1 TITLE PAGE

Title: Soil N_2O and NO emissions from land use and land-use change in the tropics and subtropics: A meta-analysis

Keywords: greenhouse gases, nitrous oxide, nitric oxide, systematic review, deforestation, REDD+, LUC, LULUC

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2 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 N_2O and 111 NO case studies), determine the trend and magnitude of flux changes with land-use change (LUC) using a meta-analysis approach (44 studies, 135 N_2O and 37 NO cases) and evaluate biophysical drivers of N_2O and NO emissions and emission changes for the tropics.

The average N_2O 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 N_2O 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 the observed NO and N_2O emissions. The sum of soil N_2O and NO fluxes and the ratio of N_2O to NO increased exponentially and significantly with increasing nitrogen availability (expressed as $NO_3^-/[NO_3^-+NH_4^+]$) and WFPS, respectively; following the conceptual Hole-In-the-Pipe model. Nitrous and nitric oxide fluxes did not overall increase significantly 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 ± 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 N_2O 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 N_2O 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).

3 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 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 agricultural 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 & 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 reforesting. In addition to carbon dioxide (CO_2), several studies on LUC in the tropics reported high non-CO_2 GHG emissions, such as nitrous oxide (N_2O) (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; Perez et al., 2007; Davidson et al., 2008). Although the absolute mass of N_2O

emissions might be small, the global warming potential for N_2O over a 100 year time horizon is 298 times greater than that of CO_2 (Forster et al., 2007). 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 N_2O as they share the same processes of production (nitrification and denitrification) in the soil and are hypothesized to be interlinked (Firestone & Davidson, 1989).

Emissions factors in the IPPC 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 N_2O and NO emissions which are known to vary diurnally, seasonally (see e.g. Meixner et al., 1997; Chen & Huang 2009; Lin et al., 2010), and locally due to micro site-specific soil variability (Dalal & 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 N_2O and NO fluxes from the soil can be a wide variety of microorganisms and processes (Anderson & Poth, 1989), but nitrification and denitrification are the main mechanisms (Davidson et al., 2000; Baggs & Philippot, 2010). Therefore, the magnitude of N_2O 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 & Smith, 2000; Heinen, 2006; Dalal & Allen, 2008). Substrates for nitrification and denitrification are ammonium and nitrate, respectively. Ammonium (NH_4^+) is the result of microbial decomposition of soil organic matter and is converted to nitrate (NO_3^-) by the nitrifying bacteria under aerobic conditions. In this process,

105 N_2O and NO are produced and partly emitted to the atmosphere. NO_3^- in return is used under
106 anaerobic conditions as a terminal electron acceptor for denitrifying bacteria that reduce NO_3^-
107 to N_2. Along this reduction gradient N_2O and NO are also produced and partly emitted to the
108 atmosphere (Anderson & Poth, 1989; Baggs & Philippot, 2010).

109 Both nitrification and denitrification produce N_2O and NO but are influenced differently
110 by the same soil variables. Therefore, models predicting N_2O and NO fluxes need to consider
111 both processes. Firestone & Davidson (1989) proposed a conceptual model – dubbed the
112 'Hole-In-the-Pipe' (HIP) model – that uses two levels of control for N_2O and NO emissions
113 in soils. The first level of control is nitrogen availability, symbolized as the amount of N
114 flowing through the pipes. The second level of control is generally represented by the soil
115 aeration status, explained as the size of the holes in the pipe through which N_2O and NO
116 "leak" into the atmosphere. The HIP-model and its underlying assumptions were tested under
117 distinct conditions, which showed that soil nitrogen availability could be expressed in
118 different ways. Davidson et al. (2000) tested several indicators and found that the C:N ratio
119 of litterfall and the ratio of NO_3^- to the sum of NO_3^- and NH_4^+ were promising proxies of N
120 cycling. Underlining the importance of rapid cycling N in N-oxide production, Purbopuspito
121 et al. (2006) showed a good correlation between $\delta^{15}N$ signatures of litter and soil and
122 emissions of N_2O in Indonesia. Veldkamp et al. (1998) suggested that, in N fertilized systems
123 of Costa Rica, the major factor controlling N_2O emissions was the soil aeration status (second
124 level of control), as N availability exceeded demand. The soil aeration status is commonly
125 expressed by the water-filled pore space (WFPS) (Linn & Doran, 1984); with a high WFPS
126 meaning a low aeration (Heinen, 2006). Nitric oxide is mainly produced when the WFPS is
127 below field capacity, whereas N_2O is produced at higher WFPS, exceeding field capacity
128 (Davidson et al., 1991, 1993; Dobbie et al., 1999; Davidson & Verchot, 2000; Bateman &

129 Baggs, 2005). Depending on soil texture, the field capacity is at a WFPS of around 60%;
130 whenever the WFPS exceeds 80%, most of the N is expected to be denitrified into N_2.
131 The goal of this study was to review how the emissions of N_2O and NO in the tropics were
132 affected by LU and LUC and to examine their variation in relation to biophysical parameters.
133 We used all studies published in the peer-reviewed literature up to 2013 to calculate
134 emissions per LU type and evaluated relationships with environmental parameters. Next, the
135 effect of LUC was assessed by using a quantitative meta-analysis statistical approach that
136 allows for a comparison between independent studies, and weights studies according to their
137 uncertainty (Hedges & Olkin, 1985). We used the Hedges' d (Koricheva et al., 2013) metric
138 to evaluate LUC effects. This is a standardized mean difference similar to the Hedges' g but
139 adjusted for small sample sizes. Finally we ran a meta-analysis regression to express the
140 changes in emission rates following LUC as a function of environmental and soil variables
141 changes.

4 MATERIAL AND METHODS

We followed three main steps to assess how soil N_2O and NO emissions were affected by LU and LUC in the tropics and subtropics: (i) compiling a database of all studies on soil N_2O 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.

4.1 Data collection and calculation

The database of Stehfest & Bouwman (2006) (available at: www.mnp.nl/en/publications/2006) was used as a basis for our research. From this dataset, 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 N_2O in the tropics. A combination of the following keywords were used in the ISI Web of Science and ScienceDirect search engines: N_2O, nitrous oxide, NO, nitric oxide, emissions, fertilizers, forest, arable, grasslands, flux, nitrification, denitrification, land use, NOx, nitrogen-oxide, tropics, subtropics. As N_2O and NO fluxes are known to vary seasonally (e.g. Meixner et al., 1997; Chen & Huang, 2009), we manually selected the studies that measured the fluxes during both dry and wet seasons. The 103 studies selected (S1), representing 392 N_2O and 111 NO LU case studies, were used to estimate annual mean N-oxides emission rates per LU category and to analyse their relationship with environmental proxies. Out of the 104 papers

167 44 measured N_2O and/or NO emissions synchronically in at least two different LUs, one of
168 which was a forest. These 44 papers represented 135 N_2O and 37 NO LUC case studies
169 which were analysed using a meta-analysis statistical approach (S2).
170 We summarized the number of studies and assessed the representation of LU per continent
171 categorizing them in five geographical areas: North-Central America, South America, Africa,
172 South Asia and Oceania. Average annual emission rates were expressed in kg NO-N or N_2O-
173 N ha^{-1} yr^{-1} using the estimates provided by the papers. Whenever annual fluxes were not
174 provided by the authors, we calculated them. For studies covering year-round measurements,
175 the annual flux was calculated by scaling up the units from hours or days to a year and cm^2 or
176 m^2 to ha. Where possible reported fluxes were weighed according to their time interval. For
177 instance, for studies covering measurements made during the dry and wet seasons, the annual
178 flux was calculated as the sum of each seasonal flux weighted by the number of days per year
179 corresponding to each season. The biophysical variables associated with N_2O and NO
180 emissions from the publications were also expressed as annual averages. Soil variables
181 (temperature, WFPS, bulk density, pH, C content, N content, NH_4^+ and NO_3^-) are from the
182 soil top layer (0-10cm). Nitrogen fertilization and litterfall are given as a mass of nitrogen per
183 hectare per year. In some cases the water-filled pore space (WFPS, %) was manually
184 calculated as a function of the gravimetric water content (m, g g^{-1} d.w.), bulk density (y_d, g
185 cm^{-3}) and particle density (y_s, g cm^{-3}) as $WFPS = 100*(m*y_d)/(1-(y_d/y_s))$ (Linn & Doran
186 1984). A y_s default value of 2.65 g cm^{-3} was used for mineral soils (Hillel, 1980), whenever
187 not provided by the studies. Nitrogen fixation was considered by using a dichotomous
188 variable indicating the presence or absence of N_2 fixing species in the LU. Nitrogen fixation
189 rates were barely reported and could not be included. For studies measuring N_2O and NO
190 simultaneously, we calculated the ratio and sum of the two and tested their correlation with

191 WFPS and soil N availability. The latter is expressed as the relative fraction of NO_3^- to total
192 inorganic N ($NO_3^-/[NO_3^-+NH_4^+]$).
193 Three LU case studies from Takakai et al. (2006) and the celery plot in Xiong et al (2006)
194 were excluded from the analysis because the very high fertilizations rates were about three
195 times higher than the International Fertilizer industry Association (IFA) recommended dose
196 for the studied crops.
197

198 **4.2 Land use and land-use change characterization**

199 The LU were classified into nine main categories: 1) forest (primary forest and secondary
200 forest older than 30 years), 2) wetland forest (swamp on peat, swamp on mineral soil and
201 riparian forest), 3) low forest cover (low canopy closure: woodlands and shrublands,
202 secondary forest younger than 30 years), 4) degraded forest (human-induced low forest cover
203 after logging and burning or fallows), 5) agroforestry systems, 6) plantations (mono-specific
204 plantations, e.g. *Acacia*, rubber, oil palm, cinnamon), 7) pastures (pastures and grasslands), 8)
205 rice fields, and 9) croplands (annual and perennial crops). For agroforestry, plantation,
206 pasture, rice and cropland both fertilized and unfertilized cases were combined and the effect
207 of fertilization was tested separately. Only a few studies included age after conversion in a
208 chronosequential sampling design; therefore we pulled together LU cases from different
209 studies to evaluate the change in emission rates as a function of time since conversion.
210 The studies either focused on a specific LUC type (e.g. forest conversion to pasture), or
211 considered several LUC types which were representative for the study region. In the latter
212 case, when only one control (forest) site was available, we used the same control for all
213 converted sites. Whenever several control sites were available in a study we averaged the
214 fluxes from all control sites. When a study measured emissions for several years, each year
215 was considered a separate case. The following LUC were analysed: 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.

4.3 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 N_2O 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 (± S.E.).

Stepwise multiple linear regression was performed to identify the environmental variables that were significantly related to soil fluxes of N_2O 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 N_2O, NO fluxes and WFPS using averages per 10% WFPS intervals.

4.3.1 Meta-analysis

A meta-analysis was used to quantify the effect of LUC on soil annual N_2O 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 N_2O or NO emissions after land-use change as being the treatment and N_2O 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 N_2O and NO fluxes. This metric is defined as:

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

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

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

Where, $\bar{X}_T$ and $\bar{X}_C$ are the average N_2O 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 & 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 N_2O or NO emission after LUC, respectively.

Calculation of *d* requires knowledge of the standard deviation and sample size associated with the average N_2O 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 (Joseph A. Huwaldt, 2011).

Publication bias for studies with significant and/or high effect sizes was assessed using a normal quantile plot (Wang & 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 dataset, 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 & 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 & Green, 2011) to assess how the changes in environmental factors affected changes in soil N_2O 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 N_2O or NO emissions. A meta-analysis regression is considered robust when it includes ten cases studies at least (Borentstein, 2009; Higgins & Green, 2011).

5 RESULTS

5.1 Exploring the dataset

The publication rate of peer-reviewed papers on LU and soil emissions of N_2O and NO in the tropics has more than doubled over the past decade (less than 2 publications y^{-1} before 2000, more than 5 y^{-1} afterwards), but remains low. The Americas (combining North-Central and South America) and South Asia represented the majority of the dataset (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.

5.2 Average land use emissions and environmental parameter values

Neither N_2O nor NO fluxes were normally distributed and about 90% of the observations were below 10 kg N_2O-N and 8 kg NO-N ha^{-1} yr^{-1}. Table 1 shows average annual N_2O and NO emissions per LU and environmental parameter associated. Croplands displayed the highest N_2O emission rate and also the highest average N fertilization rate. Both pastures and rice fields had relatively high N_2O emissions; however, these were characterized by a high

306 variation. The average NO emission rates did not show any significant difference between
307 LU.

308 The availability of environmental parameters in studies on N-oxides emissions was
309 variable. For example, only 4% of the studies reported nitrogen input through litterfall, while
310 precipitation was given in 91% of all cases. Although the comparison of values from different
311 data sources may generate inconsistencies, some generalizations per LU category can be
312 made. Overall, intact forest had a significantly lower bulk density compared to more
313 compacted soils from pastures. Wetland forest soils had a significant lower bulk density
314 compared to all other soils. Wetland forest soils were more acidic than other soils in general,
315 while cropland soils were significantly less acid than forest soils. Mineral N content did not
316 differ significantly between LU, except for high NH_4^+ and NO_3^- concentrations in wetland
317 forest and rice paddy soils. Plantation soils were the only ones where NO_3^- concentrations
318 exceeded those of NH_4^+, other LU showed the opposite trend. Carbon and nitrogen content in
319 the soils of natural wetland forest were very high and significantly higher than that in all
320 other LUs. Degraded forest soils showed a high carbon content which is due to the inclusion
321 of eleven degraded peat forests out of the twenty cases. Excluding them resulted in a soil
322 carbon content of 3.8 %.

323 The multiple linear regression analysis indicated that N fertilization, WFPS, and N
324 availability (expressed as $[NO_3^-/ (NO_3^- + NH_4^+)]$) were the best proxies for estimating overall
325 soil fluxes of N_2O (Table 2). For agricultural sites (i.e. crop and pasture) N fertilization rate
326 explained part of the variation (R^2=0.31, df=160, $p<0.01$); but (pair-wise) including the
327 WFPS more than doubled the R squared. Proxies for overall soil NO fluxes were N
328 availability and N fertilization. For agricultural sites N fertilization explained 31% of the
329 variation in NO fluxes, and the inclusion of the WFPS did not improve the relationship. In
330 non-agricultural LUs a non-linear Gaussian function of the WFPS simulated with good fit

331 N_2O and NO fluxes (Fig. 2, Table 2). The relationship indicates that NO and N_2O fluxes peak
332 at WFPS of 45% and 61%, respectively. The ratio of N_2O to NO displayed an exponential
333 relationship with the WFPS (Fig. 3, Table 2), which indicates N-oxide emissions
334 predominantly in the form of N_2O (i.e. $N_2O/NO > 1$) above a WFPS of 48%. In non-
335 agricultural sites the predominance of N_2O over NO happens at a slightly lower WFPS
336 (46%). The sum of soil N_2O and NO emissions also increased exponentially with increasing
337 N availability.
338 Time since conversion was available in 26% of the LU cases only. Nitrous oxide fluxes
339 from non-fertilized croplands appeared to be higher the first ten years after conversion and
340 thereafter decrease, whereas fluxes from fertilized croplands remained high (Fig. 4). For
341 pastures the pattern was less apparent, the first years after conversion both high and low
342 fluxes were observed.
343
344 **5.3 Land-use change effects on N_2O and NO emissions and environmental parameters**
345 Land-use change effects were evaluated by looking at differences in emissions after and
346 before LUC. This was done for each LUC type and for all LUC combined. The effect sizes of
347 LUC on N_2O emissions were not strictly normally distributed; however, all effect size ranges
348 were present. Deviation from linearity occurred for high and low effect sizes indicating a
349 potential bias for published studies measuring large effects following LUC. A normal
350 quantile plot for NO emissions as affected by LUC indicated a normal distribution; however,
351 some gaps were present in the observed values, possibly due to a biased representation of NO
352 emission changes in the literature.
353 Nitrous oxide emissions were not overall affected by LUC ($d = 0.11 \pm 0.11$); the slight
354 increasing trend was not significant because of opposing effects in different LUC trajectories
355 (Table 3). The LUC case studies overall did not share a common effect size ($Q_{overal} = 221.3$ *P*

356 < 0.01) and the majority of the variation was within case studies (1-I^2, 59%). Similarly to
357 N_2O emissions, and for the same reason, NO emissions were not overall affected by LUC;
358 with a homogeneous effect size ($Q_{overall}$ = 31.7, P = 0.67) and 47% of the variation within
359 LUC case studies (1-I^2).

360 Most studies focused on forest clearing for croplands ($n_{F\text{-}Crop}$+ $n_{WF\text{-}Crop}$+ $n_{DegF\text{-}Crop}$= 44) and
361 pastures ($n_{F\text{-}Pa}$ + $n_{WF\text{-}Pa}$ + $n_{DegF\text{-}Pa}$ = 42). Transition from intact upland forest to croplands
362 significantly increased N_2O emissions, while conversion to agroforestry showed a slight, but
363 insignificant increasing trend. Intact forest conversion to pasture (F-Pa) tended to decrease
364 N_2O emissions, whereas low forest cover conversion to pasture (LFC-Pa) showed the
365 opposite trend. Further, conversion of low forest cover overall significantly increased NO
366 emissions.

367 The Hedges' d effect size of forest conversion to fertilized LU amounted to 1.03 ± 0.31
368 and 0.52 ± 0.23 for N_2O and NO, respectively, indicating significant and high increased
369 emissions after fertilization. Evidence for increased emission following conversion to LU
370 with N fixing crops/trees was weak and fluxes of NO slightly raised but not significantly
371 (d_{NO}=0.61 ±0.33 n = 8).

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

6 DISCUSSION

6.1 Dataset representativeness and average annual LU emissions

The body of research on LULUC and N_2O 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 N_2O 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 & 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 N_2O emissions (Hadi et al., 2005; Furukawa et al., 2005; Jauhiainen et al., 2012), but the overall tendency of wetland forest conversion to increase N_2O emissions was not significant (Table 3) as observed by Hergoualc'h & 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).

The annual N_2O emission rate in intact upland forest (2.0 ± 0.2 kg N_2O-N ha^{-1} yr^{-1}, n = 88) is more than twice the value estimated by Stehfest & Bouwman (2006) (0.85 kg N_2O-N ha^{-1} yr^{-1}, n = 77) for the tropics. We excluded the cases considered by Stehfest & 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 kg N_2O-N ha^{-1} by Potter et al. (1996) and 1.2 kg N_2O-N ha^{-1} yr^{-1} by Werner et al. (2007). Dalal & Allen (2008) estimated average emissions in tropical forest of 3.0 ± 0.52 kg N_2O-N ha^{-1} yr^{-1} (n = 22) and Kim et al. (2013a, 2013b) of 1.91 kg N ±0.25 (n = 69). The annual NO emission rate in tropical forest amounts to 1.7 ±0.48 kg N-NO ha^{-1} yr^{-1} (n = 36), which is higher than previous estimates by Stehfest and Bouwman (2006) (0.39 kg NO-N ha^{-1} yr^{-1}, n = 33), Davidson and Kingerlee (1997) (0.8 kg NO-N ha^{-1} yr^{-1}, n = 15) and Potter et al. (1996) (1.2 kg NO-N ha^{-1} yr^{-1}).

Nitrous oxide emission in agricultural fields and pastures reported by Duxbury et al. (1982) were the largest in the entire dataset (average emissions of 65 kg N_2O-N ha^{-1} yr^{-1}). The study was conducted in Florida on drained organic soils under crops, grass or kept as fallows; that displayed high N mineralization rates (600-1,200 kg N ha^{-1} y^{-1}). Excluding them decreases the overall average N_2O emissions from 4.4 ± 0.6 (n = 387) to 3.5 ± 0.3 kg N_2O-N ha^{-1} yr^{-1} (n = 381), and croplands emissions from 8.6 ± 2.0 (n = 93) to 5.8 ±0.9 kg N_2O-N ha^{-1} yr^{-1} (n = 88).

6.2 Land-use change effects on the emissions

429 According to the meta-analysis LUC overall increased N_2O and NO emissions, albeit not
430 significantly. Land-use change types or practices that induced significant changes in
431 emissions all pointed towards increased rather than decreased emissions. The meta-analysis
432 confirmed that intact upland forest conversion to croplands and nitrogen fertilization after
433 LUC significantly and highly increased soil emissions of N_2O. It also corroborated high
434 increases in NO emissions after low forest cover conversion in general and when fertilizer is
435 applied after LUC. For most LUC trajectories the effect of emission change was not
436 significant even when the sample size was relatively large. For instance, the analysis
437 indicated a trend of decreased N_2O emissions following intact upland forest conversion to
438 pasture, which was not significant since the LUC studies not all agreed on the direction of
439 change. Several publications reported decreased emissions after conversion to pasture (e.g.
440 Verchot et al., 1999; Erickson et al., 2001; Garcia-Montiel et al., 2001), others reported the
441 opposite (e.g. Melillo et al., 2001; Takakai et al., 2006) and one showed no effect (Neill et al.,
442 2005). These apparent contradicting results have been explained by differences or absence of
443 differences in time after conversion of the studied pastures (Keller et al., 1993, Veldkamp et
444 al., 1999, Verchot et al., 1999, Neill et al., 2005, Wick et al., 2005) or the practiced or not
445 slash and burn technique to clear the forest, both affecting N cycling (Luizao et al., 1989;
446 Matson et al., 1990; Steudler et al., 1991; Keller & Reiners, 1994; Neill et al., 1995; Melillo
447 et al., 2001; Garcia-Montiel et al., 2001). Biomass burning produces N_2O during fires and
448 may enhance soil N_2O afterwards by stimulating N mineralisation (Skiba & Smith, 2000).
449 The paucity of field observations together with the lack of land-use history description did
450 not allow to evaluate clearing practices effects or temporal trends in soil emission dynamics
451 with LUC thoroughly. For non-fertilized croplands and pastures, the fluxes of N_2O tended to
452 increase during the first five to ten years after conversion and thereafter tended to decrease to
453 average upland forest or low canopy forest levels (Fig. 4). In fertilized croplands, however,

454 flux rates remained at a high level even beyond this period. Soil physical disturbance
455 following land clearing, high N inputs associated with clear-felling and soil preparation (e.g.
456 compaction, drainage in wetland) all combined may be at the origin of the five to ten year
457 emission peak. In fertilized croplands on the other hand, the sustained emission increase
458 seems to be driven by high mineral N inputs. This temporal variability in emission change
459 indicates that the first ten years following LUC are crucial for GHG budget calculations.
460 We used a meta-analysis statistical approach to assess the trend and magnitude of forest
461 conversion on soil emissions of N oxides. Meta-analysis consists in comparing site specific
462 (pair-wise) effects weighted according to their robustness, therefore it provides a direction
463 and a magnitude of emission change more reliable and precise than those obtained by
464 comparing average emission rates per LU category from individual papers. For example, the
465 meta-analysis effect on N_2O emissions of intact upland forest conversion to croplands (0.78)
466 was much higher than the effect calculated (0.48) using average values from Table 1 and Eq.
467 (1). The effect calculated from average emission rate derived from individual studies can also
468 lead to misleading conclusions such as in the case of intact upland forest conversion to
469 pasture. The effect calculated from average emissions (0.34) was positive indicating
470 increased emissions as opposed to the meta-analysis conclusion (-0.28). Simple assessments
471 based on average values, in general, encompass more studies than meta-analysis but are
472 biased due to the exclusion of pair-wise evaluations. In order to improve the understanding of
473 LUC on trace gas emissions in general, more studies monitoring the fluxes simultaneously in
474 control (forest) and converted sites are necessary. Whenever the conversion includes
475 intermediary stages such as short fallows with the practice of slash-and-burn, the
476 corresponding emission rates should be evaluated as well. When focusing on a specific
477 crop/tree a chronosequential approach including different ages since planting should be
478 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.

6.3 Biophysical drivers of NO and N_2O emission and emission change

An IPPC 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 N_2O 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 N_2O 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 & 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 management and properties are defined as Tier 2 level whereas Tiers 3 methods usually involves process-based models (Del Grosso et al., 2006). The multiple regression analysis of the dataset indicated that tropical N_2O 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 N_2O 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 N_2O emissions, one of the largest source of N_2O in most countries. For non-agricultural sites a more mechanistic approach appeared to fit better the observed data. The fluxes of both NO and N_2O 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 modelling (Parton et al., 2001; Parton et al., 1996; Potter et al., 1996). Its application in the context of the current tropical database confirms a maximum of N_2O 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 N_2O 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˚C and 14-31˚C for air and soil temperatures). In the temperate zone exponential increases in N_2O 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 N_2O 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 ($NO + N_2O$) flux rate and the WFPS (second level of control) controlling also in an exponential fashion the ratio of N_2O 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 N_2O 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 $NO_3^-/[NH_4^+ + NO_3^-]$ ratio of 0.5 the relationship of Davidson et al. (2000) departs from the one we

529 developed. For instance, at a 0.75 $NO_3^-/[NH_4^+ + NO_3^-]$ value, we estimate annual NO + N_2O
530 emissions of about 6 kg N ha^{-1} y^{-1} whereas the model of Davidson et al. indicates 10 kg N ha^{-1} y^{-1}. The probable reason explaining the discrepancy is the temporal scale of the data, we
532 used annual emission rates whereas Davidson et al. used hourly fluxes and thus took into
533 account punctual high emission peaks less apparent in annual budgets. Also, given the
534 nonlinear nature of the functions, an annual budget estimated by summing up fluxes
535 simulated from e.g. hourly WFPS and inorganic N ratio values would lead to a different
536 result than the one simulated from annual WFPS and inorganic N ratio values, as we did. This
537 demonstrates that relationships used in modelling exercises should be developed according to
538 the time step of the model.

539 Land-use change involves major transformations of the soil-plant-atmosphere continuum.
540 As a result of land-clearing fires, mechanical ploughing and compaction, vegetation change,
541 fertilization, etc., the soil system is highly altered from its previous state. Soil properties such
542 as bulk density, porosity, moisture, WFPS, temperature, mineral N content and pH are often
543 affected by LUC (Farquharson & Baldock, 2008; Dobbie et al., 1999; Verchot et al., 1999).
544 Fertilization N input after land-use change increases highly and significantly both N_2O and
545 NO fluxes, as reported by many studies, e.g. Stehfest & Bouwman (2006). However,
546 increased emissions after LUC were not exclusively due to fertilization, changes in
547 endogenous levels of soil nitrogen availability or WFPS were also key factors impacting the
548 changes in N_2O fluxes. These variables should therefore systematically be measured and
549 reported. Land-use change generally impacts more than one variable at a time, therefore
550 changes in emissions will most likely result from an interaction of factors. This was
551 illustrated by the interactive effect of the changes in N availability and WFPS on N_2O
552 emission changes (Fig. 5).

7 CONCLUSIONS

We estimate natural tropical forests to emit 2.0 kg N_2O-N ha^{-1} 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 see their NO emissions raise significantly after being converted. These LUC trajectories can hence contribute substantially to non-CO_2 GHG emission increases whenever they represent a substantial area for a given country. Default Tier 1 N_2O 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 N_2O and NO emissions to biophysical parameters and emission changes to biophysical parameter 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 N_2O emissions from agriculture as a function of both N fertilization rate and WFPS. Improving the scientific understanding of N_2O 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 modify N cycling. Finally, even though the body of research on LUC and N_2O 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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10 SUPPLEMENTARY MATERIAL

S1 – Database of LU study cases on N_2O and NO fluxes and environmental parameters.

S2 – Database used for the meta-analysis of LUC study cases and Hedges'*d* for N_2O and NO fluxes and environmental parameters.

11 TABLES

Table 1: Average of annual N_2O 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)	**WFPS** (%)	**Bulk density** (g d.w. cm^{-3})	**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})
						Nitrous oxide							
F	2.0[a]	2226	22.8	23.7[a,b]	56.1	.9[a]	4.9[a,b,c]	20.5[a]	10.8[a]	4.8[a]	0.4[a]	0[a]	100
	(0.2, 90)	(81, 90)	(0.4, 80)	(0.5, 29)	(3.4, 45)	(0.0, 58)	(0.1, 55)	(2.8, 47)	(1.5, 45)	(0.5, 45)	(0.0, 45)	(0, 87)	(17, 14)
WF	2.7[a,b]	2485	26.1	26.8[a,b]	44.5	0.1[b]	3.8[a]	412.0[b]	70.9[b]	49.7[b]	1.6[b]	0[a,b,d]	n.a.
	(1.9, 7)	(167, 6)	(0.4, 6)	(0.5, 4)	(7.7, 3)	(0.0, 4)	(0.2, 7)	(119.9, 4)	(12.2, 5)	(3.2, 7)	(0.1, 7)	(0, 7)	
LFC	0.5[a,b]	1546	23.9	28.8[a,b]	47.7	1.1[a,c]	5.0[a,b,c,d]	5.1[a]	3.1[a]	4.0[a]	0.3[a]	0[a,b,d]	n.a.
	(0.1, 11)	(390, 11)	(1.6, 9)	(1.2, 3)	(10.6, 8)	(0.1, 10)	(0.3, 11)	(1.1, 8)	(1, 8)	(0.9, 8)	(0.1, 8)	(0, 10)	
DegF	1.9[a,b]	2220	25.1	27.6[a]	48.4	0.9[a]	4.4[a,b]	44.4[a]	11.6[a]	30.0[c 1]	0.9[c]	0[a,b]	122
	(0.5, 30)	(123, 30)	(0.4, 28)	(0.6, 14)	(5, 19)	(0.1, 24)	(0.2, 23)	(17.4, 20)	(4.1, 20)	(6.2, 20)	(0.1, 20)	(0, 26)	(54, 3)
AGF	3.4[a,b]	2297	25.2	22.1[a,b]	77.1	1.2[a,c]	5.6[b,c,d]	10.7[a]	7.8[a,b]	2.8[a]	0.3[a,c]	39[a,b,c]	218
	(1.6, 8)	(112, 8)	(0.8, 6)	(2.3, 2)	(17.2, 3)	(0.1, 8)	(0.3, 7)	(4.6, 7)	(3.1, 7)	(0.5, 3)	(0.1, 3)	(31, 8)	(#, 1)
Pl	1.5[a,b]	2120	24.3	25.5[a,b]	59.0	1.0[a,c]	4.8[a,b,c]	11.9[a]	17.8[a,b]	6.7[a]	0.4[a]	53[a,b]	304
	(0.3, 40)	(137, 40)	(0.6, 38)	(0.6, 22)	(3.4, 26)	(0.1, 27)	(0.1, 37)	(2.3, 30)	(8.2, 27)	(2.2, 30)	(0.1, 31)	(25, 35)	(153, 5)
Pa	5.2[a,b]	1913	23.4	26.3[a,b]	64.2	1.2[c]	5.4[c,d]	26.1[a]	26.9[a,b]	5.1[a]	0.3[a]	90[b,d]	n.a.
	(1.3, 97)	(89, 90)	(0.5, 54)	(1.9, 8)	(4.6, 18)	(0, 54)	(0.1, 49)	(4.2, 29)	(13.7, 29)	(1.8, 41)	(0, 39)	(17, 70)	

R	5.1[a,b] (1.7, 17)	1562 (234, 13)	21.9 (1.9, 13)	20.9[b] (2.4, 5)	73.0 (1.2, 3)	1.2[a,c] (0, 4)	6.0[d] (0.3, 17)	788.01 (#, 1)	29.4[a,b] (2.0, 2)	13.6[a] (5.2, 17)	0.5[a,c] (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[a,b] (1.1, 23)	58.1 (5.2, 28)	1.1[a,c] (0.1, 44)	5.7[d,e] (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[c,d] (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 [bc] (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 [acd] (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 [bdef] (12, 5)	n.a.
PI	5.4 (5.3, 2)	2124 (1839, 2)	21.4 [acd] (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 [cf] (180, 2)	n.a.
Pa	2.6 (0.7, 28)	2279 (252, 26)	25.5 [bd] (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 [acd] (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.

884 Table 2: Multiple regression between soil N_2O or NO emissions and associated
885 environmental parameters; and meta-analysis regression between the standardized differences
886 after and before land-use change of N_2O emissions (or Hedges' *d*, d_{N2O}) and of environmental
887 factors ($d_{Navailable}$, d_{wfps}). The models are presented with slope and intercept ± SE; P values are
888 indicated with * (p<0.05), ** (p<0.01) and *** (p<0.001). All regression models were
889 significant (p≤0.01).
890

LU	R^2	df	Model
Linear regression LU study cases			
All	0.39	125	$Ln(N_2O+1.2)$ = 0.002*** ±0.0004 × $N_{fertilization}$ + 0.87** ±0.29 × $N_{available}$ + 0.014*** ±0.003 × *WFPS* – 0.11^{ns} ±0.22
Agr[a]	0.83	40	$Ln(N_2O+1.2)$ = 0.008*** ±0.0007 × $N_{fertilization}$ + 0.017*** ±0.003 × *WFPS* – 0.28^{ns} ±0.26
Non-Agr[b]	0.17	80	$Ln(N_2O+1.2)$ = 0.87** ±0.27 × $N_{available}$ + 0.008*** ±0.003 × *WFPS* – 0.15^{ns} ±0.21
All	0.18	64	$Ln(NO)$ = 2.27** ±0.80 × $N_{available}$ + 0.0085* ±0.0039 × $N_{fertilization}$ – 1.42*** ±0.35
Agr[a]	0.31	44	$Ln(NO)$ = 0.0081*** ±0.0019 × $N_{fertilization}$ – 0.65* ±0.26
Non-Agr[b]	0.20	36	$Ln(NO)$ = 3.02** ±1.02 × $N_{available}$ – 1.67** ±0.47
Gaussian regression WFPS			
Non-Agr[b]	0.90	102	$N_2O = 2.3 \times exp(-0.5 \times ((WFPS^c-61.8)/24.7)^2)$
Non-Agr[b]	0.89	36	$NO = 2.5 \times exp(-0.5 \times ((WFPS^c-45.3)/16.5)^2)$
HIP model regression			
All	0.48	40	$Log(1+N_2O+NO) = 0.92^{***} \pm 0.15 \times N_{available} + 0.15^{*} \pm 0.06$
All	0.39	42	$Log(1+ N_2O/NO) = 0.0129^{***} \pm 0.003 \times WFPS - 0.32^{ns} \pm 0.18$
Non-Agr[b]	0.40	29	$Log(1+ N_2O/NO) = 0.0125^{***} \pm 0.003 \times WFPS - 0.27^{ns} \pm 0.20$
Meta-analysis regression LUC study cases			
All	0.23	89	d_{N2O} = 0.65** ±0.14 × $d_{Navailable}$ -0.04 ±0.13
All	0.15	69	d_{N2O} = 0.55** ±0.22 × d_{wfps} +0.05 ±0.16

891 N_2O and NO are expressed in kg N2O-N yr^{-1} or N-NO ha-1 yr^{-1}, $N_{available}$ is (NO_3^-/[NO_3^-+NH_4^+]) without units, NO_3^-
892 and NH_4^+ in µg N g^{-1} d.w., $N_{fertilization}$ in kg N ha^{-1} yr^{-1} and WFPS in %.
893 [a]Agr includes cropland and pasture.
894 [b]Non-Agr includes forest, low forest cover, degraded forest, agroforestry and plantation.
895 [c]WFPS intervals of 10%.

Table 3 – Hedges' d ± SE (n) of N_2O (d_{N2O}) and NO (d_{NO}) emission change following land-use change (LUC). Hedges' d is the standardized mean difference of N_2O (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_{N2O}	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 N_2 fixing trees/crops.

12 FIGURE LEGENDS

Figure 1: Spatial distribution of land use case studies on soil fluxes of (a) N_2O 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, Pl: 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 N_2O 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 1,000 ha. Adapted from FAO (2010).

Figure 2: Gaussian relationships (dashed lines) between the WFPS and N_2O and NO emissions in non-agricultural land uses. N_2O and NO fluxes are averaged in 10% WFPS intervals. Error bars are N flux standard errors in each WFPS interval.

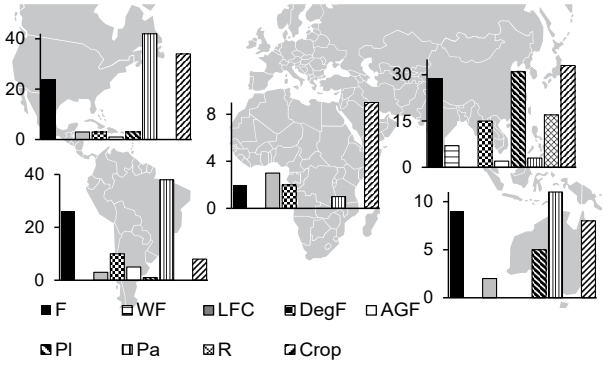
Figure 3: Relationships between (a) the WFPS and the ratio of N_2O to NO; (b) $N_{available}$ (NO_3^- /[NO_3^-+NH_4^+]) and the sum of N_2O and NO. The domains of definition are (a) [0.02; 44.71] in N_2O to NO ratio and [30.4; 94.4] in WFPS; (b) [0.00;12.80] in N_2O + NO (kg N ha^{-1} yr^{-1}) and [0.01;0.77] in $N_{available}$.

Figure 4: Effect of time since conversion on N_2O fluxes in (a) croplands and (b) pastures. Average N_2O 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.

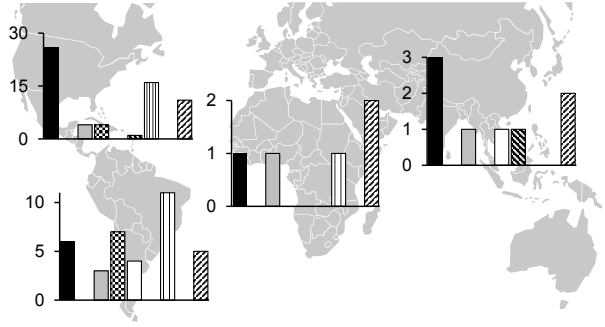
931

932 Figure 5: N_2O Hedges'd as affected by the interactive changes in $N_{availability}$ and WFPS. The
933 meta-analysis regression between d_{N2O} and $d_{Navailability}$ was performed for all cases (solid line)
934 and for cases when $d_{WFPS}>0$ or $d_{WFPS}<0$ (dashed lines).Closed and open circles represent
935 increased and decreased WFPS, respectively.

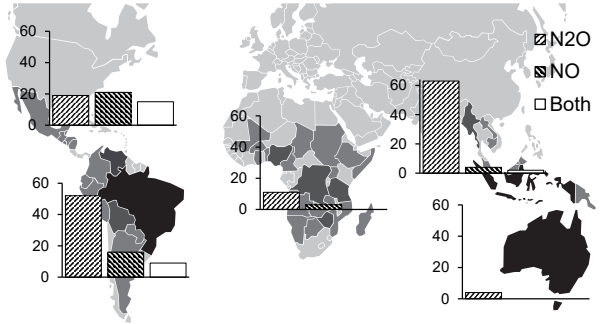
A. Nitrous oxide LU study cases

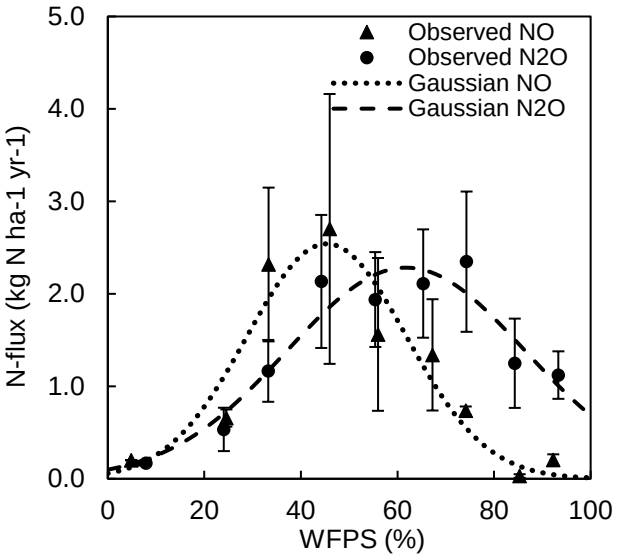


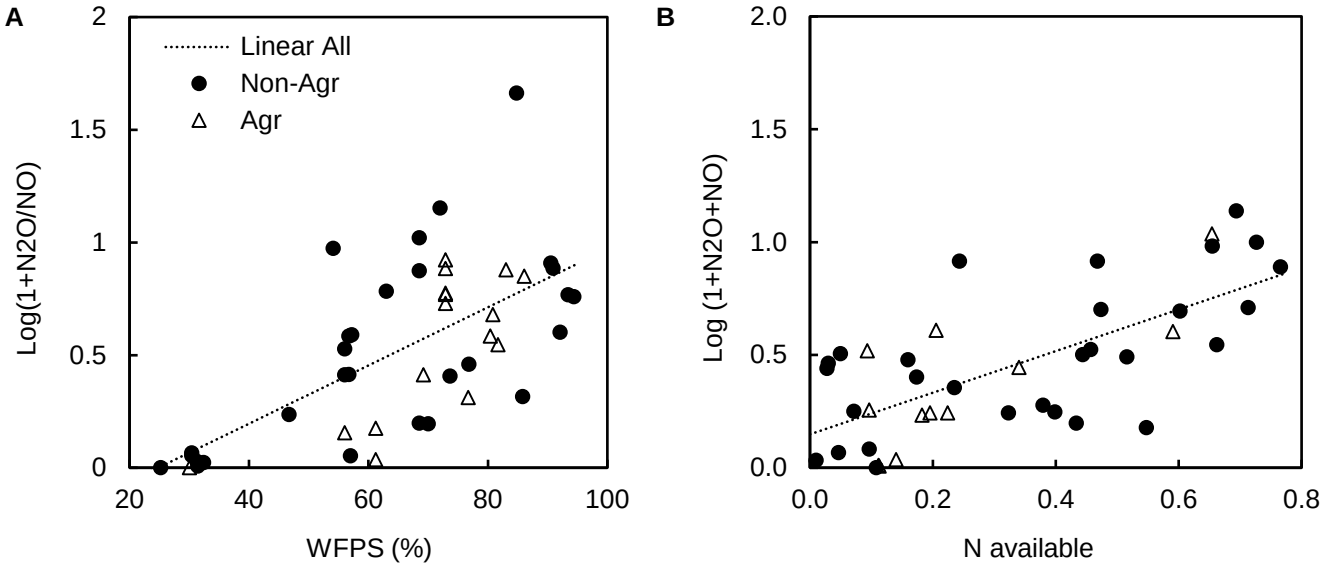
B. Nitric oxide LU study cases

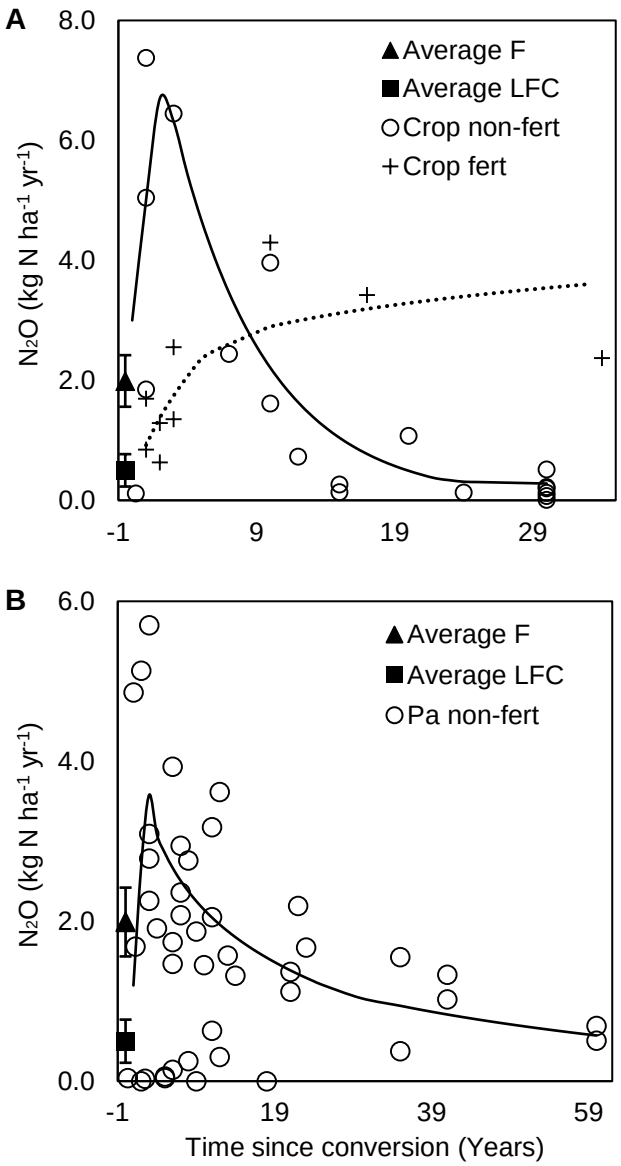


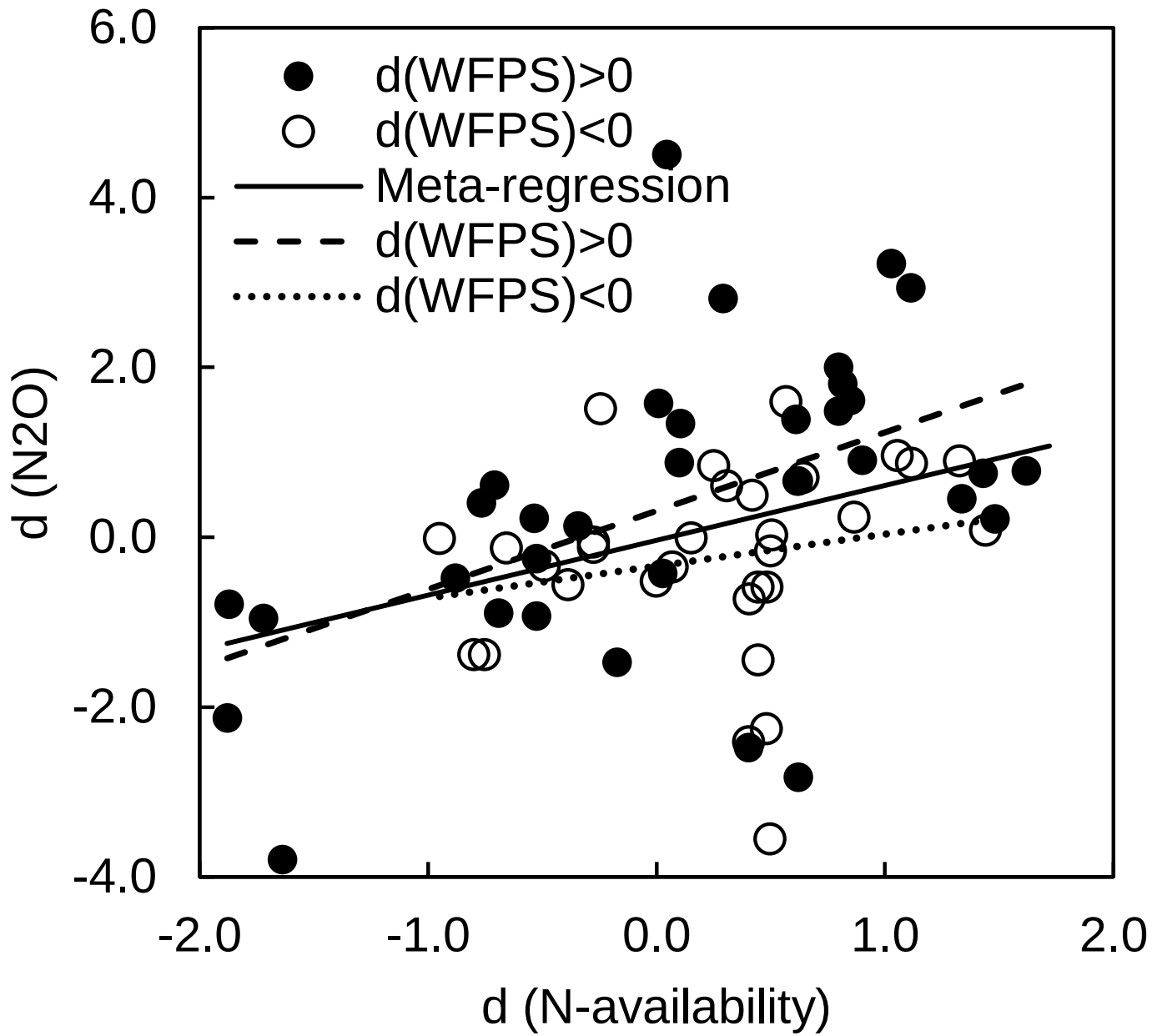
C. LUC study cases




Observed NO
Observed N2O
Gaussian NO
Gaussian N2O
N-flux (kg N ha-1 yr-1)
WFPS (%)
0.0
1.0
2.0
3.0
4.0
5.0
0
20
40
60
80
100


A
Linear All
Non-Agr
Agr
Log(1+N2O/NO)
WFPS (%)
B
Log (1+N2O+NO)
N available


A
8.0
6.0
4.0
2.0
0.0
N2O (kg N ha-1 yr-1)
Average F
Average LFC
Crop non-fert
Crop fert
-1
9
19
29
B
6.0
4.0
2.0
0.0
N2O (kg N ha-1 yr-1)
Average F
Average LFC
Pa non-fert
-1
19
39
59
Time since conversion (Years)


6.0
4.0
2.0
0.0
-2.0
-4.0
d (N2O)
-2.0
-1.0
0.0
1.0
2.0
d (N-availability)
d(WFPS)>0
d(WFPS)<0
Meta-regression
d(WFPS)>0
d(WFPS)<0