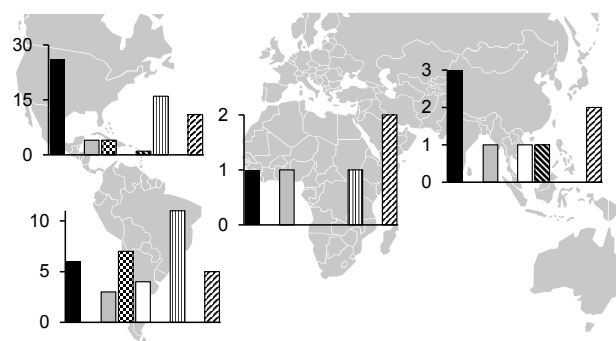
Neither N₂O nor NO fluxes were normally distributed and about 90 % of the observations were below 10 kg N₂O-N and 8 kg NO-N ha⁻¹ yr⁻¹. Table 1 shows average annual N₂O and NO emissions per LU and environmental parameter associated. Croplands displayed the highest N₂O emission rate and also the highest average N fertilization rate. Both pastures and rice fields had relatively high N₂O emissions; however, these were characterized by a high variation. The average NO emission rates did not show any significant difference between LU.

The availability of environmental parameters in studies on N-oxides emissions was variable. For example, only 4 % of the studies reported nitrogen input through litterfall, while precipitation was given in 91 % of all cases. Although the comparison of values from different data sources may generate inconsistencies, some generalizations per LU category can be made. Overall, intact forest had a significantly lower bulk density compared to more compacted soils from pastures. Wetland forest soils had a significant lower bulk den-

(a) Nitrous oxide LU study cases



(b) Nitric oxide LU study cases



(c) LUC study cases

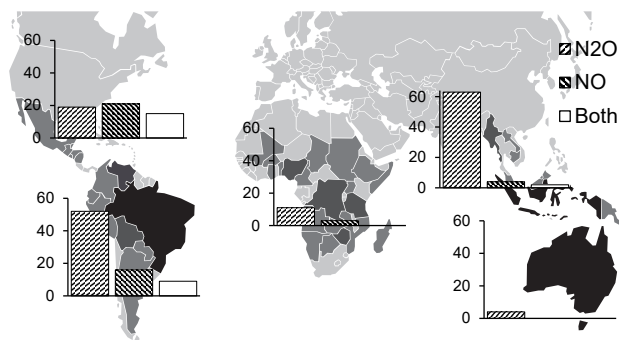


Figure 1. Spatial distribution of land use case studies on soil fluxes of (a) N₂O and (b) NO per land use category in the tropics. Land uses are abbreviated as F: forest, WF: wetland forest, LFC: low forest cover, DegF: degraded forest, AGF: agroforestry, PI: plantation, Pa: pasture, R: rice and Crop: cropland. y axes of the diagrams represent number of case studies per land use. Land use case studies from Europe are omitted ($n = 2$). (c) Spatial distribution of land-use change case studies on soil N₂O and NO fluxes, compared to a map of annual loss of forest area by country between 2005 and 2010. The four shades of grey, from black to light grey, respectively represent > 500, 500–250, 250–50 and < 50 net loss of area in 1000 ha. Adapted from FAO (2010).

Table 1. Average of annual N₂O and NO emissions in the Tropics and associated environmental parameter values. Land uses are F: forest, WF: wetland forest, LFC: low forest cover, DegF: degraded forest, AGF: agroforestry, Pl: plantation, Pa: pasture, R: rice and Crop: cropland. NA: not available, no nitric oxide cases were available for WF. Standard error and sample size are indicated in brackets, # indicates no statistics were possible. Letters in superscript indicate significant differences among land uses, whenever differences were not significant no letter was indicated.

Land use	Flux (kg N ha ⁻¹ yr ⁻¹)	Annual precipitation (mm)	Annual temperature (°C)	Soil temperature (°C)	WPPS (%)	Bulk density (g d.w. cm ⁻³)	Nitric oxide						
							pH	NH ₄ ⁺ (µg N g ⁻¹ d.w.)	NO ₃ ⁻ (µg N g ⁻¹ d.w.)	C (%)	N (%)	Fertilization (kg N ha ⁻¹ yr ⁻¹)	Litterfall (kg N ha ⁻¹ yr ⁻¹)
F	2.0 ^a (0.2, 90)	2226 (81, 90)	22.8 (0.4, 80)	23.7 ^{ab} (0.5, 29)	56.1 (3.4, 45)	0.9 ^a (0.0, 58)	4.9 ^{abc} (0.1, 55)	20.5 ^a (2.8, 47)	10.8 ^a (1.5, 45)	4.8 ^a (0.5, 45)	0.4 ^a (0.0, 45)	0 ^a (0, 87)	100 (17, 14)
WF	2.7 ^{ab} (1.9, 7)	2485 (167, 6)	26.1 (0.4, 6)	26.8 ^{ab} (0.5, 4)	44.5 (7.7, 3)	0.1 ^b (0.0, 4)	3.8 ^a (0.2, 7)	412.0 ^b (119.9, 4)	70.9 ^b (12.2, 5)	4.9 ^{7b} (3.2, 7)	1.6 ^b (0.1, 7)	0 ^{ab} (0, 7)	n.a.
LFC	0.5 ^{ab} (0.1, 11)	1546 (390, 11)	23.9 (1.6, 9)	28.8 ^{ab} (1.2, 3)	47.7 (10.6, 8)	1.1 ^{ac} (0.1, 10)	5.0 ^{abc} (0.3, 11)	5.1 ^a (1.1, 8)	3.1 ^a (1.1, 8)	4.0 ^a (0.9, 8)	0.3 ^a (0.1, 8)	0 ^{ab} (0, 10)	n.a.
DegF	1.9 ^{ab} (0.5, 30)	2220 (123, 30)	25.1 (0.4, 28)	27.6 ^a (0.6, 14)	48.4 (5, 19)	0.9 ^a (0.1, 24)	4.4 ^{ab} (0.2, 23)	44.4 ^a (17.4, 20)	11.6 ^a (4.1, 20)	30.0 ^c (6.2, 20)	0.9 ^c (0.1, 20)	0 ^{ab} (0, 26)	122 (54, 3)
AGF	3.4 ^{ab} (1.6, 8)	2297 (112, 8)	25.2 (0.8, 6)	22.1 ^{ab} (2.3, 2)	77.1 (17.2, 3)	1.2 ^{ac} (0.1, 8)	5.6 ^{bcd} (0.3, 7)	10.7 ^a (4.6, 7)	7.8 ^{ab} (3.1, 7)	2.8 ^a (0.5, 3)	0.3 ^{ac} (0.1, 3)	39 ^{abc} (31, 8)	218 (#, 1)
Pl	1.5 ^{ab} (0.3, 40)	2120 (137, 40)	24.3 (0.6, 38)	25.5 ^{ab} (0.6, 22)	59.0 (3.4, 26)	1.0 ^{ac} (0.1, 27)	4.8 ^{abc} (0.1, 37)	11.9 ^a (2.3, 30)	17.8 ^{ab} (8.2, 27)	6.7 ^a (2.2, 30)	0.4 ^a (0.1, 31)	53 ^{ab} (25, 35)	30.4 (153, 5)
Pa	5.2 ^{ab} (1.3, 97)	1913 (89, 90)	23.4 (0.5, 54)	26.3 ^{ab} (1.9, 8)	64.2 (4.6, 18)	1.2 ^c (0.5, 4)	5.4 ^{cd} (0.1, 49)	26.1 ^a (4.2, 29)	2.6 ^{9ab} (13.7, 29)	5.1 ^a (1.8, 41)	0.3 ^a (0.39)	90 ^{bd} (17, 70)	n.a.
R	5.1 ^{ab} (1.7, 17)	1562 (234, 13)	21.9 (1.9, 13)	20.9 ^b (2.4, 5)	73.0 (1.2, 3)	1.2 ^{ac} (0.4)	6.0 ^d (0.3, 17)	788.01 (#, 1)	29.4 ^{ab} (2.0, 2)	13.6 ^a (5.2, 17)	0.5 ^{ac} (0.1, 17)	228 ^c (61, 17)	n.a.
Crop	8.6 ^b (2.0, 92)	1965 (123, 76)	24.4 (0.6, 60)	25.3 ^{ab} (1.1, 23)	58.1 (5.2, 28)	1.1 ^{ac} (0.1, 44)	5.7 ^{de} (0.1, 78)	21.3 ^a (10.9, 36)	12.2 ^a (2.6, 36)	7.5 ^a (1.6, 55)	0.4 ^a (0.55)	155 ^{cd} (25, 92)	77 (28, 2)
Nitric oxide													
F	1.7 (0.5, 36)	2342 (166, 35)	21.6 ^a (0.8, 30)	24.9 ^a (0.4, 13)	60.1 (4.5, 24)	0.75 ^a (0.07, 24)	5.3 (0.3, 25)	15.4 (2.5, 21)	12.2 ^a (2.0, 21)	5.1 ^a (0.7, 15)	0.4 (0.1, 19)	0 ^{ab} (0, 36)	79 (16, 10)
DegF	2.9 (1.9, 20)	2119 (281, 19)	25.4 ^{b,c} (0.9, 12)	26.4 ^{ab} (0.8, 9)	53.7 (7.8, 11)	1.08 ^b (0.09, 17)	5.6 (0.3, 17)	15.1 (3.1, 13)	5.6 ^{ab} (1.5, 13)	3.1 ^{ab} (0.8, 13)	0.3 (0.1, 10)	0 ^b (0, 20)	68 (6, 2)
AGF	2.3 (0.8, 5)	2219 (147, 5)	26.0 ^{ac,d} (0.0, 4)	24.4 [#] (#, 1)	56.0 (#, 1)	1.32 ^b (0.03, 5)	5.9 (0.2, 5)	9.5 (4.6, 4)	4.9 ^{ab} (3.1, 4)	2.5 (#, 1)	0.2 (#, 1)	12 ^{bcd} (12, 5)	n.a.
Pl	5.4 (5.3, 2)	2124 (1839, 2)	21.4 ^{ac,d} (4.4, 2)	n.a.	70.0 (#, 1)	1.23 ^{ab} (0.43, 2)	7.6 (#, 1)	n.a.	n.a.	n.a.	n.a.	180 ^c (180, 2)	n.a.
Pa	2.6 (0.7, 28)	2279 (252, 26)	25.5 ^{b,d} (0.1, 13)	27.8 ^b (0.7, 8)	66.8 (6.0, 14)	1.22 ^b (0.07, 16)	5.8 (0.3, 17)	27.0 (5.9, 17)	5.4 ^b (1.1, 17)	1.2 ^b (0.4, 13)	0.2 (0.1, 6)	91 ^{ce} (26, 26)	n.a.
Crop	3.1 (0.8, 20)	1686 (268, 14)	24.7 ^{ac,d} (1.1, 3)	27.8 ^b (0.4, 11)	43.0 (12.3, 6)	1.31 ^b (0.09, 13)	5.7 (0.2, 20)	28.2 (14.5, 12)	12.1 ^{ab} (2.3, 12)	2.5 ^{ab} (1.0, 9)	0.3 (0.1, 4)	88 ^{cd} (17, 20)	n.a.

¹ Including 10 degraded peat forests, soil carbon content for non-peat soils was 3.8.

sity compared to all other soils. Wetland forest soils were more acidic than other soils in general, while cropland soils were significantly less acidic than forest soils. Mineral N content did not differ significantly between LU, except for high NH₄⁺ and NO₃⁻ concentrations in wetland forest and rice paddy soils. Plantation soils were the only ones where NO₃⁻ concentrations exceeded those of NH₄⁺, other LU showed the opposite trend. Carbon and nitrogen content in the soils of natural wetland forest were very high and significantly higher than that in all other LUs. Degraded forest soils showed a high carbon content which is due to the inclusion of eleven degraded peat forests out of the twenty cases. Excluding them resulted in a soil carbon content of 3.8 %.

The multiple linear regression analysis indicated that N fertilization, WFPS, and N availability (expressed as $[\text{NO}_3^- / (\text{NO}_3^- + \text{NH}_4^+)]$) were the best proxies for estimating overall soil fluxes of N₂O (Table 2). For agricultural sites (i.e. crop and pasture) N fertilization rate explained part of the variation ($R^2 = 0.31$, $df = 160$, $p < 0.01$); but (pair-wise) including the WFPS more than doubled the R squared. Proxies for overall soil NO fluxes were N availability and N fertilization. For agricultural sites N fertilization explained 31 % of the variation in NO fluxes, and the inclusion of the WFPS did not improve the relationship. In non-agricultural LUs a non-linear Gaussian function of the WFPS simulated with good fit N₂O and NO fluxes (Fig. 2, Table 2). The relationship indicates that NO and N₂O fluxes peak at WFPS of 45 and 61 %, respectively. The ratio of N₂O to NO displayed an exponential relationship with the WFPS (Fig. 3, Table 2), which indicates N-oxide emissions predominantly in the form of N₂O (i.e. N₂O / NO > 1) above a WFPS of 48 %. In non-agricultural sites the predominance of N₂O over NO happens at a slightly lower WFPS (46 %). The sum of soil N₂O and NO emissions also increased exponentially with increasing N availability.

Time since conversion was available in 26 % of the LU cases only. Nitrous oxide fluxes from non-fertilized croplands appeared to be higher the first 10 years after conversion and thereafter decreasing, whereas fluxes from fertilized croplands remained high (Fig. 4). For pastures the pattern was less apparent, the first years after conversion both high and low fluxes were observed.

3.3 Land-use change effects on N₂O and NO emissions and environmental parameters

Land-use change effects were evaluated by looking at differences in emissions after and before LUC. This was done for each LUC type and for all LUC combined. The effect sizes of LUC on N₂O emissions were not strictly normally distributed; however, all effect size ranges were present. Deviation from linearity occurred for high and low effect sizes indicating a potential bias for published studies measuring large effects following LUC. A normal quantile plot for NO emissions as affected by LUC indicated a normal distribu-

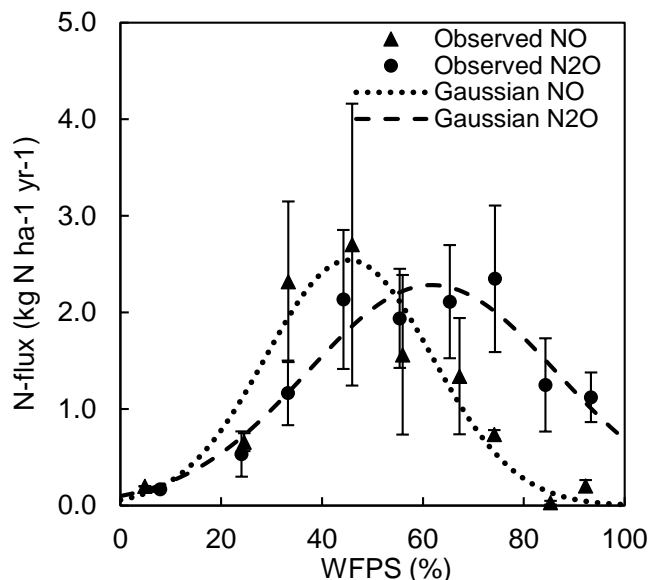


Figure 2. Gaussian relationships (dashed lines) between the WFPS and N₂O and NO emissions in non-agricultural land uses. N₂O and NO fluxes are averaged in 10 % WFPS intervals. Error bars are N flux standard errors in each WFPS interval.

tion; however, some gaps were present in the observed values, possibly due to a biased representation of NO emission changes in the literature.

Nitrous oxide emissions were not affected overall by LUC ($d = 0.11 \pm 0.11$); the slight increasing trend was not significant because of opposing effects in different LUC trajectories (Table 3). The LUC case studies overall did not share a common effect size ($Q_{\text{overall}} = 221.3$, $P < 0.01$) and the majority of the variation was within case studies ($1 - I^2$, 59 %). Similarly to N₂O emissions, and for the same reason, NO emissions were not overall affected by LUC; with a homogeneous effect size ($Q_{\text{overall}} = 31.7$, $P = 0.67$) and 47 % of the variation within LUC case studies ($1 - I^2$).

Most studies focused on forest clearing for croplands ($n_{\text{F-Crop}} + n_{\text{WF-Crop}} + n_{\text{DegF-Crop}} = 44$) and pastures ($n_{\text{F-Pa}} + n_{\text{WF-Pa}} + n_{\text{DegF-Pa}} = 42$). Transition from intact upland forest to croplands significantly increased N₂O emissions, while conversion to agroforestry showed a slight, but insignificant increasing trend. Intact forest conversion to pasture (F-Pa) tended to decrease N₂O emissions, whereas low forest cover conversion to pasture (LFC-Pa) showed the opposite trend. Further, conversion of low forest cover significantly increased NO emissions overall.

The Hedges' d effect size of forest conversion to fertilized LU amounted to 1.03 ± 0.31 and 0.52 ± 0.23 for N₂O and NO, respectively, indicating significant and high increased emissions after fertilization. Evidence for increased emission following conversion to LU with N fixing crops/trees was weak and fluxes of NO slightly raised but not significantly ($d_{\text{NO}} = 0.61 \pm 0.33$, $n = 8$).

Table 2. Multiple regression between soil N₂O or NO emissions and associated environmental parameters; and meta-analysis regression between the standardized differences after and before land-use change of N₂O emissions (or Hedges' *d*, d_{N_2O}) and of environmental factors ($d_{N_{available}}$, d_{WFPS}). The models are presented with slope and intercept \pm SE; *P* values are indicated with * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$. All regression models were significant ($p \leq 0.01$).

LU	R ²	df	Model
Linear regression LU study cases			
All	0.39	125	$\text{Ln}(N_2O + 1.2) = 0.002^{***} \pm 0.0004 \times N_{\text{fertilization}} + 0.87^{**} \pm 0.29 \times N_{\text{available}} + 0.014^{***} \pm 0.003 \times \text{WFPS} - 0.11^{\text{ns}} \pm 0.22$
Agr ^a	0.83	40	$\text{Ln}(N_2O + 1.2) = 0.008^{***} \pm 0.0007 \times N_{\text{fertilization}} + 0.017^{***} \pm 0.003 \times \text{WFPS} - 0.28^{\text{ns}} \pm 0.26$
Non-Agr ^b	0.17	80	$\text{Ln}(N_2O + 1.2) = 0.87^{**} \pm 0.27 \times N_{\text{available}} + 0.008^{***} \pm 0.003 \times \text{WFPS} - 0.15^{\text{ns}} \pm 0.21$
All	0.18	64	$\text{Ln}(\text{NO}) = 2.27^{**} \pm 0.80 \times N_{\text{available}} + 0.0085^* \pm 0.0039 \times N_{\text{fertilization}} - 1.42^{***} \pm 0.35$
Agr ^a	0.31	44	$\text{Ln}(\text{NO}) = 0.0081^{***} \pm 0.0019 \times N_{\text{fertilization}} - 0.65^* \pm 0.26$
Non-Agr ^b	0.20	36	$\text{Ln}(\text{NO}) = 3.02^{**} \pm 1.02 \times N_{\text{available}} - 1.67^{**} \pm 0.47$
Gaussian regression WFPS			
Non-Agr ^b	0.90	102	$N_2O = 2.3 \times \exp(-0.5 \times ((\text{WFPS}^c - 61.8)/24.7)^2)$
Non-Agr ^b	0.89	36	$\text{NO} = 2.5 \times \exp(-0.5 \times ((\text{WFPS}^c - 45.3)/16.5)^2)$
HIP model regression			
All	0.48	40	$\text{Log}(1 + N_2O + \text{NO}) = 0.92^{***} \pm 0.15 \times N_{\text{available}} + 0.15^* \pm 0.06$
All	0.39	42	$\text{Log}(1 + N_2O / \text{NO}) = 0.0129^{***} \pm 0.003 \times \text{WFPS} - 0.32^{\text{ns}} \pm 0.18$
Non-Agr ^b	0.40	29	$\text{Log}(1 + N_2O / \text{NO}) = 0.0125^{***} \pm 0.003 \times \text{WFPS} - 0.27^{\text{ns}} \pm 0.20$
Meta-analysis regression LUC study cases			
All	0.23	89	$d_{N_2O} = 0.65^{**} \pm 0.14 \times d_{N_{available}} - 0.04 \pm 0.13$
All	0.15	69	$d_{N_2O} = 0.55^{**} \pm 0.22 \times d_{WFPS} + 0.05 \pm 0.16$

N₂O and NO are expressed in kg N₂O-N yr⁻¹ or N-NO ha⁻¹ yr⁻¹, N_{available} is (NO₃⁻ / [NO₃⁻ + NH₄⁺]) without units, NO₃⁻ and NH₄⁺ in μg N g⁻¹ d.w., N_{fertilization} in kg N ha⁻¹ yr⁻¹ and WFPS in %.
^a Agr includes cropland and pasture. ^b Non-Agr includes forest, low forest cover, degraded forest, agroforestry and plantation. ^c WFPS intervals of 10 %.

The results of the meta-regression, which was run pooling all LUC case studies together, are presented in Table 2. The change in N₂O fluxes as affected by LUC was positively related to changes in N availability and WFPS. No significant relationships were found for NO. The interactive effect of WFPS and N availability change on N₂O flux change is illustrated in Fig. 5. Whenever N availability increased after LUC ($d_{N_{available}} > 0$) the increase in N₂O emissions ($d_{N_2O} > 0$) was exacerbated if the WFPS also increased ($d_{WFPS} > 0$), or diminished if the WFPS was decreased ($d_{WFPS} < 0$). The slope of the regression between d_{N_2O} and $d_{N_{available}}$ was raised by 143 % for the $d_{WFPS} > 0$ cases, reduced by 58 % for $d_{WFPS} < 0$ cases.

4 Discussion

4.1 Data set representativeness and average annual LU emissions

The body of research on LULUC and N₂O and NO emissions in the Tropics has increased during the past decade; however, Africa and Oceania remain strongly underrepresented. Most of Africa's LU case studies were from (converted) savannahs although Africa has a variety of forest types unaccounted for at present in the literature. Furthermore, a comparison between the spatial distribution of LUC case studies and global forest conversion for 2005–2010 (FAO, 2010) shows that highest deforested areas overlapped well with studies on N

emissions from LUC except for Oceania and Africa (Fig. 1c). These regions need more research on soil N₂O and NO emissions, in representative LULUC categories. Sampling bias was not only geographical; some biofuel or food crops such as oil palm and soy were also underrepresented ($n_{oil\ palm} = 7$ and $n_{soy} = 4$) although they are the most rapidly expanding perennial and annual crop in the tropics (Phalan et al., 2013). Land-use change categories were also not equally represented; there was a dominance of studies on forest conversion to croplands and pastures. Only a few cases (10–13 %) assessed the effect of nitrogen fertilization or the use of N-fixing species after LUC. Those studies took place in Latin America (Matson et al., 1996; Veldkamp and Keller 1997; Veldkamp et al., 1998) and Asia (Verchot et al., 2006; Veldkamp et al., 2008). Some wetland forest conversion study cases showed high effect sizes for N₂O emissions (Hadi et al., 2005; Furukawa et al., 2005; Jauhiainen et al., 2012), but the overall tendency of wetland forest conversion to increase N₂O emissions was not significant (Table 3) as observed by Hergoualc'h and Verchot (2014). However, the sample size was small and none of the converted case studies were fertilized or intensively monitored following fertilization. Future research direction should consider conversion to fertilized land uses, using an experimental design adequate for capturing fertilization effects on N oxide emissions, and wetland forests in and outside of South Asia. Likewise, few papers studied forest degradation; a topic that needs more attention (Mertz et al., 2012).

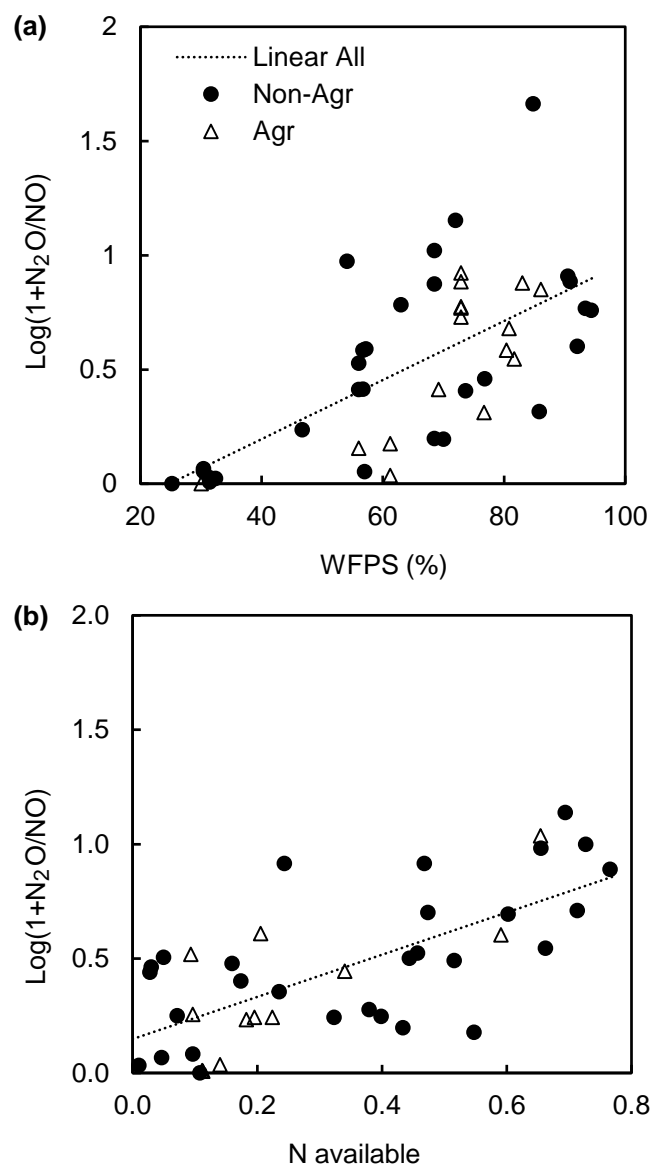


Figure 3. Relationships between (a) the WFPS and the ratio of N₂O to NO; (b) $N_{\text{available}}$ ($\text{NO}_3^- / [\text{NO}_3^- + \text{NH}_4^+]$) and the sum of N₂O and NO. The domains of definition are (a) [0.02; 44.71] in N₂O to NO ratio and [30.4; 94.4] in WFPS; (b) [0.00; 12.80] in N₂O + NO ($\text{kg N ha}^{-1} \text{ yr}^{-1}$) and [0.01; 0.77] in $N_{\text{available}}$.

The annual N₂O emission rate in intact upland forest ($2.0 \pm 0.2 \text{ kg N}_2\text{O-N ha}^{-1} \text{ yr}^{-1}$, $n = 88$) is more than twice the value estimated by Stehfest and Bouwman (2006) ($0.85 \text{ kg N}_2\text{O-N ha}^{-1} \text{ yr}^{-1}$, $n = 77$) for the tropics. We excluded the cases considered by Stehfest and Bouwman (2006) that did not cover seasonal variation, but ended up with a higher sample size by adding studies published after 2005. Our value is also larger than the model estimations of $1.4 \text{ kg N}_2\text{O-N}$ by Potter et al. (1996) and $1.2 \text{ kg N}_2\text{O-N ha}^{-1} \text{ yr}^{-1}$ by Werner et al. (2007). Dalal and Allen (2008) estimated average emissions in tropical for-

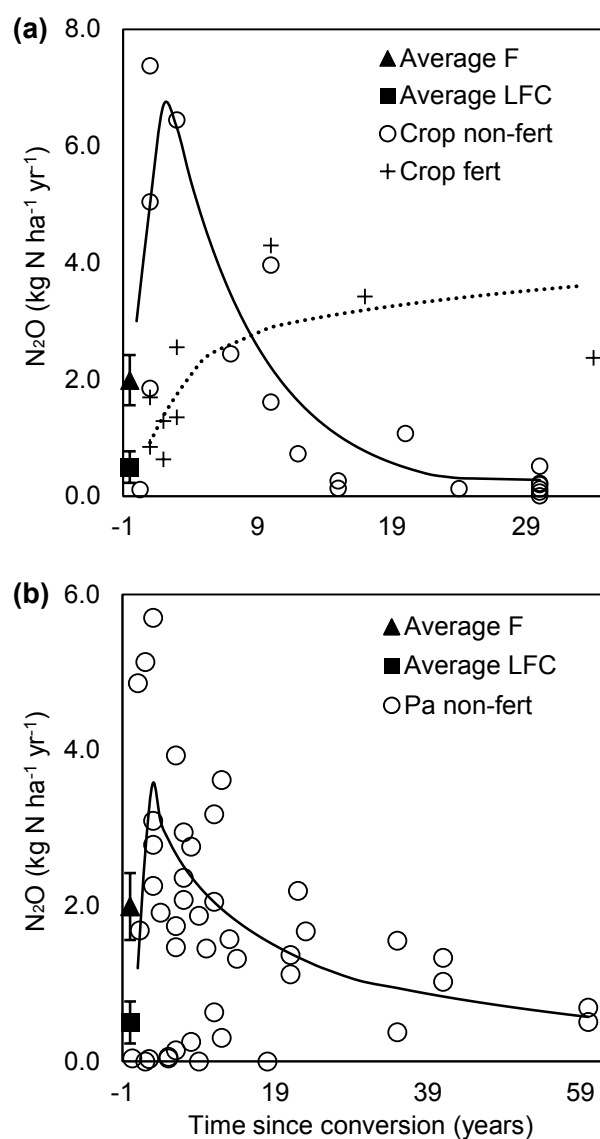


Figure 4. Effect of time since conversion on N₂O fluxes in (a) croplands and (b) pastures. Average N₂O flux and 95 % confidence intervals are given for upland forests (triangle) and low canopy forests (square). The solid and dashed lines represent a conceptual trend for non-fertilized and fertilized cases, respectively.

est of $3.0 \pm 0.52 \text{ kg N}_2\text{O-N ha}^{-1} \text{ yr}^{-1}$ ($n = 22$) and Kim et al. (2013a, b) of $1.91 \text{ kg N} \pm 0.25$ ($n = 69$). The annual NO emission rate in tropical forest amounts to $1.7 \pm 0.48 \text{ kg N-NO ha}^{-1} \text{ yr}^{-1}$ ($n = 36$), which is higher than previous estimates by Stehfest and Bouwman (2006) ($0.39 \text{ kg NO-N ha}^{-1} \text{ yr}^{-1}$, $n = 33$), Davidson and Kingerlee (1997) ($0.8 \text{ kg NO-N ha}^{-1} \text{ yr}^{-1}$, $n = 15$) and Potter et al. (1996) ($1.2 \text{ kg NO-N ha}^{-1} \text{ yr}^{-1}$).

Nitrous oxide emission in agricultural fields and pastures reported by Duxbury et al. (1982) were the largest in the entire data set (average emissions of $65 \text{ kg N}_2\text{O-N ha}^{-1} \text{ yr}^{-1}$). The study was conducted in Florida on drained organic

Table 3. Hedges' $d \pm \text{SE}$ (n) of N₂O ($d_{\text{N}_2\text{O}}$) and NO (d_{NO}) emission change following land-use change (LUC). Hedges' d is the standardized mean difference of N₂O (or NO) flux rates after and before LUC. A $d < 0$ indicates a reduction in emission; a $d > 0$ an increase. Land uses are: F-forest, WF-wetland forest, LFC-low forest cover, DegF-degraded forest, AGF-agroforestry, Pl-plantation, Pa-pasture, R-Rice and Crop-cropland.

LUC	$d_{\text{N}_2\text{O}}$	d_{NO}
F-DegF	0.09 ± 0.29 (15)	0.08 ± 0.34 (5)
F-AGF	0.34 ± 0.29 (4)	– (1) ^a
F-Pl	0.06 ± 0.37 (12)	–
F-Pa	–0.28 ± 0.17 (36)	–0.56 ± 0.67 (9)
F-Crop	0.78* ± 0.24 (19)	– (2) ^a
Overall F	0.11 ± 0.14 (86)	–0.19 ± 0.37 (17)
WF-DegF	–0.17 ± 0.31 (9)	–
WF-Pl	1.07 ± 0.42 (3)	–
WF-Pa	2.37 ± 1.80 (3)	–
WF-R	–0.06 ± 0.62 (9)	–
Overall WF	0.31 ± 0.34 (24)	–
DegF-AGF	0.27 ± 0.19 (4)	0.72 ± 0.28 (4)
LFC-Pl	– (2) [#]	–
LFC-Pa	0.47 ± 0.37 (3)	–0.06 ± 0.31 (5)
LFC-Crop	–0.29 ± 0.40 (16)	0.57* ± 0.09 (11)
Overall LFC ^b	–0.07 ± 0.25 (25)	0.44* ± 0.13 (20)
Overall LUC	0.11 ± 0.11 (135)	0.16 ± 0.19 (37)
Fertilization ^c	1.03* ± 0.31 (17)	0.52* ± 0.23 (12)
N fixation ^c	–0.14 ± 0.33 (13)	0.61 ± 0.33 (8)

* $p < 0.05$; no statistics calculated for studies with $n < 3$. ^a no statistics possible. ^b including 4 DegF-AGF LUC cases. ^c Fertilization and N fixation indicate cases of forest conversion to fertilized LU and LU with N₂ fixing trees/crops.

soils under crops, grass or kept as fallows; that displayed high N mineralization rates (600–1200 kg N ha^{–1} yr^{–1}). Excluding them decreases the overall average N₂O emissions from 4.4 ± 0.6 ($n = 387$) to 3.5 ± 0.3 kg N₂O-N ha^{–1} yr^{–1} ($n = 381$), and croplands emissions from 8.6 ± 2.0 ($n = 93$) to 5.8 ± 0.9 kg N₂O-N ha^{–1} yr^{–1} ($n = 88$).

4.2 Land-use change effects on the emissions

According to the meta-analysis LUC overall increased N₂O and NO emissions, albeit not significantly. Land-use change types or practices that induced significant changes in emissions all pointed towards increased rather than decreased emissions. The meta-analysis confirmed that intact upland forest conversion to croplands and nitrogen fertilization after LUC significantly and highly increased soil emissions of N₂O. It also corroborated high increases in NO emissions after low forest cover conversion in general and when fertilizer is applied after LUC. For most LUC trajectories the effect of emission change was not significant even when the sample size was relatively large. For instance, the analysis indicated a trend of decreased N₂O emissions following in-

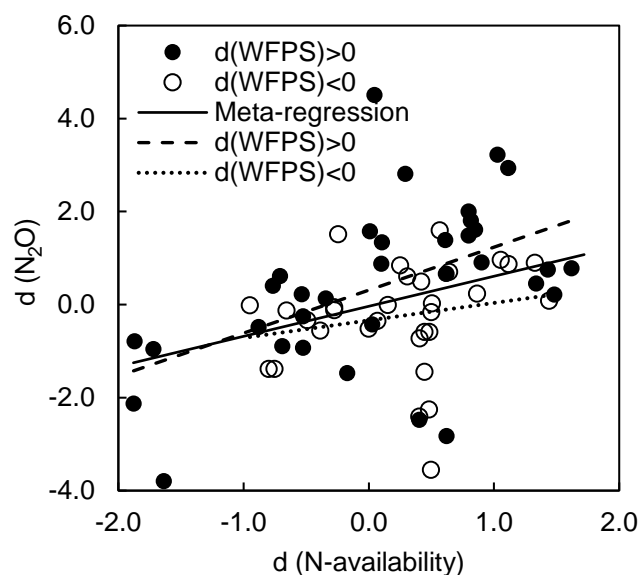


Figure 5. N₂O Hedges' d as affected by the interactive changes in N_{availability} and WFPS. The meta-analysis regression between $d_{\text{N}_2\text{O}}$ and $d_{\text{Navailability}}$ was performed for all cases (solid line) and for cases when $d_{\text{WFPS}} > 0$ or $d_{\text{WFPS}} < 0$ (dashed lines). Closed and open circles represent increased and decreased WFPS, respectively.

tact upland forest conversion to pasture, which was not significant since the LUC studies not all agreed on the direction of change. Several publications reported decreased emissions after conversion to pasture (e.g. Verchot et al., 1999; Erickson et al., 2001; Garcia-Montiel et al., 2001), others reported the opposite (e.g. Melillo et al., 2001; Takakai et al., 2006) and one showed no effect (Neill et al., 2005). These apparent contradicting results have been explained by differences or absence of differences in time after conversion (Keller et al., 1993; Veldkamp et al., 1999; Verchot et al., 1999; Neill et al., 2005; Wick et al., 2005), or the optional practice of slash and burn technique to clear the forest, both affecting N cycling (Luizao et al., 1989; Matson et al., 1990; Steudler et al., 1991; Keller and Reiners, 1994; Neill et al., 1995; Melillo et al., 2001; Garcia-Montiel et al., 2001). Biomass burning produces N₂O during fires and may enhance soil N₂O afterwards by stimulating N mineralization (Skiba and Smith, 2000). The paucity of field observations together with the lack of land-use history description did not allow to evaluate clearing practices effects or temporal trends in soil emission dynamics with LUC thoroughly. For non-fertilized croplands and pastures, the fluxes of N₂O tended to increase during the first 5 to 10 years after conversion and thereafter tended to decrease to average upland forest or low canopy forest levels (Fig. 4). In fertilized croplands, however, flux rates remained at a high level even beyond this period. Soil physical disturbance following land clearing, high N inputs associated with clear-felling and soil preparation (e.g. compaction, drainage in wetland) all combined may be at the origin of the 5 to

10-year emission peak. In fertilized croplands on the other hand, the sustained emission increase seems to be driven by high mineral N inputs. This temporal variability in emission change indicates that the first 10 years following LUC are crucial for GHG budget calculations.

We used a meta-analysis statistical approach to assess the trend and magnitude of forest conversion on soil emissions of N oxides. Meta-analysis consists in comparing site-specific (pair-wise) effects weighted according to their robustness, therefore it provides a direction and a magnitude of emission change more reliable and precise than those obtained by comparing average emission rates per LU category from individual papers. For example, the meta-analysis effect on N₂O emissions of intact upland forest conversion to croplands (0.78) was much higher than the effect calculated (0.48) using average values from Table 1 and Eq. (1). The effect calculated from average emission rate derived from individual studies can also lead to misleading conclusions such as in the case of intact upland forest conversion to pasture. The effect calculated from average emissions (0.34) was positive indicating increased emissions as opposed to the meta-analysis conclusion (−0.28). Simple assessments based on average values, in general, encompass more studies than meta-analysis but are biased due to the exclusion of pair-wise evaluations. In order to improve the understanding of LUC on trace gas emissions in general, more studies monitoring the fluxes simultaneously in control (forest) and converted sites are necessary. Whenever the conversion includes intermediary stages such as short fallows with the practice of slash-and-burn, the corresponding emission rates should be evaluated as well. When focusing on a specific crop/tree a chronosequential approach including different ages since planting should be considered, especially if fertilization rates evolve with time. The first few years after conversion are likely to be hotspots for N oxide emissions and time since conversion is an important factor to be included.

4.3 Biophysical drivers of NO and N₂O emission and emission change

An IPCC Tier 1 approach is generally used by countries in the Tropics to estimate their annual emissions of GHG. Average LU-based emission rates as provided in this paper or the contribution of N applied released as N₂O from agricultural soils (IPCC, 2006) illustrate the type of emission factors applied to activity data at a Tier 1 level. This approach is useful to compare anthropogenic emissions from different countries but does not capture the variations across climate regions for instance (Skiba et al., 2012). Soil fluxes of N₂O and NO are known to be controlled by climate (rainfall, temperature), soil conditions (drainage, aeration, texture, pH, etc.) and management (land cover, fertilization rate and type, etc.) (Skiba and Smith, 2000; Ludwig et al., 2001; Butterbach-Bahl et al., 2013). Country- or regional LU-specific emission factors that better account for local climate, soil manage-

ment and properties are defined as Tier 2 level whereas Tier 3 methods usually involves process-based models (Del Grosso et al., 2006). The multiple regression analysis of the data set indicated that tropical N₂O and NO fluxes could be expressed as a combination of nitrogen availability and/or application and WFPS; even though the predictive power for simulating overall N₂O emissions was low ($R^2 = 0.39$). However, the predictive power of the regressions increases when the database is split up in agriculture and non-agriculture cases (Table 2). The establishment of an emission factor for agricultural soils that includes the WFPS in addition to N fertilization rate is likely to improve estimates of direct agricultural N₂O emissions, one of the largest sources of N₂O in most countries. For non-agricultural sites a more mechanistic approach appeared to fit better with the observed data. The fluxes of both NO and N₂O followed a Gaussian type relationship with the WFPS – a key determinant for soil anaerobiosis. This type of relationship was hypothesized by Davidson (1991), demonstrated in case studies (Davidson et al., 2000; Davidson and Verchot, 2000; Veldkamp et al., 1998) and used in modeling (Parton et al., 2001; Potter et al., 1996). Its application in the context of the current tropical database confirms a maximum of N₂O emissions around a WFPS of 60 % and indicates maximum NO emissions at a lower WFPS (45 %) than that reported by Davidson et al. (2000) (55 %). It also points out that N₂O emissions remain high at an 80 % WFPS and diminish towards 100 % WFPS. Neither air nor soil temperature were found to affect soil N-oxide fluxes across LUs, although the LU annual average span was wide (12–34 and 14–31 °C for air and soil temperatures). In the temperate zone exponential increases in N₂O emissions with increasing temperature have been reported, whereas in the tropics the evidence is mixed (Skiba and Smith, 2000). Substrate (e.g. N, P) and moisture constraints of microbial processes influencing N-oxide fluxes may reduce the temperature effect. Werner et al. (2006), for instance, demonstrated that variations in N₂O emissions from tropical rainforest soils were mainly affected by soil moisture changes and that temperature changes were of minor importance.

The data confirmed the concepts formulated in the HIP model (Davidson et al., 2000); with the availability of mineral N in the system (first level of control) controlling in an exponential fashion the (NO + N₂O) flux rate, and the WFPS (second level of control) controlling also in an exponential fashion the ratio of N₂O to NO. Although our exponential models are similar to those obtained by Davidson and Verchot (2000) using the TRAGNET database and by Davidson et al. (2000) using fluxes from forest to pasture conversions in the American Tropics, the magnitude of the coefficient is different. For a WFPS between 30 and 60 % the N₂O to NO ratio obtained using the relationship of Davidson and Verchot (2000) is five to nine times lower than the one obtained with the relationship developed here. Above a $\text{NO}_3^- / [\text{NH}_4^+ + \text{NO}_3^-]$ ratio of 0.5 the relationship of Davidson et al. (2000) departs from the one we developed. For

instance, at a $0.75 \text{ NO}_3^- / [\text{NH}_4^+ + \text{NO}_3^-]$ value, we estimate annual NO + N₂O emissions of about $6 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ whereas the model of Davidson et al. indicates $10 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. The probable reason explaining the discrepancy is the temporal scale of the data, we used annual emission rates whereas Davidson et al. used hourly fluxes and thus took into account punctual high emission peaks less apparent in annual budgets. Also, given the nonlinear nature of the functions, an annual budget estimated by summing up fluxes simulated from e.g. hourly WFPS and inorganic N ratio values would lead to a different result than the one simulated from annual WFPS and inorganic N ratio values, as we did. This demonstrates that relationships used in modeling exercises should be developed according to the time step of the model.

Land-use change involves major transformations of the soil-plant-atmosphere continuum. As a result of land-clearing fires, mechanical ploughing and compaction, vegetation change, fertilization, etc., the soil system is highly altered from its previous state. Soil properties such as bulk density, porosity, moisture, WFPS, temperature, mineral N content and pH are often affected by LUC (Farquharson and Baldock, 2008; Dobbie et al., 1999; Verchot et al., 1999). Fertilization N input after land-use change increases highly and significantly both N₂O and NO fluxes, as reported by many studies, e.g. Stehfest and Bouwman (2006). However, increased emissions after LUC were not exclusively due to fertilization, changes in endogenous levels of soil nitrogen availability or WFPS were also key factors impacting the changes in N₂O fluxes. These variables should therefore systematically be measured and reported. Land-use change generally impacts more than one variable at a time, therefore changes in emissions will most likely result from an interaction of factors. This was illustrated by the interactive effect of the changes in N availability and WFPS on N₂O emission changes (Fig. 5).

5 Conclusions

We estimate natural tropical forests to emit $2.0 \text{ kg N}_2\text{O-N ha}^{-1} \text{ yr}^{-1}$ on average and emission rates to be significantly increased after conversion to cropland, and to a smaller degree to agroforestry. Low forest cover also sees their NO emissions raise significantly after being converted. These LUC trajectories can hence contribute substantially to non-CO₂ GHG emission increases whenever they represent a substantial area for a given country. Default Tier 1 N₂O and NO emission factors currently proposed by the IPCC for the tropical region are based on a limited number of studies and rely essentially on N inputs. However, mechanisms of N-oxide production are the result of microbial processes controlled by a combination of factors; thus the IPCC Tier 1 approach is somewhat flawed. Here we established a set of predictive relationships linking annual soil N₂O and NO emissions to biophysical parameters and emission changes to biophysical pa-

rameter changes. The analysis established that N availability or N inputs as well as the soil WFPS were the key explanatory factors of emissions or emission changes. In particular, we developed a statistical model for tropical countries allowing the calculation of N₂O emissions from agriculture as a function of both N fertilization rate and WFPS. Improving the scientific understanding of N₂O and NO fluxes and how they relate to environmental parameters requires the design of experiments considering the high spatio-temporal variation of the fluxes and associated parameters and the use of standardized measurement methods. Also, studies considering a LUC transition pathway should include in their design all intermediate land use stages (e.g. degraded forest) susceptible to modifying N cycling. Finally, even though the body of research on LUC and N₂O and NO emissions has steadily increased over the past decades, knowledge gaps are still important especially in Africa and Oceania, and for wetland forest (notably on peat), degraded forest and important world crops such as oil palm plantations and soy fields.

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