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 explored what soil and environmental factors influenced 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. Reverting to natural ecosystems did not fully reverse those effects, even after 80 years (except for CH_4 fluxes by –12 µg m^{-2} h^{-1}). In general, neither the type of natural ecosystem that was converted, nor the type of anthropogenic land use it was converted to, affected the magnitude of increase in soil emissions. The exception to this is when natural ecosystems were converted to pastures or croplands (emissions increased by +23 and +5 µg CH_4 m^{-2} h^{-1}). A complex suite of variables interacted to influencing CH_4 and N_2O fluxes, but availability of soil inorganic nitrogen (i.e. extractable ammonium and nitrate), texture, pH, and microclimate were the strongest mediators of effects of land-use change. Land-use changes in wetter ecosystems resulted in greater CH_4 fluxes, and effects of land-use change on soil nitrate, total organic C, and pH emerged as the greatest drivers of changes in CH_4 fluxes. Effects of land-use change on N_2O fluxes decreased in wetter ecosystems, and the land-use change effect was regulated primarily via changes in soil inorganic N and water content. Understanding the complicated effects of land-use changes on soil-atmosphere CH_4 and N_2O fluxes, and the mechanisms underpinning such emissions, could inform land management actions to mitigate increased greenhouse gas emissions after changing land uses.

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 key 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 GHGs, highlight the need to more fully understand the consequences of LUC.

Soils in natural and more 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 these LUC features have the potential to significantly alter GHG fluxes between soils and the atmosphere.

Amongst the better-known effects of LUC on soils are changes in soil carbon (C) stocks (Guo and Gifford 2002; Nyawira and others 2016), but 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 are often 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 also 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; for example, up to 80% of the upward diffusive flux of CH_4 can be consumed 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 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 conversion 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). However, some studies have found LUC can reduce fluxes (Verchot and others 2000; Galbally and others 2010; Mapanda and others 2010; Benanti and others 2014). Within types of LUC, such as cropland or pasture, practices like tillage and fertilization can alter the CH_4

sink (Ball and others 1999; Venterea and others 2005; Sainju and others 2012), but the direction (increase or decrease) and magnitude vary from study to study. The large variation in response of GHG emissions to LUC highlights the need for more research.

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 can 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 53-76%, if N additions increase emissions of CH_4 and N_2O (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 opposite trends for fluxes of CH_4 and N_2O, or, in other words, LUC can result in greater contributions to the atmosphere of one gas but reduce contribution of the other (Keller and Reiners 1994; Galbally and others 2010; Livesley and others 2011; Carmo and others 2012; Benanti and others 2014). These striking inconsistencies in effects of LUC, and lack of understanding of driving mechanisms, further emphasise the need for a comprehensive, quantitative review. Furthermore, recent use of machine learning algorithms and regression tree analysis of soil GHG fluxes have allowed us to predict complex, interacting variables and form new hypotheses that were unavailable with previous multivariate techniques (e.g. Saha and others

2017). 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 is the overall LUC effect on soil CH_4 and N_2O fluxes, and does reversing a LUC cause a full recovery?
2. Which land-use change cause 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?

One aspect that differentiates this meta-analysis from others is our approach to elucidate mechanisms through which LUC alters soil processes, ultimately contributing to the changes these studies observe in CH_4 and N_2O fluxes (Question #3). We collected a large suite of environmental and soil data, along with the CH_4 and N_2O fluxes, in order to help explain 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-filled pore space, and volumetric. Since we are concerned with changes due to LUC, we represent all measures of soil moisture as relative ratio or relative change from LUC making it unitless. 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 number 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 ($\bar{U}$) were calculated as:

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

Where $\bar{U}$ 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). The 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. The 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}). However, it is important to keep in mind that the 40 measurements from the urban soils came from 2 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 '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 changed 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 human land use to another tended to decrease 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 used a weighted approach for our meta-analysis because it is most common and the type of experimental designs and replication varied considerably across the 62 included studies. Nonetheless, there are arguments for and against this weighted approach (Gurevitch and Hedges 1999; Philibert and others 2012; Koricheva and Gurevitch 2014). For example, one common weighting issue in meta-analyses is whether or not to give extra emphasis on studies with more precision when variances are given. We present the calculated, global warming potential (GWP) data in both weighted and unweighted format (Table 2) to allow readers to choose which approach is best for overall effect of LUC. Weighting tended to decrease the mean GWP from LUC due to CH_4 and N_2O (except for Reversed LUCs on N_2O fluxes), indicating it is the more conservative approach to estimating overall LUC effect on the two GHGs. When the two GHGs were summed, conversion of land from a natural to a 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 neither were significantly different to zero indicating reversing LUC does not decrease GWP.

Types of LUC, or the 'natural' vegetation the LU was converted from, had very little effect on both greenhouse gases (Fig. 2). Converting forests to human uses had a significantly greater effect on CH_4 fluxes than converting herbaceous ecosystems, but only when the final land use was tree plantations in which case there was a large decrease in fluxes for herbaceous ecosytems (+18 μg CH_4 m^{-2} h^{-1} for forests, and -9 μg CH_4 m^{-2} h^{-1} for SSG, Fig. 2). Conversions among previous and current land uses (forest or herbaceous) had no significant effect on N_2O fluxes (Fig. 2). This is largely due to the high variability (e.g. forest to plantation) and low number of studies measuring soil N_2O fluxes relative to those measuring CH_4 fluxes.

Pooling all prior land uses revealed few differences in CH_4 fluxes among new land uses – irrespective if the new use was either under human management or a restored natural use (Fig. S2). Out of four contrasts combining both 'natural systems', only change to a pasture (+23 μg CH_4 m^{-2} h^{-1}) was significantly greater than forest to crop agriculture (+11 μg CH_4 m^{-2} h^{-1}, $P = 0.008$, Fig. S2). Cropping system type had little effect on CH_4 fluxes, although converting to barley (24 μg CH_4 m^{-2} h^{-1}) produced a greater effect than converting to wheat (-1 μg CH_4 m^{-2} h^{-1}). Despite many studies not reporting if fertilizer N was added (nearly 50% of studies), studies that did include this information showed a marginally significant positive effect (+13 μg N_2O m^{-2} h^{-1}) of adding N fertilizer on N_2O (P= 0.053, Fig. S2).

Drivers of LUC effects on CH_4 and N_2O

Effects of "elapsed time since land-use change" on emissions were significant for forests (Ps < 0.014) but not herbaceous ecosystems, albeit only for conversions from natural 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, fluxes when modelled stabilized and remained about 28 µg CH_4 m^{-2} h^{-1} above 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 and stabilized at ~ 40 years where fluxes were nearly equivalent to prior 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 of land uses to 'natural' conditions was negatively related ($P < 0.001$). Changing land use to agriculture or plantations from previously 'natural' use resulted in N_2O fluxes being negatively related to MAP ($P = 0.011$). Soil texture (% clay) was not significantly related to LUC effect on fluxes of either gas. We found only 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. When human LUs are converted back to 'natural systems', effects on CH_4 fluxes were greatest 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 human land-uses 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 better correlated, individually, with fast-changing soil variables (Fig. 6). LUCs that increased soil temperature, on average, increased CH_4 fluxes by 0.34 µg CH_4 m^{-2} h^{-1} per 1 °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 clearly drivers of the LUC effects on both CH_4 and N_2O fluxes (Fig. 6). LUC effects on soil NH_4^+ correlated well with U_{N2O}, but not as well with U_{CH4}. LUCs that increased soil NH_4^+ also increased fluxes of the two greenhouse gases – U_{CH4} marginally ($P = 0.092$) and U_{N2O} significantly ($P = 0.024$). Reversion of human land use (to natural vegetation) however, 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 human uses ($P < 0.001$, Fig. 6).

Biogeochemical processes responsible for soil N_2O and CH_4 emissions are dynamic in nature and involve multiple interacting factors, which univariate linear models often fail to explain. Using the Random Forest model, and multiple interacting variables, the data show that fast-changing variables such as soil NH_4^+ and NO_3^- are the most important 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 ($R^2 > 0.90$, $P < 0.05$). Nonetheless, the Random Forest model underestimated at higher ranges of U_{CH4} and U_{N2O} (Fig. S4). This model explained 58% and 58.1 % of the variation in observed U_{CH4} and U_{N2O}, respectively. Other variables, such as soil clay and direction of LUC, were more important to U_{CH4} than to U_{N2O}. Regression tree analyses provided a classification of the LUC effect on GHG emissions. Both U_{CH4} and U_{N2O} regression trees show clear splits based on changes in soil mineral NH_4^+ and NO_3^- due to LUC (Fig. 7 and 8). Converting one human LU to another (Neutral), or if human land-use is restored to natural land-use with concomitant reductions in soil NO_3^-, then CH_4 uptake is increased (Nodes 1 and 2, Fig. 7). In general, and as expected, LUCs that increased soil NH_4^+ and NO_3^- also increased N_2O fluxes (Nodes 3 and 5-8, Fig. 8).

Discussion

Converting natural ecosystems to anthropogenic land uses is causing biological, chemical, and physical changes to large parts of the biosphere (Wohl 2013). Drawing conclusions about LUC impacts 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 LUC. 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 is the overall LUC effect of soil CH_4 and N_2O fluxes, and does reversing a LUC cause a full recovery?

Converting land to human use increased CH_4 fluxes by 14 µg m^{-2} h^{-1}, and N_2O fluxes by 7 µg m^{-2} h^{-1} (Fig. 2), but when converted to CO_2-equivalents the LUC effect on N_2O was nearly three times that of CH_4 (Table 2). Conversely, reversing LUC (e.g. to native vegetation) did not fully return fluxes to pre-land-use condition when considering both GHGs (Table 2). However, reversing LUC for recovery of soil CH_4 uptake (or negative fluxes) appears promising (Figs. 2 & 3, Table 2), especially in forests (Priemé and others 1997; Hiltbrunner and others 2012). On the other hand, N_2O fluxes increased after both converting to new LUCs and reversing or restoring native vegetation (Fig. 2 and S2). These findings suggest it is likely that the original strength of the soil sink for CH_4 can be readily recovered via simple reversal of LUC to an ecosystem's natural land use, but N_2O emissions will remain high. The reason for this discrepancy remains unknown, but could be due to a shift in steady state of the ecosystem brought about due to the initial disturbance of converting land uses that only affects the soil N cycling microbial community (Erickson and others 2001; Scheffer and others 2001; Hiltbrunner and others 2012) or 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 microaggregate structure, also not accounted for in this meta-analysis, might explain this new steady state idea (Meurer and others 2016). One study, however, showed converting cropland back to native vegetation could reduce N_2O emissions by up to 29% (Robertson and others 2000). The lack of studies on effects of restoration (or reversing LUC) on soil N_2O emissions, limits our ability to resolve this discrepancy, elucidate specific mechanisms, and make clear recommendations.

We predicted that time elapsed since LUC would have significant effects on GHG fluxes, and found that elapsed time did influence the negative effects on fluxes of converting to human LU, but not returning land to 'natural' conditions (Fig. 3). Soil GHG emissions after conversion from forests were much more responsive than from herbaceous ecosystems, but fewer studies are represented, especially those > 50 years. The greatest effects of LUC on both GHG fluxes were found in the first 1-10 years after land-use changed (Fig. 3), with the greatest effects of LUC immediately after conversion as best fit with an exponential decay model. Methane fluxes due to LUC dropped rapidly after conversion, but remained high for nearly 100 years (~29 μg CH_4 m^{-2} h^{-1}). We compared our model to data from Meurer and others (2016) and Neill and others (2005) that looked at U_{N2O} over time when forests were converted to pasture in Brazil (Fig. 3). Both models show rapid declines in LUC effect on N_2O fluxes after conversion (and confirmed by conceptual curve in van Lent and others (2015)); but the major difference between the trend lines is that we show a converted land, regardless of what it is converted too, will have N_2O fluxes that approach that of native vegetation (or U_{N2O} = ~0 μg m^{-2} h^{-1}). Meurer and others (2016) and van Lent and others (2015), however, show that lands converted to pasture will eventually have lower N_2O fluxes than (sub-tropical) forests (U_{N2O} = ~-15 μg m^{-2} h^{-1}). This discrepancy, and an issue with LUC in general, is that the difference in GHG emissions will largely depend on the type of native vegetation you are comparing the new land use to. Tropical forests are known to have high N_2O fluxes (discussed further below), and many pastures are degraded and not fertilized, therefore have low N_2O fluxes (Meurer and others 2016).

Individual studies on forest harvesting and N_2O find that disturbance-induced fluxes of N_2O are greatest within the first few months to a year or two (Steudler and others 1991; Keller and others 1993; Tate and others 2006; McDaniel and others 2014a). Conditions during these land use transition periods, often major disturbances like whole-tree harvesting, are ideal for large GHG emissions. For instance, soils are typically warmer and moister after the initial disturbance to a new land use, there is a flush of carbon and nutrients from vegetation debris, and fallow ground where there is no plants to take up nutrients (Hendrickson and others 1989; Johnson 1992; Mariani and others 2006). van Lent and others (2015), in a meta-analysis restricted to tropical forests, showed a similar trend with N_2O fluxes peaking at ~ 4 kg N_2O-N ha^{-1} y^{-1} shortly after harvest and 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 during the second year after warm-season grasses were established for bioenergy production in a previously cool-season grassland. Studies relying on measurements long after this initial disturbance period are likely to significantly underestimate effects of LUC on total soil N_2O (and CH_4) fluxes. Consistently declining LUC effects over time for CH_4 and N_2O also suggest that subsequent management actions (e.g. tillage or fertilization) may not be as important as the biogeochemical changes during this initial disturbance from LUC.

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

Our synthesis surprisingly showed that increases in CH_4 and N_2O from LUC are largely independent of both the type of human LU an ecosystem is converted to (Fig. 2), and the type of previous LU (Fig. 2 and S2). This was especially true for N_2O fluxes. Soil CH_4 fluxes in forests are more sensitive to LUC (Fig. S2), albeit for unknown reasons (possibly a sensitivity of soil microbes to disturbance, soil microclimate changes, and/or microbial substrate availability). Since CH_4 fluxes are often tightly linked to soil moisture (Keller and Reiners 1994; Steudler and others 1996; Hiltbrunner and others 2012), we would expect changes in vegetation that reduce soil moisture should reduce CH_4 fluxes; however, relationships among plant life forms and soil moisture are complicated. Soil moisture is often lower in grasslands than forests (Köchy and Wilson 2000; James and others 2003), but is strongly seasonal (James and others 2003). Soil temperatures and rates of evaporation are usually lower in forests, meaning greater soil moisture in forests relative to non-woody vegetation (Köchy and Wilson 1997). Taken together, it is thus slightly paradoxical that the most negative CH_4 fluxes are measured in forests (Fig. 1). Introduction of tree plantations to areas previously covered by herbaceous vegetation (grasses, crops) would be expected to reduce CH_4 emissions to the atmosphere, and this meta-analysis provides some support for this (Fig. 2). Nonetheless, our analysis still allows room for non-soil water influences on CH_4 emissions from forests. These are discussed further below.

Regardless of the original LU, when converted to pasture, CH_4 fluxes increased strongly by about 23 µg CH_4 m^{-2} h^{-1} (Fig. 2). The data presented here provide a partial explanation as to the cause(s) of the strength of this finding. Most likely are differences in soil moisture due to vegetation type and/or increased bulk density (Keller and others 1993; Steudler and others 1996; Tate and others 2007; Price and others 2010; Carmo and others 2012; Grover and others 2012). Univariate regressions also provide some support for these physical and chemical mechanisms (Fig. 5 and 6). Fluxes of N_2O changed strongly when LU changed to tree plantations (23 µg N_2O m^{-2} h^{-1}), followed by changing to cropland (9 µg N_2O m^{-2} h^{-1}). The large increase from converting any land use to tree plantations might be due to two potential factors: 1) enhanced decomposition of soil organic matter and thus increased gross N mineralization either from drying soils or 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 with tree plantations is difficult since nitrification is a strong contributor to decreasing pH (i.e. co-varying).

With an increasing human population, it is inevitable that more urban and suburban land uses will encroach upon native and agriculture land uses (Foley and others 2005). This rapidly increasing land use was largely underrepresented in this study was urban (only four studies), but has the potential to be a major contributor to overall CH_4 and N_2O fluxes due to LUC based on our limited data set (Fig. 1). Even converting land uses already under human management to a different human use tends to increase both CH_4 and N_2O emission – 9.5 and 6.2 µg m^{-2} h^{-1} of CH_4 and N_2O, respectively (Fig. 2). Only by understanding the mechanisms behind these changes in land use will we be able to mitigate increased GHG emissions.

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). MAP exerted a strong and distinct univariate relationship with CH_4 and N_2O fluxes (Fig. 4). Apart from its direct influence on soil microbial activity, soil moisture often dictates rates of O_2 diffusion that in turn are 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 Random Forest analysis (Table 3). For CH_4 fluxes, LUC effects were strongest in wetter ecosystems – more positive when converting to human 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 soil moisture plays in CH_4 dynamics (Carmo and others 2012; Tate 2015), but also how it interacts with LUC. LUC effects on CH_4 fluxes in particular are heavily dependent on the effects of LUC on soil moisture, as has been shown in many previous studies (Keller and Reiners 1994; Steudler and others 1996; Hiltbrunner and others

2012). Our meta-analysis adds to existing knowledge that demonstrates the strong and consistent sensitivity of CH_4 fluxes to LUC under wet conditions.

N_2O fluxes were more variable with MAP and types of LUC, and arguably better related to the controlling influence of NO_3^- production/consumption (i.e. nitrification and denitrification), rather than land use itself. Indeed, while negative relationships between LUC effects on N_2O fluxes and MAP might seem counter-intuitive, 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 tropical soils in general (both natural and agricultural; ~3 Tg y^{-1}, Reay and others, 2007). Our data support this with a mean forest N_2O emission of 25 μg N_2O m^{-2} h^{-1} across our studies (Fig. 1). With the exception of the initial disturbance effect (Fig. 3), overall effects of LUC on N_2O can be obscured by strong background fluxes in these ecosystems and others have shown that measuring only N_2O emissions might miss other impacts of LUC on the N cycle (like NO emissions, Neill and others 2005). Consequently, the magnitude of change in N_2O fluxes in drier ecosystems appears greater than that in wet systems, as a result of LUC (Kaye and others 2004; Scheer and others 2008; Mapanda and others 2010). In large part this may be due to production of larger "pulses" of N_2O after rain events in arid ecosystems, which could likely comprise a larger proportion of overall annual N_2O emissions (Davidson 1992; Kessavalou and others 1998).

LUC effects on soil microclimate, and relationships to CH_4 and N_2O fluxes, are not simple. LUCs that increased soil moisture showed a strong increase in CH_4 fluxes, but not in N_2O fluxes (Fig. 6). Small LUC effects on soil moisture (response ratios between -0.25 and +0.25, Fig. 8) coincided with the greatest GHG responses. This unimodal trend in LUC effects may, in fact, be related to the unimodal relationship of N_2O fluxes with soil moisture (Linn and Doran 1984; Castellano and others 2010). Drier soils produce little N_2O, but once moisture increases beyond a matric potential of ~ -5 kPa, conditions begin to favour complete conversion to N_2, and N_2O production declines commensurately (Linn and Doran 1984; Davidson 1993; Castellano and others 2010).

Generally speaking, our results suggest that when accompanied by increased soil mineral N availability, conversion of land to human uses increased both CH_4 and N_2O fluxes (Figs. 6, 7, 8). Here we concur with Liu and Greaver (2009). However, when human land uses are reversed to 'native' vegetation the opposite relationship is true – with an increase in soil mineral N from LUC, follows lower fluxes of CH_4 and N_2O (Fig. 6). This finding highlights the complexity of N cycling, and arguably reflects long-term consequences of N fertilizers for microbial processes. LUC effects on soil carbon is also likely linked to changes in soil GHGs. Soils rich in organic matter harbor more soil microbes (Fierer and others 2009) – this can, for example, be extended to methanotrophs and by implication to the effects of LUC as well. We still lack the ability to eliminate alternatives such as substrate-specific limitation of CH_4 oxidation. While there is evidence that 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), this is not yet supported by substantial evidence of the effects of LUC on dissolved organic C, let alone specific substrates used in 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 concentrations of both N species show strong relationships with the LUC effect on CH_4 and N_2O (Fig. 6). 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. LUCs that increased concentrations of inorganic N species also tended to increase N_2O fluxes. Addition of surplus N fertilizer probably underpins this relationship (Shcherbak and others 2014), and the complex nature of these relationships is reflected in the data presented here (Figs. 7 and 8).

In support of univariate analyses, the Random Forest analysis presented here also revealed the important role of mineral N availability on CH_4 and N_2O emissions (Table 3 and Figs. 7 and 8). For N_2O fluxes, increasing mineral N availability increases N_2O emissions, more so when LUC also increases soil moisture (Nodes 6 vs 7, Fig. 8). Increased mineral N supply negatively affects N_2O reduction to di-nitrogen 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), but we showed that the inorganic N effect on CH_4 is also regulated by LUC effects on soil pH and total organic carbon too.

Finally, a subset of our studies (n = 8) measured soil microbial functional genes (*pmo*A, *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 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 unique to this meta-analysis – Spatiotemporal variability of soil greenhouse gas emissions

The experimental designs and methods of the studies included here varied widely (Table 1 and S1), but one major limitation with all soil GHG studies is temporal and spatial variability. Nearly all of our 62 studies used paired-site approaches, or where GHG emissions were measured at two or more sites in close proximity. The average replication of these paired sites was n=4 (range from 1 to 15), and average sampling frequency was more than about once per month (range 1/week to 1/8 weeks). Unfortunately, spatial and temporal variability of CH_4 and N_2O fluxes can be extraordinarily large (Barton and others 2015; McDaniel and others 2017) and even the highest sampling density (i.e. replication) and frequencies from these studies could under- or over-estimate true mean fluxes from LUC. 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 from the same field, and that to get a best estimate for the field's GHG flux (10% of mean) would require nearly 2000 measurements for CH_4 and over 8000 measurements for N_2O. Likewise, Barton et al. (2015) found that daily measurements of N_2O are required to get within best estimates of 9 studies over three continents, but a minimum of once per week with proper sampling strategies was recommended. Sampling frequency or density in time and space are just two issues contributing to uncertainty in soil GHG emissions, others have shown that even number of measurements or model used per sampling event can alter flux estimation and contribute to uncertainty too (Levy and others 2011; Jungkunst and others 2018).

Ignoring underlying spatial and temporal variability or, worse, confounding it with other treatment variables (e.g. LUC type, time elapsed since LUC), limits our ability to detect treatment effects. This is especially the case for critical periods, such as after fertilization, where missing N_2O fluxes after fertilization could severely underestimate fluxes (Barton and others 2015; Guardia and others 2016). Thus we must place greater emphasis on the many fewer, well-replicated studies that likely capture these events. For example, studies by Dobbie and others (1995, n = 15) and Merino and others (2004, n = 56) are very valuable as they alleviate some of the uncertainty and improve our ability to detect broad trends. 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. Given that soil GHG fluxes are highly variable in both time and space (Velthof and others 1996; Barton and others 2015; Kravchenko and Robertson 2015; McDaniel and others 2017), future studies need to explicitly acknowledge the problems, and preferably utilize the 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 LUC will continue, and that some soils currently under natural vegetation will eventually be used to provide food, fibre, and fuel to a likely 9 billion people by 2050. 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 still a small fraction of the total CO_2 loss from LUC (estimated at 2%, Hansen 2013), our meta-analysis suggests that restoring these lands to ‘natural’ vegetation would have little effect on fluxes of CH_4 and N_2O, at least on a 0 – 50 year time scale. Land management practices that help increase CH_4 oxidation or reduce N_2O fluxes are good options for land already under human use or future land converted to human uses. 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 LUC effects on methane (UCH4). 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 (NO3), 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 UCH4 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 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), 5^{th} percentile (bottom circle), 10^{th} percentile (whisker), 25^{th} percentile (bottom of box), 75^{th} percentile (top of box), 90^{th} percentile (whisker), and 95^{th} percentile (top circle).

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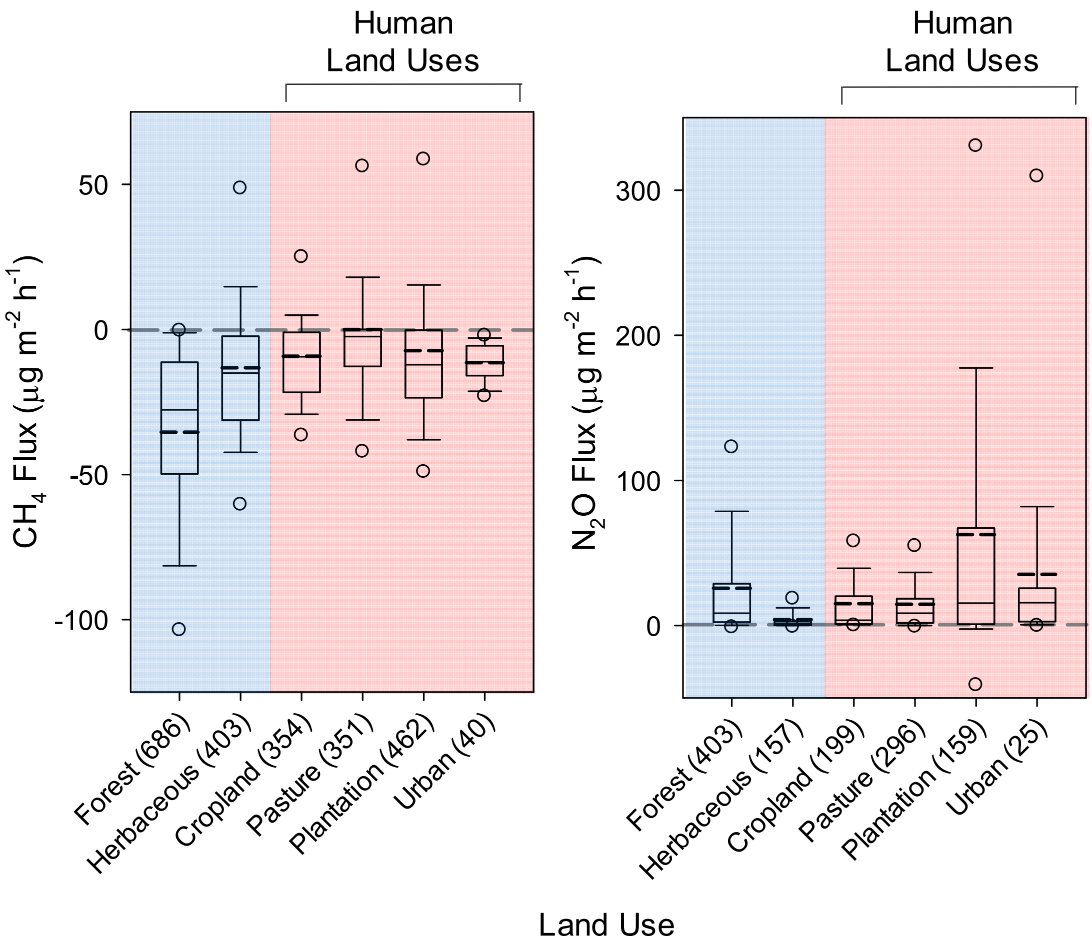


Figure 1. Box plots of soil methane (CH_4) and nitrous oxide (N_2O) fluxes. Herbaceous vegetation includes: shrubland, savanna, and grasslands. Box plots show mean (dashed line), median (solid line), 5th percentile (circle), 10th percentile (whisker), 25th percentile, 75th percentile, 90th percentile (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.

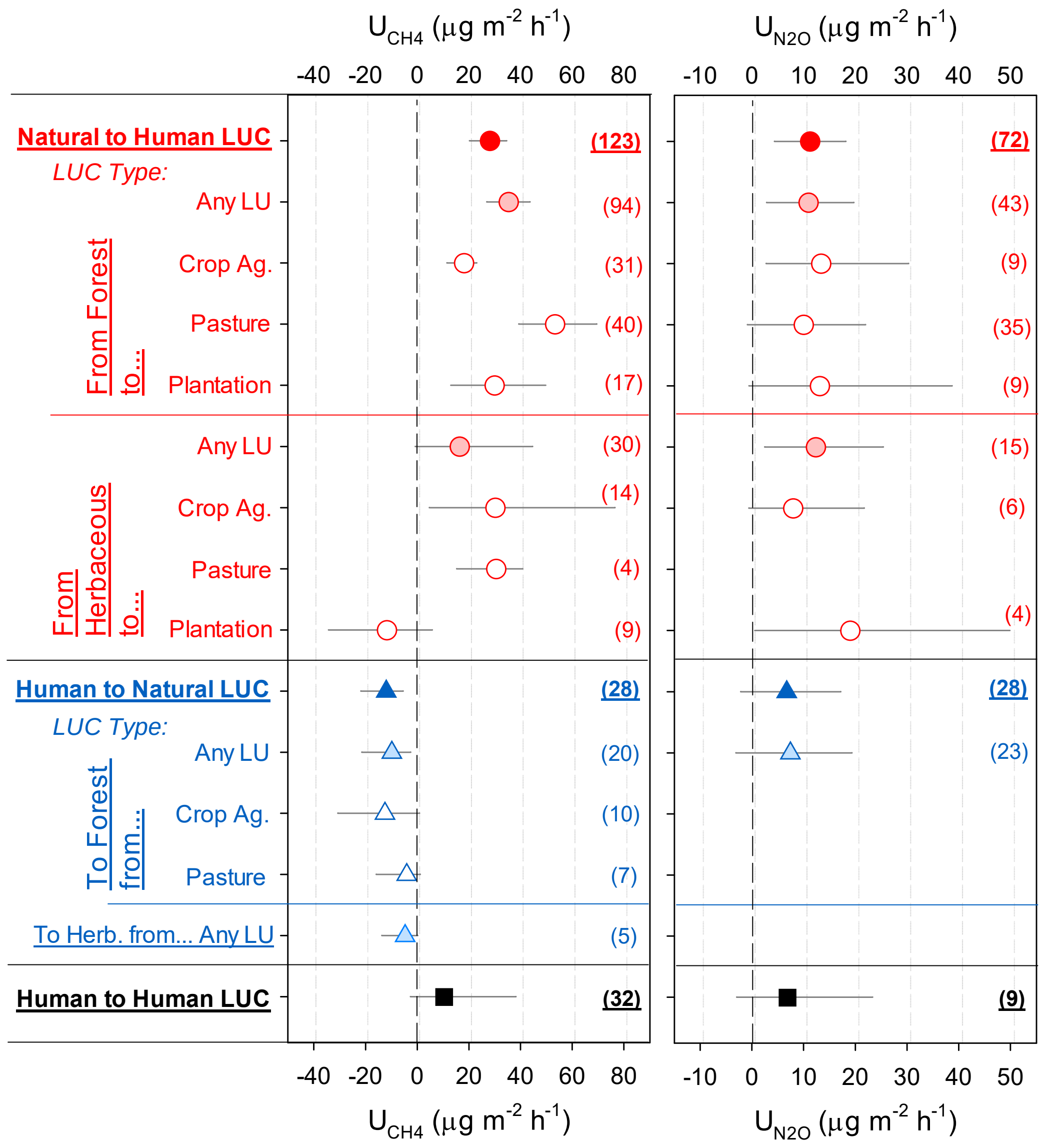


Figure 2. Effect of land-use change on soil methane (CH4) and nitrous oxide (N2O) fluxes. The overall data (filled symbols) and data separated by type of land-use (open symbols). These data are further separated by two ecosystem types: Forests and herbaceous ecosystems (shrubland, savanna, and grasslands). U is the difference in greenhouse gas flux between the new and previous land use. The numbers in parentheses are number of overall comparisons.

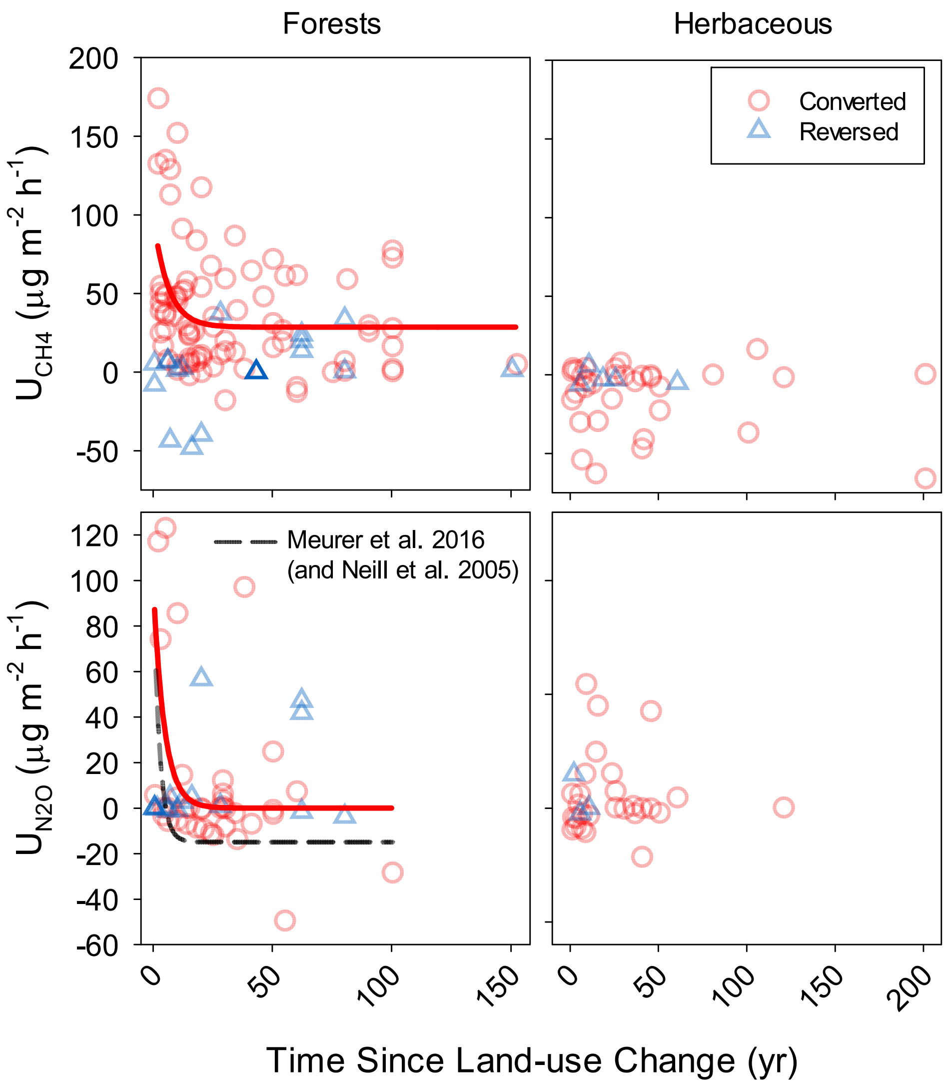


Figure 3. The effect of land-use change on soil methane (CH4) and nitrous oxide (N2O) expressed over the number of years since conversion to the new land use. U is the difference in greenhouse gas flux between the new and previous land use. Herbaceous ecosystems are shrublands, savannahs and grasslands. 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.

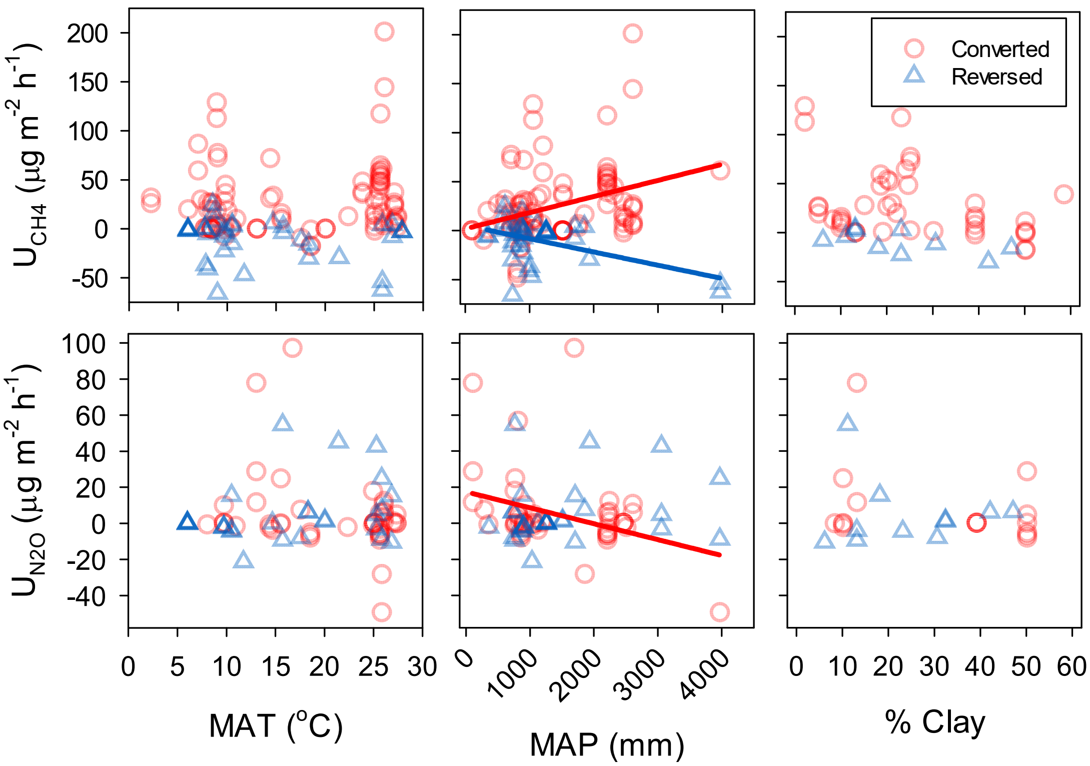


Figure 4. Correlations among land-use change effects on soil methane (U_{CH4}) and nitrous oxide (U_{N2O}) with environmental variables: mean annual temperature (MAT), mean annual precipitation (MAP), and percentage of clay in the soil. U is the difference in greenhouse gas flux between the new and previous 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.

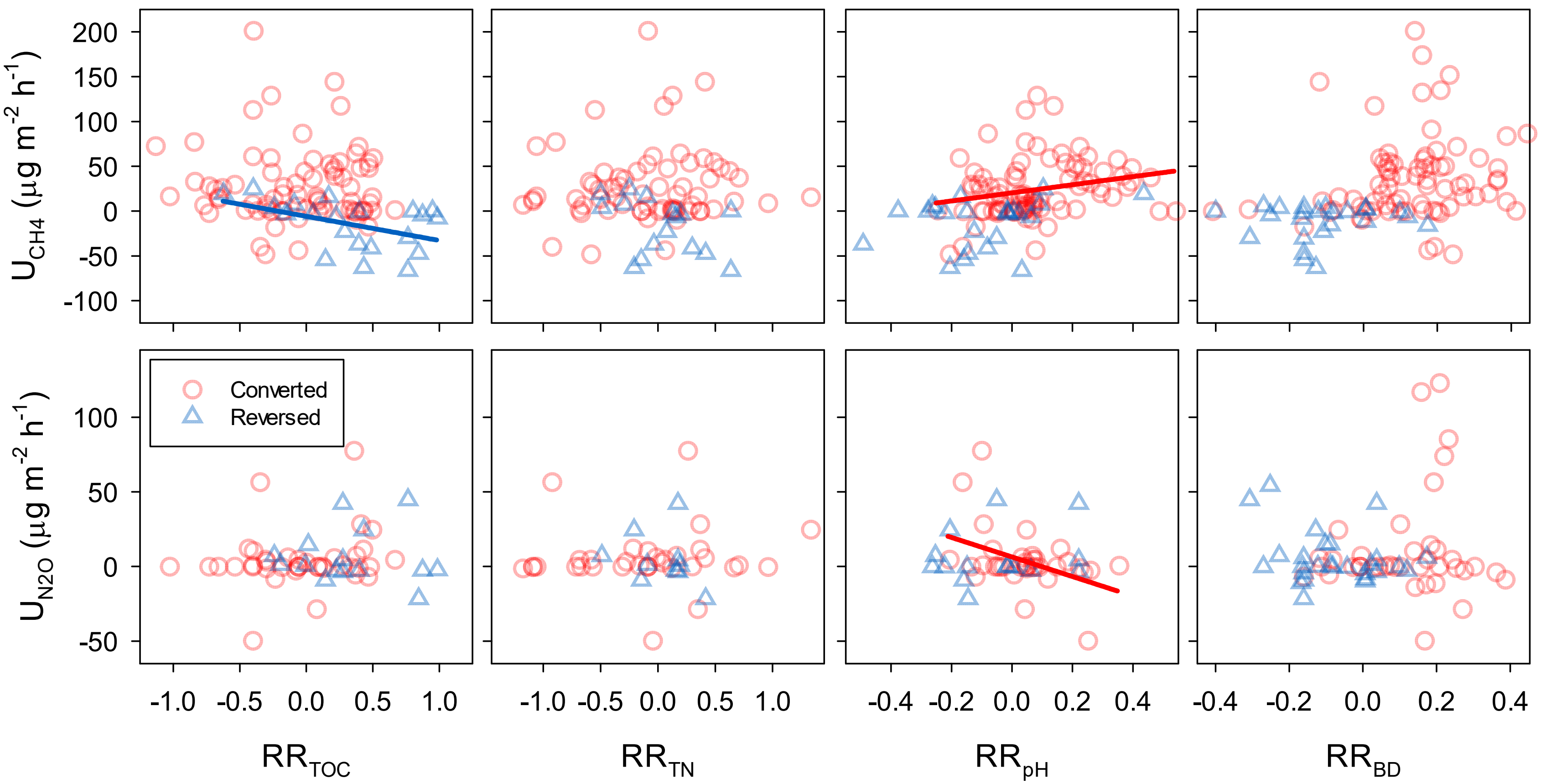


Figure 5. Correlations among land-use change effects on soil methane (CH4) and nitrous oxide (N2O) with slow-changing variables: total organic carbon (TOC), total nitrogen (TN), pH, and bulk density (BD). RR is the response ratio of that soil variable to land use change – a positive value is increase 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.

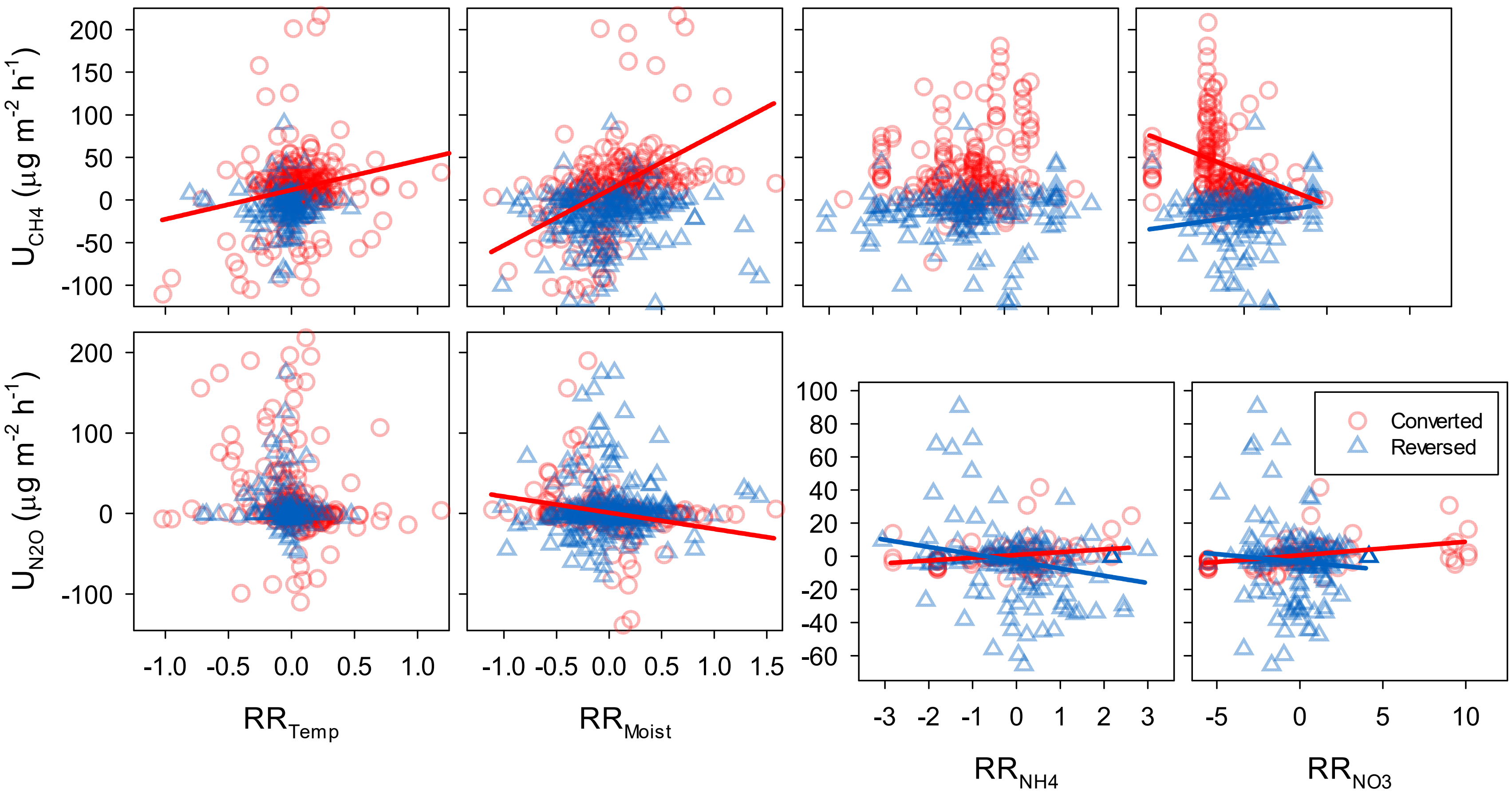


Figure 6. Correlations among land-use change effects on soil methane (CH4) and nitrous oxide (N2O) with fast-changing or dynamic variables: temperature (Temp), soil moisture (Moist), ammonium (NH4), and nitrate (NO3). RR is the response ratio of that soil variable to land use change – a positive value 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.

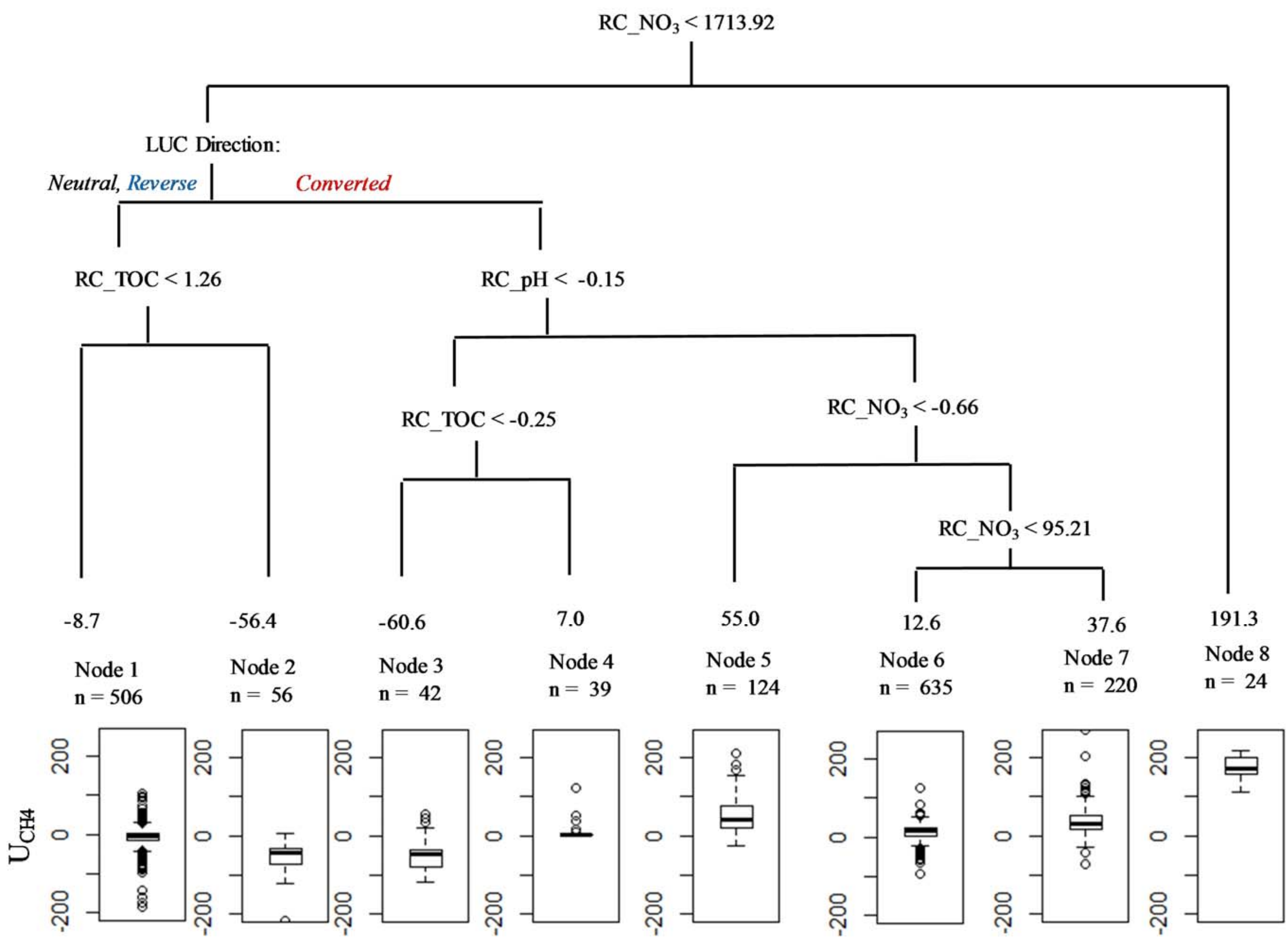
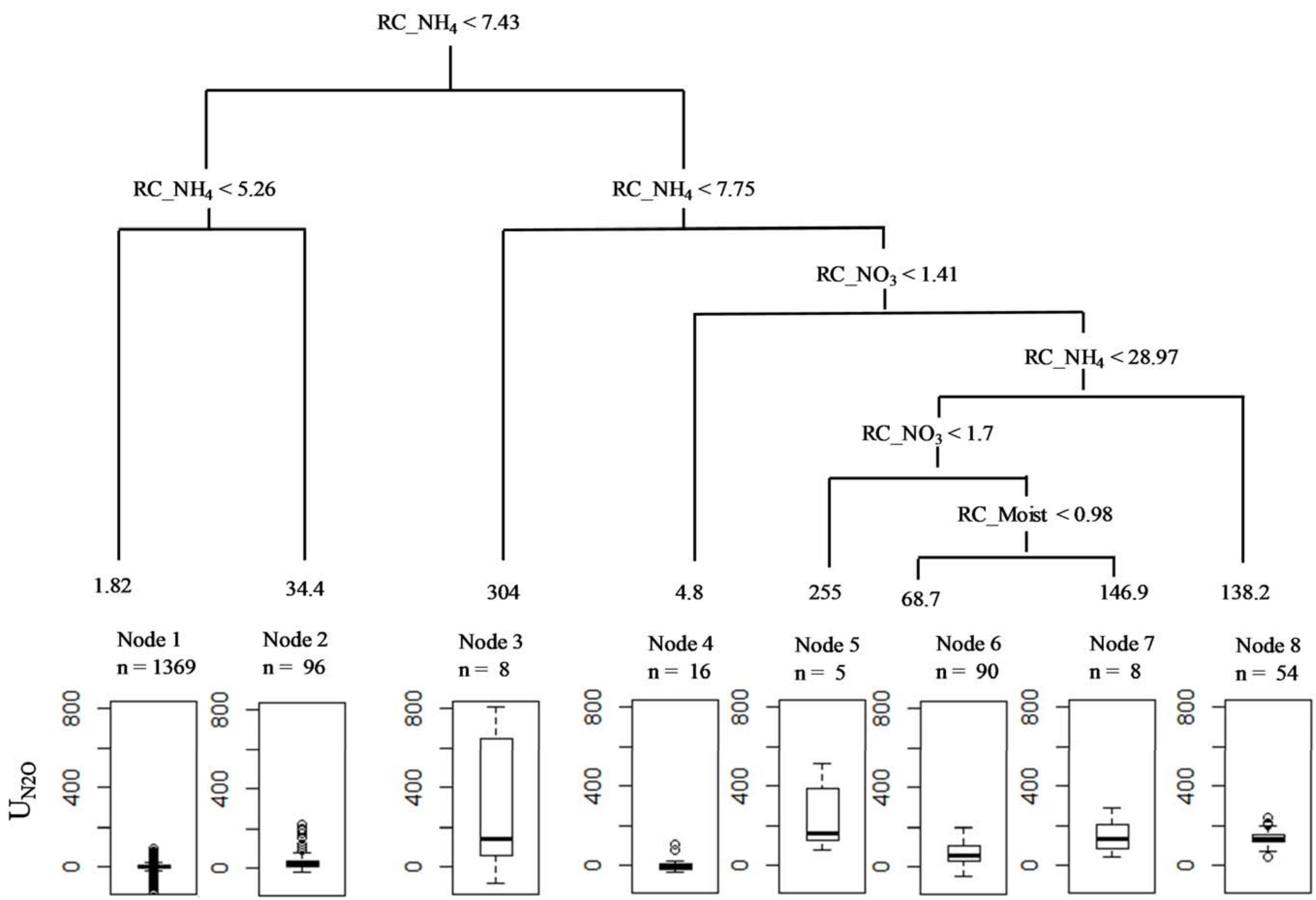

RC_NO3 < 1713.92
LUC Direction:
Neutral, Reverse
Converted
RC_TOC < 1.26
RC_pH < -0.15
RC_TOC < -0.25
RC_NO3 < -0.66
RC_NO3 < 95.21
-8.7
Node 1
n = 506
-56.4
Node 2
n = 56
-60.6
Node 3
n = 42
7.0
Node 4
n = 39
55.0
Node 5
n = 124
12.6
Node 6
n = 635
37.6
Node 7
n = 220
191.3
Node 8
n = 24
UCH4
200
0
-200

Figure 7. Random Forest regression tree analysis for the 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).



RC_NH4 < 7.43
RC_NH4 < 5.26
RC_NH4 < 7.75
RC_NO3 < 1.41
RC_NH4 < 28.97
RC_NO3 < 1.7
RC_Moist < 0.98
1.82
34.4
304
4.8
255
68.7
146.9
138.2
Node 1 n = 1369
Node 2 n = 96
Node 3 n = 8
Node 4 n = 16
Node 5 n = 5
Node 6 n = 90
Node 7 n = 8
Node 8 n = 54
UN2O
0
400
800

Figure 8. Random Forest regression tree analysis for the 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).