The effect of land-use change on soil CH_4 and N_2O fluxes: a global meta-analysis

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Abstract (Max 300 words)

Land-use change is a prominent feature of the Anthropocene. Transitions between natural and human-managed ecosystems affect biogeochemical cycles in many ways, but soil processes are amongst the least understood. We used a global meta-analysis (62 studies, 1670 paired comparisons) to examine effects of land conversion on soil-atmosphere fluxes of methane (CH_4) and nitrous oxide (N_2O) from upland soils, and determine soil and environmental factors driving these effects. Conversion from a natural ecosystem to any anthropogenic land use increased soil CH_4 and N_2O fluxes by 234 kg CO_2-equivalents ha^{-1} y^{-1}, on average. Reversion of managed ecosystems to that resembling natural ecosystems did not fully reverse those effects, even after 80 years. In general, neither the type of ecosystem converted, nor the type of subsequent anthropogenic land use, affected the magnitude of increase in soil emissions. Land-use changes in wetter ecosystems resulted in greater increases in CH_4 fluxes, but reduced N_2O fluxes. An interacting suite of soil variables influenced CH_4 and N_2O fluxes, with availability of inorganic nitrogen (i.e. extractable ammonium and nitrate), pH, total carbon, and microclimate being strong mediators of effects of land-use change. In addition, time after a change in land use emerged as a critical factor explaining the effects of land-use change – with increased emissions of both greenhouse gases diminishing rapidly after conversion. Further research is needed to elucidate complex biotic and abiotic mechanisms that land-use change, and in particularly during this initial disturbance when greenhouse gas emissions are increased the most relative to native vegetation. Efforts to mitigate emissions will be severely hampered by this gap in knowledge.

Keywords: afforestation; climate change; cultivation; deforestation; global change; greenhouse gas emissions; methane; nitrous oxide;

Abbreviations: carbon, C; carbon dioxide, CO_2; greenhouse gases, GHG; methane, CH_4; land use change, LUC; mean annual temperature, MAT; mean annual precipitation, MAP; nitrogen, N; nitrous oxide, N_2O; response ratio, RR;

Introduction

Producing food and fibre for 9 billion people by 2050 will be one of this century's most critical and formidable challenges (Godfray and others 2010). Past solutions to the on-going challenge to produce more food has been to convert more natural ecosystems to agro-ecosystems, a type of land-use change (LUC). Many now question the sustainability of continuing LUC to increase food and fibre supply (e.g. Brussaard and others, 2010; Power, 2010; Mueller and others, 2012), in large part due to both known and unknown consequences for ecosystem attributes (e.g. soil structure, carbon storage in soil and vegetation, biodiversity) and processes (e.g. nutrient cycling, water yield and quality, primary productivity). Soil greenhouse gas (GHG) emissions are an obvious and important example of the latter. The importance of soils in global cycles of C and N, highlight the need to more fully understand the consequences of LUC.

Soils in natural and intensively managed ecosystems differ in many ways. Some of the more significant differences are: i) lasting physical effects of the initial disturbance when a natural ecosystem is converted to a managed agroecosystem, ii) flora or fauna in managed systems are often markedly different to natural systems (and often have reduced diversity), and iii) external inputs of nutrients (e.g. fertilizer) are usually much larger in managed systems. There are also secondary effects, such as prolonged disturbance (i.e. tillage, use of heavy machinery) or introductions of flora with different biophysical characteristics (e.g. introduced annuals or legumes). All have the potential to significantly alter GHG fluxes between soils and the atmosphere.

Amongst the better-known effects of LUC on soils is change in soil carbon (C) stocks (Guo and Gifford 2002; Nyawira and others 2016). Nonetheless, actual changes in soil C depend on the type of LUC. Native forest converted to tree plantations decreased soil C by

13%, while conversion to crops decreased soil C by 42%. On the other hand, a native forest converted to pasture resulted in an increase in soil C (+8%, Guo & Gifford, 2002). These changes in soil C can be reflected in changes in CO_2 fluxes after conversion to human uses (Dale and others 1991; Raich and Schlesinger 1992; Tate and others 2006). Non-CO_2 greenhouse gases of biogenic origins – methane (CH_4) and nitrous oxide (N_2O) – are sensitive to LUC, because both soil CH_4 and N_2O fluxes are regulated by highly-specialized groups of microorganisms (Firestone and Davidson 1989; Conrad 2009; Tate 2015).

Globally, soils are a net source of atmospheric CH_4 as a result of emissions from flooded soils where anoxic conditions lead to methanogenesis; a microbial process that reduces CO_2 to CH_4 under anaerobic condition. On the other hand, methanotrophic (CH_4-oxidizing) bacteria mitigate CH_4 emissions by consuming endogenous CH_4 before it is released to the atmosphere. Up to 80% of the upward diffusive flux of CH_4 can be consumed by methanotrophs before reaching the atmosphere (Conrad and Rothfuss 1991). Furthermore, well-drained aerobic (upland) soils are a known sink for atmospheric CH_4 (Harriss and others 1982) and make up an estimated 6% of the total global CH_4 sink (Smith and others 2000; Solomon 2007). This is largely due to the abundance and activity of CH_4-oxidizing bacteria in these soils (Bender and Conrad 1992; Kolb 2009; Knief 2015). This small, yet important sink is also highly sensitive to anthropogenic activities (Tate 2015), and likely a result of the sensitivity of the high-affinity CH_4 oxidizers to a range of environmental factors (Dunfield 2007).

LUC can increase CH_4 fluxes, or decrease the strength of the CH_4 sink in upland soils (Keller and others 1990; Priemé and Christensen 1999; Nazaries and others 2011). Other studies have reported that LUC reduces fluxes (Verchot and others 2000; Galbally and others 2010; Mapanda and others 2010; Benanti and others 2014). Within land-use categories, such as croplands or pastures, practices like tillage and fertilization have significant effects on CH_4

sinks (Ball and others 1999; Venterea and others 2005; Sainju and others 2012), but the direction (increase or decrease) and magnitude of change varies strongly from study to study.

Nitrous oxide - a GHG 300 times more potent than CO_2 (Solomon 2007) - is produced during both nitrification and denitrification processes (Firestone and Davidson 1989). As with CH_4, some soils also act as sinks for N_2O (Chapuis-Lardy and others 2007). Even pristine ecosystems can be significant contributors of N_2O to the atmosphere depending on climate, soil type, and vegetation. Forested ecosystems in the tropics, for example, are often strong contributors of N_2O to the atmosphere (Keller and Reiners 1994; Verchot and others 2000). Fertilizer nitrogen (N) addition to agroecosystems are amongst the strongest drivers of increased global emissions of N_2O (van Lent and others 2015; Stehfest and Bouwman 2006; Liu and Greaver 2009; Aronson and Allison 2012; Shcherbak and others 2014). A previous meta-analysis showed that CO_2 sequestration via increased biomass, may be offset by as much as 53-76%, if emissions of CH_4 and N_2O are increased by additions of fertilizer N (Liu and Greaver 2009). But what other features of LUC could alter CH_4 and N_2O emissions?

Much like the LUC effect on methanotrophs, we poorly understand the LUC effect on soil microorganisms that regulate N_2O. Many LUC studies have shown opposing trends for fluxes of CH_4 and N_2O. In other words, LUC can result in greater contributions to the atmosphere of one gas, while reducing contributions of the other (Keller and Reiners 1994; Galbally and others 2010; Livesley and others 2011; Carmo and others 2012; Benanti and others 2014). Recently, machine learning algorithms and regression tree analyses have been applied to predicting GHG outcomes of complex, interacting soil processes (e.g. Saha and others 2017). The striking inconsistencies in effects of LUC, and lack of understanding of driving mechanisms, further emphasise the need for a comprehensive, quantitative review.

We used a global meta-analytical approach to help resolve key critical questions surrounding land-use change effects on upland soil CH_4 and N_2O fluxes. In particular:

1. What are the overall LUC effects on soil CH4 and N2O fluxes and can they be reversed?
2. Which land-use change causes the greatest change to soil CH_4 and N_2O fluxes, and which ecosystems are most vulnerable to LUC?
3. What variables regulate LUC effects on soil CH_4 and N_2O fluxes?

This meta-analysis differs from others in seeking to elucidate mechanisms underpinning observed CH_4 and N_2O fluxes, and how LUC alters soil processes, (Question #3). We thus collated a large suite of environmental and soil data, along with CH_4 and N_2O flux data, in order to explore the LUC effect on these two greenhouse gases (Table 1).

Materials and Methods

Literature Search and Data Collection

We searched ISI Web of Science in 2014 for the operators *(soil AND (methane OR CH4)) AND (soil AND ("nitrous oxide" OR N2O))* for all of the manuscripts containing soil CH_4 and N_2O fluxes (8,593 results). Then we narrowed this selection with the refining operators - *"land use change" OR "land use"* (353 results). These results were then screened to 62 studies that met our criteria. These criteria included: 1) measured soil CH_4 and/or N_2O from at least two land uses, and 2) studies that had at least one treatment representing native vegetation or a natural ecosystem that had not been recently converted, or a human land use (e.g. agriculture). These studies were often 'side-by-side' or paired land use comparisons, typically comparing a human land use to that of a natural ecosystem. There are also a number of studies of reversing from human land use back to 'natural ecosystems'.

We included a handful of studies that have experimentally manipulated conversions of land use, and then measured the effects on GHGs immediately afterward. 3) Finally, we focused on upland soils due to their importance as a global CH_4 sink (Tate 2015). We thus excluded wetland studies. We only included peer-reviewed literature, and 'grey literature' was not included due to it being difficult to find (not appearing in ISI Web of Science), and also often not having the scientific rigor of peer-reviewed publications. In addition to a broad search and selective screening, we used publications' reference sections as a guide to further potential publications.

Our primary data set consisted of soil CH_4 and N_2O fluxes. We included additional soil properties, moderating variables, and study characteristics that might influence land use effects on soil GHG emissions (Table 1). We thus collected data on eight soil variables that are commonly measured in coordination with GHGs. We divided these variables into two types: slow-changing and fast-changing. Slow-changing variables are those that are unlikely to change within one year (or perhaps a decade or more), such as total organic carbon (TOC), total nitrogen (TN), soil pH, and bulk density (BD). The fast-changing variables are those that change from day to day, or perhaps even within one day. These include soil temperature, soil moisture, and extractable inorganic N (or ammonium and nitrate). Soil moisture (Moist) was reported in papers as % gravimetric water content, water-filled pore space, and volumetric water content. Since we are concerned with changes due to LUC, we represent all measures of soil moisture as relative ratio or change (unitless) as a result of LUC.
Moderating environmental variables were defined as those that influence effect sizes in other soil meta-analyses (Tonitto and others 2006; Aronson and Allison 2012; Dooley and Treseder 2012; McDaniel and others 2014b); mostly climate variables and soil type (commonly approximated by texture). All data were collected either from text or tables or were extracted from graphs using GetData Graph Digitizer 2.26 (Sergei Fedorov, Russia).

Data handling and Meta-analysis

CH_4 and N_2O data were first converted to common units (μg GHG m^{-2} h^{-1}). Once converted, a land-use response metric was calculated for each individual observation for each gas. In order to cope with both negative and positive fluxes of CH_4 and N_2O, that invalidate the use of a 'response ratio' as a metric of effect size (Koricheva and Gurevitch 2014), we used the metric U_{GHG} (U_{CH4} and U_{N2O}, van Groenigen and others, 2011).

$$U_{GHG} = GHG_{new} - GHG_{prev}$$

U_{GHG} is the difference between the flux for a new land use (GHG_{new}) and the previous (GHG_{prev}). This metric remains in the common units of gas flux. For non-negative soil variables, we calculated a land-use effect via the response ratio (RR).

$$\ln RR_{soil} = \ln X_{new} - \ln X_{prev} = ln \frac{X_{new}}{X_{prev}}$$

Where RR_{soil} is the response ratio between means either at the observation level or between the new and previous land use.

A weighted approach was used to calculate effect sizes at the comparison level. This weighting approach incorporated replication and the number of observations for each comparison. Weightings were used owing to the variation in numbers of replications and observations. We gave more weight to studies with greater spatial or temporal replication. We gave less weight to individual studies with large numbers of comparisons so as to not have a disproportionate effect on global means. Similar to van Groenigen and others (2011), we weighted by replication with $W_R = (n_{new} \times n_{prev}) / (n_{new} + n_{prev})$, where n_{new} and n_{prev} are the replication in the new and previous land uses. Then we weighted by number of observations per comparison $W_{F,i} = W_R / n_c$, where the final weights (W_F) are calculated by dividing the number of i^{th} observations. Then the mean effect sizes for each comparison ($\overline{U}$) were calculated as:

$$\overline{U} = \sum_i (U_i \times W_{F,i}) \Big/ \sum_i W_{F,i}$$

Where $\overline{U}$ is the mean effect size for each gas. Mean effect sizes were then used in the overall meta-analysis, whereas observation effect sizes were used only for correlations with fast-changing soil variables, where these variables were measured in coordination with each greenhouse gas measure. Global warming potential (GWP) was calculated for each gas using the ratios of 34 and 298 for CH_4 and N_2O, respectively (Myhre and others 2013).

Final mean effect sizes and 95% bootstrapped confidence intervals were calculated using MetaWin v2.1 (Rosenberg and others 2000). All categorical comparisons conducted in MetaWin were set on random effects and the 95% bootstrapped confidence intervals (CI) were calculated with 9999 iterations. The overall effect was deemed significant if the CI did not overlap with zero. Total group heterogeneity (Q_T) was partitioned into within-group (Q_w) and between-group (Q_b) heterogeneity, similar to partitioning of variance in ANOVAs. A minimum of five comparisons were used to calculate Q_b, and differences between groups (or comparisons) were deemed significant if the CI did not overlap.

Factors controlling LUC effects on CH_4 and N_2O fluxes

Univariate correlations among effect sizes of soil variables with GHGs were conducted in SAS 9.3 (SAS Institute, Cary, NC) with *proc corr* and Pearson correlation coefficients are reported. We also used non-parametric Random Forest analysis to understand the variables, and their interactions, that best explain the variations in CH_4 and N_2O fluxes as influenced by LUC (Breiman 2001). The relative change (RC), or per cent change, in a soil variable was calculated with respect to the control treatment as (GHG_{new} –

GHG_{old}) / GHG_{old} × 100. The RC > 0 indicates greater value of the variable under consideration in the converted LU, or new, than that in the control, or old LU. Missing data were imputed by *missForest* package in R (Stekhoven and Bühlmann 2011). Out-of-bag error estimates of the imputation method was 0 (proportion of falsely classified entries) and 0.28 (normalized root mean square error) for the categorical and continuous variables, respectively. The *randomForest* function from R *randomForest* package (Liaw and Wiener 2002) was used on the imputed data with the control parameters *ntree* = 500 (number of trees) and *mtry* = 3 (number of variables considered for splitting at each node). Explanatory variables considered in the analysis were: direction of LUC (neutral, converted, and reverse), time since LUC (years), fertilization (yes/no), mean annual temperature (MAT, °C), mean annual precipitation (MAP, mm), soil clay (%), and relative changes in soil pH (RC_pH), soil ammonium (RC_NH_4), soil nitrate (RC_NO_3), total N (RC_TN), total soil organic carbon (RC_TOC), soil moisture content (RC_Moist), soil bulk density (RC_BD), soil temperature (RC_Temp). The *importance* function in R *randomForest* was used for variable importance scores. Importance for a variable is interpreted as increase in mean square error (%IncMSE) due to random permutation on that variable. The R *tree* package was used to construct conditional inference tree for U_{N2O} and U_{CH4}. Upon satisfaction of each node, the tree moves to the left branch to the next node. Each terminal node represents average U_{N2O} or U_{CH4} and number of observation corresponding to that node (n).

Results

Effects of LUC on CH_4 and N_2O

The 62 studies included in this meta-analysis spanned all six inhabited, continental regions – 5% Africa, 11% Asia, 15% Australia & New Zealand, 21% Europe, 33% North America, and 15% South America (Table S1). The studies included broad ranges in climate:

mean annual temperatures (MAT) from 2.2 - 27.8 °C, and mean annual precipitation (MAP) from 97 – 3962 mm. More than 70% of the studies that reported soil classification data, were from within eight of the 12 USDA soil orders (absent were Gelisols, Spodosols, Vertisols, and Mollisols). Soils ranged in clay content from 2 to 58%. We classified studies according to land uses: cropland, tree plantations, pastures, and urban (Fig. 1). There were very few studies that had urban land uses (n = 4), but urban ecosystems would be characterized as being in highly-populated residential areas, urban or suburban, with lawn or turf and ornamental trees. The time after land-use change ranged from 0.33 to ~200 years. We could not determine the exact time elapsed since LUC for several longer-term studies.

There was large variability in CH_4 and N_2O fluxes (Fig. 1, Fig. S1). Methane fluxes ranged from -322 to 588 µg CH_4 m^{-2} h^{-1} across all land uses. The greatest CH_4 uptake (most negative flux) was recorded for a loamy grassland (Boeckx and others 1997), while the strongest contribution to the atmosphere was recorded for a 20 year-old pasture (Steudler and others 1996). N_2O fluxes ranged from -194 to 1063 µg N_2O m^{-2} h^{-1}, albeit that both extreme values were measured in the same bamboo plantation in China (Liu and others 2011). Forest soils generally consumed atmospheric CH_4 - median (-28) and mean (-35 µg CH_4 m^{-2} h^{-1}) fluxes reflecting the dominance of negative fluxes in forests (~95% of studies, Fig. 1). Overall, pastures were also sinks for CH_4 (median flux = -0.01 µg CH_4 m^{-2} h^{-1}, mean flux = -2 µg CH_4 m^{-2} h^{-1}). We grouped all herbaceous-dominant ecosystems (shrubland, savannah, and grasslands) into one category: herbaceous ecosystems. Herbaceous ecosystems produced the smallest median and mean N_2O fluxes (1 and 4 µg N_2O m^{-2} h^{-1}). Urban soils produced the greatest median N_2O flux (35 µg N_2O m^{-2} h^{-1}), and tree plantations had the greatest mean flux (62 µg N_2O m^{-2} h^{-1}). All 40 measurements of urban soils were derived from just two studies (Kaye and others 2004; Chen and others 2014).

Changing land uses from a ‘natural’ system to any human use, increased CH_4 fluxes by 14 µg CH_4 m^{-2} h^{-1}, and N_2O fluxes by 7 µg N_2O m^{-2} h^{-1} (Fig. 2). Comparisons among studies suggest that reversing land use (to a more ‘natural ecosystem’) could reduce CH_4 fluxes by 11 µg CH_4 m^{-2} h^{-1}. However, reversion had little effect on N_2O fluxes. N_2O fluxes actually increased when land use was reversed to that resembling a natural system, by an average of 6 µg N_2O m^{-2} h^{-1}, but not significantly (CI overlaps with zero). Changing from one intensive land use to another tended to reduce CH_4 fluxes (but not significantly, based on four studies or 32 observations), and there were too few data to assess this influence on N_2O fluxes (Fig. 2).

We adopted the widely used weighted approach for meta-analysis. This approach allows for the wide range of experimental designs and replication across the 62 included studies. Nonetheless, there are arguments for and against this such approaches (Gurevitch and Hedges 1999; Philibert and others 2012; Koricheva and Gurevitch 2014). For example, a common issue in meta-analyses is whether or not to give extra emphasis on studies with more precision, if variances are known. We present the calculated, global warming potential due to LUC (GWP, from CH_4 and N_2O) in both weighted and unweighted format (Table 2) so that readers may thus choose their preferred approach. Weighting mostly reduced mean GWPs, consistent with a conservative approach to estimating overall effects of LUC. Conversion of land from a state of ‘natural ecosystem’ to intensive human use, resulted in a net increase of 234 kg CO_2-equivalents ha^{-1} y^{-1} (or 376 if unweighted, Table 2). Reversing this conversion also increased GWP by 132 kg CO_2-equivalents ha^{-1} y^{-1} (or 104 if unweighted), albeit this result was not significantly different to zero.

The type of the original ‘natural’ vegetation, had very little effect on both greenhouse gases (Fig. 2). Only when the final land use was tree plantations, was converting forests to human uses more significant for CH_4 fluxes than converting herbaceous ecosystems (+13 and

-8 µg CH_4 m^{-2} h^{-1}, respectively, Fig. 2). Conversions among previous and current land uses (forest or herbaceous) had no effect on N_2O fluxes (Fig. 2), albeit largely due to variability and the small number of studies of N_2O fluxes relative to CH_4 fluxes.

Pooling prior land uses revealed few differences in CH_4 fluxes among new land uses – irrespective if the new use was either intensive management or a restored natural use (Fig. S2). Of four contrasts combining 'natural systems', only changes in herbaceous ecosystems to a pasture (+25 µg CH_4 m^{-2} h^{-1}), had a significantly greater effect than a change to tree plantations (-8 µg CH_4 m^{-2} h^{-1}, P = 0.008, Fig. 2). Cropping system type had little effect on CH_4 fluxes (Fig. S2), although converting to barley (24 µg CH_4 m^{-2} h^{-1}) had a greater effect than converting to wheat (-1 µg CH_4 m^{-2} h^{-1}). Many studies did not report if fertilizer N was included in the human land use (nearly 50% of studies). When that data were available, there was a marginally significant effect (+13 µg N_2O m^{-2} h^{-1}) of added N on N_2O emissions (P= 0.053, Fig. S2).

Drivers of LUC effects on CH_4 and *N_2O*

Effects of "elapsed time since land-use change" on GHG emissions were significant (Ps < 0.014) for conversions from natural forests to human land use (Fig. 3). The best fit model for both GHGs was exponential decay. Mean U_{CH4} was ~ 50 µg CH_4 m^{-2} h^{-1} immediately after conversion, but this then declined by about 0.1 µg CH_4 m^{-2} h^{-1} per year. After roughly 30 years, modelled fluxes stabilized and remained about 28 µg CH_4 m^{-2} h^{-1} above that of the previous land use. Mean U_{N2O} was 27 µg N_2O m^{-2} h^{-1} immediately after conversion, and then declined more quickly, by about 0.2 µg N_2O m^{-2} h^{-1} per year before stabilizing after ~ 40 years. At that point, N_2O fluxes were roughly equivalent to those of the previous land use.

Univariate analysis shows that amongst climate and edaphic factors, MAP had the clearest influence on CH_4 fluxes (Fig. 4). The LUC effect on CH_4 was positively related to precipitation ($P < 0.001$), while reversion to 'natural' land uses was negatively related ($P < 0.001$). N_2O fluxes were negatively related to MAP ($P = 0.011$) when land use changed to cropland or plantations. Soil texture (% clay) had no influence on the role of LUC in fluxes of either gas, however, there was a marginally significant (negative) correlation between U_{CH4} and % clay ($P = 0.052$, Fig. 4). We also examined interactions of MAT and MAP on U using contour graphs (Fig. S3). When natural vegetation was converted, CH_4 fluxes increased most in cold-wet and warm-wet conditions, whereas N_2O fluxes increased most at moderate MAT and MAP (15-20 °C, 1500-2500 mm) and cold-dry conditions. Reversion of land use to 'natural ecosystems' had greatest effects on CH_4 fluxes under moderate MAT and dry conditions; while N_2O fluxes respond most strongly on warm and wet sites.

There were unexpected and inconsistent univariate relationships among slow-changing variables and effects of land use change on soil CH_4 and N_2O fluxes. For example, LUC had effects on soil pH (Fig. 5), but gas fluxes showed divergent responses – U_{CH4} increased while U_{N2O} decreased with pH. Effects on CH_4 fluxes resulting from reversing LUC were negatively related to effects on total organic C (TOC, $P = 0.036$) – land uses that increase TOC reduce CH_4 fluxes. However, there was no relationship between LUC effects on total soil nitrogen and fluxes of either gas. Although there was no clear linear relationship with soil bulk density (Fig. 5), where LUC results in increased bulk density CH_4 fluxes are mostly increased (except for three observations – Simona and others, 2004; Mapanda and others, 2010; Galbally and others, 2010).

Land-use effects were best correlated with fast-changing soil variables (Fig. 6). Changes in use that increased soil temperature, on average increased CH_4 fluxes by 0.34 µg CH_4 m^{-2} h^{-1} per °C increase in soil temperature ($P = 0.034$). Even so the strongest effect of

LUC was through its influence on soil moisture ($P < 0.0001$, Fig. 6). For every 1 % increase in soil moisture, CH_4 fluxes increased by 0.65 µg CH_4 m^{-2} h^{-1}. LUC effects on N_2O were also closely related to soil moisture ($P < 0.001$), albeit negatively. Concentrations of extractable inorganic N (nitrate, ammonium) in soils were clear drivers of the LUC effects on both CH_4 and N_2O fluxes (Fig. 6). LUCs that increased soil NH_4^+ increased fluxes of the two greenhouse gases – U_{CH4} marginally ($P = 0.092$) and U_{N2O} significantly ($P = 0.024$). Reversion of land use produced a negative correlation between NH_4^+ and U_{CH4} (Fig. 8, $P = 0.077$) and U_{N2O} (Fig. 8, $P = 0.004$). If LUC reduced concentrations of soil NO_3^-, then CH_4 fluxes increased ($P = 0.004$). Extractable NO_3^- had a different relationship with LUC and N_2O fluxes. U_{N2O} was positively related to the LUC effect on NO_3^- for conversions from natural to intensive uses ($P < 0.001$, Fig. 6).

Using multiple interacting variables within a regression tree model, again shows that fast-changing variables such as soil NH_4^+ and NO_3^- are key drivers of LUC effects on CH_4 and N_2O emissions (Table 3). Predicted U_{CH4} and U_{N2O} were significantly correlated with observed values ($R^2 > 0.90$, $P < 0.05$). The regression tree model underestimated at higher ranges of U_{CH4} and U_{N2O} (Fig. S4) yet still explained 58% of the variation in observed U_{CH4} and U_{N2O}.. Regression tree analyses provided a classification of the LUC effect on GHG emissions. Changes in soil mineral NH_4^+ and NO_3^- due to LUC produced clear bifurcation in both U_{CH4} and U_{N2O} regression trees (Fig. 7 and 8). If there are reductions in soil NO_3^- associated with converting one intensive land use to another, or with reversion of a land use to natural conditions, then CH_4 uptake is increased (Nodes 1 and 2, Fig. 7). In general, and as expected, LUCs that increase soil NH_4^+ and NO_3^- also increase N_2O fluxes (Nodes 3 and 5-8, Fig. 8).

Discussion

Land-use change is just one direct way in which humans are altering soil processes. In the Anthropocene, however, many human activities now have a global reach so that even what appear to be 'natural' ecosystems (which humans have not begun to physically manage) are now in some way affected by human activities (Wohl 2013). Nonetheless, drawing conclusions about impacts of LUC on GHG fluxes from soils, based on comparisons with so-called 'natural' or 'undisturbed' ecosystems, must be conditioned by recognition that human influence is not restricted to land use. Pollution and invasive species, for example, are just two ways humans indirectly influence all ecosystems (Akimoto 2003; Vilà and others 2011; Cronk and Fuller 2014). Our analysis is focused on synthesizing and quantifying broad effects of LUC on soil-atmosphere CH_4 and N_2O fluxes, *beyond* those caused by indirect human activity.

What are the overall LUC effects on soil CH_4 and N_2O fluxes and can they be reversed?

Converting land to more intensive uses increased CH_4 fluxes by 14 µg m^{-2} h^{-1}, and N_2O fluxes by 7 µg m^{-2} h^{-1} (Fig. 2). When converted to CO_2-equivalents, the LUC effect on N_2O was nearly three times that of CH_4 (Table 2). Conversely, when land use reverts to more natural conditions, gas fluxes often remained greater than under the original use (Table 2). However, active reversion of land use (e.g. from agriculture to native forest) remains a likely means of regenerating net CH_4 uptake primarily via increased oxidation (Figs. 2 & 3, Table 2; see Priemé and others 1997; Hiltbrunner and others 2012). On the other hand, N_2O fluxes increased after LUC *and* after reversing or restoring native vegetation (Fig. 2 and S2). Although, there are studies which show that converting cropland back to native vegetation could reduce N_2O emissions (by up to 29%, Robertson and others 2000). Our meta-analysis demonstrates that simply reverting back to ‘natural’ ecosystems may not always mitigate soil GHG emissions.

The differences between LUC effects on CH_4 and N_2O fluxes are not fully understood. Persistent changes in N_2O fluxes have been discussed mostly in terms of overall changes in the N cycle (Erickson and others 2001; Scheffer and others 2001; Hiltbrunner and others 2012), and as legacy effects of N addition on nitrification and denitrification. A recent analysis of LUC effects on N_2O emissions in Brazil speculated that changes in soil micro-aggregate structure, might explain a new “steady state” (Meurer and others 2016). This long-term change in soil structure could have cascading effects on soil water content and movement, and thus also impact GHG emissions.

Changes in the fluxes of both gases were greatest in first ten years after a change in land use (Fig. 3), and an exponential decay model best explains the global patterns in this period. We compared our global N_2O model to Meurer and others (2016) and Neill and others (2005) studies which focus on Brazilian ecosystems (Fig. 3). Both show rapid declines in the LUC effect on N_2O fluxes (also confirmed by conceptual curve in van Lent and others (2015)). Our global synthesis suggests that LUC will result in N_2O fluxes that approach that of native vegetation (or U_{N2O} = ~0 µg m^{-2} h^{-1}) at around 12 years after conversion. Meurer and others (2016) and van Lent and others (2015) model suggest that if subtropical forest land is converted to pasture, N_2O fluxes will eventually be lower than had the land remained forest (U_{N2O} = ~ -15 µg m^{-2} h^{-1}). A general problem with LUC studies is that selection of the ‘reference’ (or native) land use, can dramatically change the outcome. For example, some tropical forests are known for their fast rates of N turnover and relatively high N_2O emissions (discussed further below). By contrast, the pastures created by converting such forests can quickly become degraded, seldom receive N fertilizer, and can have low N_2O emission relative to native tropical forests (Meurer and others 2016). .

Forest harvesting studies have some relevance to the issues of LUC discussed here. Harvesting-induced changes in fluxes of N_2O are greatest within the first few months (Steudler and others 1991; Keller and others 1993; Tate and others 2006; McDaniel and others 2014a). During this period, when a flush of carbon and nutrients is added to the soil in vegetation debris, soil microbial activity is stimulated by warmer and wetter conditions in the absence of plant 'sinks' for N and water – such that nitrification and denitrification are enhanced (Hendrickson and others 1989; Johnson 1992; Mariani and others 2006). In a meta-analysis restricted to tropical forests, van Lent and others (2015) showed a similar trend with N_2O fluxes peaking at ~ 4 kg N_2O-N ha^{-1} y^{-1} shortly after harvest, then declining over 50 years to < 1 kg N_2O-N ha^{-1} y^{-1}. Saha and others (2017) also observed increased N_2O emissions in the second year after LUC. Effects of LUC on total soil N_2O (and CH_4) fluxes are likely underestimated if this initial period is not properly considered. Consistently declining effects of LUC on CH_4 and N_2O fluxes also suggests that subsequent management actions (e.g. tillage or fertilization) may not be as important as the original disturbance.

Which land-use change causes the greatest change to soil CH_4 and N_2O fluxes, and which ecosystems are most vulnerable to LUC?

Somewhat surprisingly, our synthesis suggests that LUC effects on fluxes of CH_4 and N_2O (especially) are largely independent of both final land use (Fig. 2), and previous land use (Fig. 2 and S2). The exception to this is conversion effects on CH_4 fluxes in herbaceous ecosystems. For instance, herbaceous-to-cropland and herbaceous-to-pasture conversions increased CH_4 emissions by +16 and +26 µg CH_4 m^{-2} h^{-1}, on average, versus herbaceous-to-plantation which decreased emissions by -8 µg CH_4 m^{-2} h^{-1} (Fig. 2). The most likely explanation for this finding are changes in soil moisture or quantity/quality of C inputs to soils. Methane fluxes are tightly linked to soil moisture and even changes to land uses that are managed more intensively that might decrease soil moisture (e.g. via changes to leaf area) might be expected to decrease CH_4 fluxes, mostly through increased CH_4 oxidation (Keller and Reiners 1994; Steudler and others 1996; Hiltbrunner and others 2012). Changing from natural herbaceous vegetation, to woody trees will undoubtedly change distribution, quantity and quality of C inputs to soils. There is now good evidence showing CH_4 oxidation is linked to labile soil C (Sullivan and others 2013). Both of these factors, soil moisture and changes in soil carbon, will be discussed further below.

We are limited in predicting sensitivity of GHG emissions from natural to managed ecosystem for many reasons (some discussed further below); but this is especially the case for N_2O which had fewer studies and amongst the studies we included there was much more variation than CH_4. This is unfortunate due to N_2O's outsized contribution to overall GHG emissions (Table 2). Furthermore, some important land uses are notably underrepresented here – like urban and suburban land uses (just four studies), which rapidly replacing native vegetation and agricultural land uses worldwide (Foley and others 2005). Urban land use has the potential to be a major contributor to overall GHG fluxes (Fig. 1), especially since even conversion from agricultural use to urban increases CH_4 emission by 9.5 μg m^{-2} h^{-1} and N_2O emissions by 6.2 μg m^{-2} h^{-1} (Fig. 2).

What variables moderate LUC effects on soil CH_4 and N_2O fluxes?

Our approach to address this question includes both univariate and multivariate non-parametric analyses. Across the 62 studies included in this meta-analysis, a range of edaphic and climate variables modified effects of LUC on CH_4 and N_2O. No single variable, nor even pair of variables (Fig. S3), had identical influence on both GHGs, and their interactions were complex (Figs. 7 and 8, Table 3). However, soil extractable inorganic N and soil moisture emerged as two of the most salient drivers of LUC effects on both gases through both univariate and multivariate regression approaches.

Mean annual precipitation (MAP) exerted a strong and distinct relationship with LUC effects on CH_4 fluxes (Fig. 4). Apart from its direct influence on soil microbial activity, soil moisture often dictates rates of O_2 diffusion is critical to both rates of CH_4 production and oxidation. Relationships between CH_4 and soil moisture can fluctuate with time (Verchot and others 2000) and are often strongly dependent on soil texture, as reflected in our regression tree analysis (Table 3). For CH_4 fluxes, LUC effects were strongest in wetter ecosystems – or more positive when converting to intensive land uses (+50 μg CH_4 m^{-2} h^{-1}) and more negative when reversing to 'natural' vegetation (-50 μg CH_4 m^{-2} h^{-1}). These trends emphasize the critical role of soil moisture in CH_4 dynamics (Keller and Reiners 1994; Steudler and others 1996; Carmo and others 2012; Hiltbrunner and others 2012; Tate 2015).

N_2O fluxes, as affected by LUC, were much more variable with MAP, and arguably better related to the direct controlling influence of NO_3^- production/consumption (i.e. nitrification and denitrification) rather than land use itself (Figs. 6 & 8). Indeed, while negative relationships between LUC effects on N_2O fluxes and MAP might seem counter-intuitive (Fig. 4), primary tropical forests (Reiners and others 1994; Arai and others 2014), as well as late-successional tropical forests (Erickson and others 2001), can be significant global sources of N_2O, as are many tropical soils (Reay and others, 2007). Our data synthesis suggests a mean rate of emission of 25 μg N_2O m^{-2} h^{-1} from all forests (Fig. 1). Such high N_2O fluxes in 'natural' forests, but especially in wetter ecosystems (> 2000 mm), ensures that any LUC to human land use will be lower (on average). This statement must be cautioned, however, since many studies do not account for N_2O pulse seen after initial conversion, nor do they accurately account for periodic 'hot moments' like fertilization or tillage events.

Other gaseous N losses, like NO emissions (Neill and others 2005), remain too poorly studied to be included here. The effects of LUC on N_2O fluxes in drier ecosystems appears greater than that in wet systems (Kaye and others 2004; Scheer and others 2008; Mapanda and others 2010). This may be largely due to actually accounting for these "pulses" of N_2O emission after rain events in drier ecosystems. Such pulses comprise a large proportion of annual N_2O emissions in drier ecosystems (Davidson 1992; Kessavalou and others 1998).

Generally speaking, our results suggest that when conversion of land increases soil mineral N availability, increases of both CH_4 and N_2O fluxes also follow (Figs. 6, 7, 8). We must concur with Liu and Greaver (2009). In a global meta-analysis, they found N additions increased CH_4 emission by 97% (reducing CH_4 uptake by 38%), and increased N_2O emissions by 216%. Increased mineral N supply can negatively affect N_2O reduction to N_2 and increases N_2O emissions (Weier and others 1993; Gillam and others 2008). Greater mineral N availability (from N fertilization) has also been reported to slow CH_4 uptake by inhibiting methanotroph activity (Steudler and others 1989; Wang and Ineson 2003). Methane oxidation is N-limited in some cases, but inhibited by N in others (Bodelier and Laanbroek 2004; Aronson and Helliker 2010), with the response determined by many site-specific factors as well as the type and amount of fertilizer N applied.

Using soil NH_4 and NO_3 as proxies for any fertilization, along with any other LUC features affecting N dynamics, allowed us to evaluate the two N species importance in regulating GHG emissions (even though many studies did not include fertilization information). Converted-to and reverted-from managed ecosystems showed opposite, divergent relationships with mineral N and N_2O emissions (Fig. 6). Land use changes that increased N availability, either NH_4 or NO_3, increased N_2O emissions when transitioning from natural-to-human land uses *but* decreased emissions when reversing (human-to-natoral or reversed). Even in unfertilized soils, concentrations of NH_4^+ and NO_3^- in soil reflect a range of competing processes by plants and soil microbes (Kaye and Hart 1997; Schimel and Bennett 2004), and our data show clear opposing trends when land is either converted to and reversed from a managed ecosystem (Fig. 6). This finding highlights the complexity of N cycling, and arguably reflects long-term consequences of N fertilizers for microbial processes.

Soil C and pH have well-established links to CH_4 and N_2O emissions, and here we provide some supporting evidence that concomitant changes in these soil properties and GHG emissions from LUC are related (Fig. 5). The effect LUC has on both of these soil properties, and subsequent effect on GHG emissions, could be through an altered soil microbial community. At the global scale both soil C and pH have shown strong relationships diversity and abundance of soil microbes (Fierer and others 2009; Lauber and others 2009) – this can, for example, be extended to methanotrophs and N-cycling bacteria and archaea. Another possibility, is that changes in soil pH or C quantity or quality, via LUC, increase the activity of methane oxidation or N cycling with little to no effect on abundance or diversity of organisms. Some high-affinity CH_4 oxidizers may use acetate as a substrate (Pratscher and others 2011), and that there is a positive relationship between dissolved organic C and CH_4 oxidation (Sullivan and others 2013). Nitrous oxide emissions can be dually regulated by: 1) enhanced decomposition of soil organic matter and thus increased gross N mineralization either from increased C inputs from greater gross primary production (Benanti and others 2014) – leading to larger pools of NH_4^+ and NO_3^- to be converted to N_2O , or 2) possible reductions in soil pH, especially from coniferous trees, where acidification can inhibit the last step in denitrification leading to more N_2O relative to N_2 (Firestone and others 1980; ŠImek and Cooper 2002; Wang and others 2018). Resolving which of these factors is driving the increase in N_2O is difficult since nitrification frequently covaries with pH. Further research into the driving mechanisms for both gases are needed.

Finally, a subset of our studies (n = 8) measured soil microbial functional genes (*pmoA*, *nirK*¸and *nirS*) involved in soil GHG emissions (Table S2). Seven studies assessed abundance of the *pmoA* gene, which encodes the ß-subunit of the particulate methane monooxygenase enzyme, and is the most common, and perhaps only genetic marker available for detection of all atmospheric CH_4 oxidizers. *pmoA* genes associated with atmospheric CH_4 oxidizers are typically referred to as upland soil clusters, of which there are several. A strong negative relationship between LUC effect on the *pmoA* gene and CH_4 fluxes highlights the importance of these organisms in regulating LUC effects (Fig. S5). Many authors of studies of soil CH_4 fluxes have speculated that these organisms are particularly sensitive to disturbance. This meta-analysis provides some cross-study evidence for such sensitivity, but, again, we lack knowledge at the finer scale.

Limitations of meta-analysis – Spatiotemporal variability of soil greenhouse gas emissions

There is large variation in the experimental designs and methods encompassed here (Table 1 and S1). Temporal and spatial variability remains a major limitation in all studies of soil-atmosphere fluxes of GHG (Velthof and others 1996; Barton and others 2015; Kravchenko and Robertson 2015; McDaniel and others 2017). Nearly all of our 62 studies used paired-site approaches, or reported GHG emissions from two or more sites in close proximity. Paired sites were generally replicated four times (range 1 to 15), while sampling frequency was typically once per month (range: 1 to 8 measurements/week). Spatial and temporal variability of CH_4 and N_2O fluxes can be extreme (Barton and others 2015; McDaniel and others 2017) and all included fluxes could be significant over- or under-estimates. For instance, McDaniel and others (2017) showed that spatial variability in a 16 ha agriculture field can rival that of five months of temporal variability within the same field. To reduce the standard error in reported GHG fluxes to within 10% of their mean values would have required nearly 2000 measurements for CH_4 and over 8000 measurements for N_2O. Barton et al. (2015) reported that daily measurements of N_2O were essential given the known temporal variability, and the uncertainty of flux estimation extends to the methods used in individual flux measurements too (Levy and others 2011; Jungkunst and others 2018).

Spatial and temporal variability limits our ability to detect treatment effects. This is especially the case for critical periods, such as immediately after fertilizer application. N_2O fluxes in this period are frequently many fold, or even order of magnitude, larger than at other times, so not capturing these data could severely underestimate fluxes (Barton and others 2015; Guardia and others 2016). We must thus place greater emphasis on the relatively few, well-replicated studies that capture such events. For example, studies by Dobbie and others (1995, n = 15) and Merino and others (2004, n = 56) are highly valuable. Many studies included here (15 of the 62) had spatial replication of n=3 or less, and half of all included studies (31) had temporal replication of 2 or less. Future studies should explicitly acknowledge the problems of spatiotemporal variability, and utilize known solutions via appropriate sampling and statistical techniques (Barton and others 2015; Kravchenko and Robertson 2015; McDaniel and others 2017; Saha and others 2017a).

Conclusion

It seems inevitable that land uses will continue to change around the globe, and that some soils currently under natural vegetation will be converted to the production of food, fibre, and fuel. Converting more land to production could increase fluxes of methane (CH_4) and nitrous oxide (N_2O) by 234 kg CO_2-eq ha^{-1} y^{-1} (95% confidence range: 84-447). While this is small relative to total CO_2 losses that emanate from LUC (~ 2%, Hansen 2013), our meta-analysis suggests that restoring these lands to 'natural' vegetation would have little effect, at least on decadal time scales. Land management practices that serve to increase CH_4

oxidation or reduce N_2O emissions are good options for land under human use (including further converted land). Future research that focuses on a better understanding of the proximal biotic drivers of the responsible processes seems to be of greater value than more studies quantifying fluxes alone.

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Tables

Table 1. Soil properties, environmental moderating variables, and site and treatment characteristics for studies included in this meta-analysis.

Table 2. Overall effects of land-use change on CH_4 and N_2O greenhouse gas global warming potential (GWP).

Table 3. Importance of interacting variables to effects of LUC on fluxes of CH_4 and N_2O.

Figures

Figure 1. Box plots of soil methane (CH_4) and nitrous oxide (N_2O) fluxes. Herbaceous vegetation includes: shrubland, savanna, and grasslands. Box plots show mean (dashed line), median (solid line), 5th percentile (circle), 10th percentile (whisker), 25th percentile, 75th percentile, 90th percentile (whisker), and 95th percentile (circle). Natural vegetation shown in blue, and converted land uses are in red. The number in parentheses are number of observations from the ecosystem or land-use types.

Figure 2. Effect of land-use change on soil methane (CH_4) and nitrous oxide (N_2O) fluxes. The overall data (filled symbols) and data separated by type of land use (open symbols). These data are further separated by two ecosystem types: Forests and herbaceous ecosystems (shrubland, savanna, and grasslands). U is the difference in greenhouse gas flux between the new and previous land use. The numbers in parentheses are number of overall comparisons.

Figure 3. The effect of land-use change on soil methane (CH_4) and nitrous oxide (N_2O) expressed over the number of years since conversion to the new land use. U is the difference in greenhouse gas flux between the new and previous land use. Herbaceous ecosystems are shrublands, savannahs and grasslands. Natural-to-human (Converted, red circles) and human-to-natural (Reversed, blue triangles) land use changes are shown. Significant ($P < 0.05$) correlations are shown with exponential decay trend lines. Data from Meurer and others (2016) and Neill and others (2005), focused on pasture conversions from Brazilian forests, were adapted to fit our UN_2O format for comparison.

Figure 4. Correlations among land-use change effects on soil methane (UCH_4) and nitrous oxide (UN_2O) with environmental variables: mean annual temperature (MAT), mean annual precipitation (MAP), and percentage of clay in the soil. U is the difference in greenhouse gas flux between the new and previous land use. Natural-to-human (Converted, red circles) and

human-to-natural (Reversed, blue triangles) land use changes are shown. Significant ($P < 0.05$) correlations are shown with linear trend lines.

Figure 5. Correlations among land-use change effects on soil methane (CH4) and nitrous oxide (N2O) with slow-changing variables: total organic carbon (TOC), total nitrogen (TN), pH, and bulk density (BD). RR is the response ratio of that soil variable to land use change – a positive value is increase from new land use, negative is a decrease from the new land use. U is the difference in greenhouse gas flux between the new and previous land use. Natural-to-human (Converted, red circles) and human-to-natural (Reversed, blue triangles) land use changes are shown. Significant ($P < 0.05$) correlations are shown with linear trend lines. Significant ($P < 0.05$) correlations are shown with linear trend lines.

Figure 6. Correlations among land-use change effects on soil methane (CH4) and nitrous oxide (N2O) with fast-changing or dynamic variables: temperature (Temp), soil moisture (Moist), ammonium (NH4), and nitrate (NO3). RR is the response ratio of that soil variable to land use change – a positive value is increase from new land use, negative is a decrease from the new land use. U is the difference in greenhouse gas flux between the new and previous land use. Natural-to-human (Converted, red circles) and human-to-natural (Reversed, blue triangles) land use changes are shown. Significant ($P < 0.05$) correlations are shown with linear trend lines.

Figure 7. Random Forest regression tree analysis for the land-use change (LUC) effects on methane (U_{CH4}). U is the difference in greenhouse gas flux between the new and previous land use. Nodes in the tree are moderating variables expressed as relative change (RC) in percent, which was calculated as: new LU – old LU/ old LU × 100. Variables in this tree include: soil nitrate (NO_3), land use change direction (LUC), and soil total organic carbon (TOC). To read the tree, at each node if the LUC effect is true (e.g. < XX relative change)

then move to the left branch, if not then move to the right. At the ends of the branches are the mean U_{CH4} values associated with that path, and number of comparisons (n) for each terminal node, and box and whisker plots. Box and whisker plots show median (solid line), 5th percentile (bottom circle), 10th percentile (whisker), 25th percentile (bottom of box), 75th percentile (top of box), 90th percentile (whisker), and 95th percentile (top circle).

Figure 8. Random Forest regression tree analysis for the land-use change (LUC) effects on nitrous oxide (U_{N2O}). U is the difference in greenhouse gas flux between the new and previous land use. Nodes in the tree are moderating variables expressed as relative change (RC) in percent, which was calculated as: new LU – old LU/ old LU × 100. Variables in this tree include: soil ammonium (NH_4), soil nitrate (NO_3), and gravimetric water content (GWC). To read the tree, at each node if the LUC effect is true (e.g. < XX relative change) then move to the left branch, if not then move to the right. At the ends of the branches are the mean U_{N2O} values associated with that path, number of comparisons (n) for each terminal node, and box and whisker plots. Box and whisker plots show median (solid line), 5th percentile (bottom circle), 10th percentile (whisker), 25th percentile (bottom of box), 75th percentile (top of box), 90th percentile (whisker), and 95th percentile (top circle).

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