Tree stem bases are sources of CH_4 and N_2O in a tropical forest on upland soil during the dry to wet season transition

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Abstract

Tropical forests on upland soils are assumed to be a methane (CH_4) sink and a weak source of nitrous oxide (N_2O), but studies of wetland forests have demonstrated that tree stems can be a substantial source of CH_4, and recent evidence from temperate woodlands suggests that tree stems can also emit N_2O. Here, we measured CH_4 and N_2O fluxes from the soil and from tree stems in a semi-evergreen tropical forest on upland soil. To examine the influence of seasonality, soil abiotic conditions, and substrate availability (litter inputs) on trace greenhouse gas (GHG) fluxes, we conducted our study during the transition from the dry to the wet season in a long-term litter manipulation experiment in Panama, Central America. Trace GHG fluxes were measured from individual stem bases of two common tree species and from soils beneath the same trees. Soil CH_4 fluxes varied from uptake in the dry season to minor emissions in the wet season. Soil N_2O fluxes were negligible during the dry season but increased markedly after the start of the wet season. By contrast, tree stem bases emitted CH_4 and N_2O throughout the study. Although we observed no clear effect of litter manipulation on trace GHG fluxes, tree species and litter treatments interacted to influence CH_4 fluxes from stems and N_2O fluxes from stems and soil, indicating complex relationships between tree species traits and decomposition processes that can influence trace GHG dynamics. Collectively, our results show that tropical trees can act as conduits for trace GHGs that most likely originate from deeper soil horizons, even when they are growing on upland soils. Coupled with the finding that the soils may be a weaker sink for CH_4 than previously thought, our research highlights the need to reappraise trace gas budgets in tropical forests.

Introduction

Methane (CH_4) and nitrous oxide (N_2O) are important trace greenhouse gases (GHGs) with radiative effects 25 and 298 times greater than CO_2, respectively (Houghton et al., 2001). Interest in trace GHG exchange in tropical forests has grown in recent years, particularly in saturated wetland areas of the tropics such as the Amazon floodplain (Graffman et al., 2008; Pangala et al., 2017) and mangrove swamps (Kreuzwieser et al., 2003; Krithika et al., 2008). Natural wetlands are the single largest individual source of atmospheric methane contributing 177-284 Tg CH_4 yr^{-1} (IPCC, 2013), to which tropical wetland emissions from a variety of sources (including waterlogged soils) are a significant contributor, but the contribution of tropical forests on upland soils (i.e. soils that are rarely flooded and only temporarily water-saturated) has not yet been quantified. Globally, emissions of nitrous oxide from soils in natural ecosystems account for 37% of total global surface emissions (IPCC, 2007), estimated at 3.37-6.60 Tg N yr^{-1} (Zhuang et al., 2012) and tropical rainforests are the single biggest natural source of N_2O (Bouwman et al., 1995).

Tree stems can also emit significant amounts of CH_4 in temperate (Gauci et al., 2010) and tropical (Pangala et al., 2013; Pangala et al., 2017) wetland ecosystems, and mesocosm experiments showed that black alder trees, typical of European temperate wetlands, can also act as a pathway for N_2O emissions to the atmosphere (Rusch and Rennenberg, 1998). CH_4 and N_2O are produced under anoxic conditions in waterlogged soils by methanogenic consortia of archaea or denitrifying bacteria, respectively, and the gases diffuse into soil water, and then from water into roots as either a solute or a gas. The gases move up the tree stem by either mass flow (transpiration or pressurized ventilation) or diffusion, then diffuse from the xylem through the stem tissue to the atmosphere via lenticels and other structures that aid gas exchange (Carmichael et al., 2014). Findings extrapolated from glasshouse experiments suggest that wetland hardwood trees could account for emissions of around 60 Tg CH_4 yr^{-1} (Rice et al.,

2010); tree stem fluxes accounted for 62-87% of total ecosystem CH_4 flux in tropical peat forests in Indonesia (Pangala et al. 2013) and contribute half of all emitted methane in the Amazon floodplain (~20 Tg; Pangala et al., 2017).

We are only just beginning to understand the role of tropical tree stems as conduits of soil-produced trace GHGs, and the vast majority of research on this subject to date has been in forested wetlands. Wetland tree species have evolved a variety of specialist tissues to aid oxygen transport to roots in anoxic soils such as aerenchyma, increased stem lenticel density (Pangala et al., 2014) and adventitious roots, which can transport soil-generated CH_4 in mangrove tree species (Purvaja et al., 2004). Inter-species variations in wood specific density and stem lenticel numbers could be important controls of stem emissions, as tree stem CH_4 flux is negatively related to wood density and positively related to lenticel number (Pangala et al., 2013). Tree stem emissions of trace GHGs can occur on upland soils when such soils become saturated with water, which reduces soil oxygen concentrations and facilitates the activity of anoxic methanogenic archaea and denitrifying bacteria that thrive in such soil conditions. Tree stem emissions of CH_4 and N_2O have been observed in temperate trees that lack aerenchyma and other adaptations to wet, anoxic soil conditions (Machacova *et al*., 2013, 2016; Wen et al., 2017). In addition, recent work demonstrates production of CH_4 within tree stems (Wang et al., 2016) and high abundance of methanogens in heartwood (Yip et al., 2018). However, despite the global importance of tropical forests in GHG budgets, we know very little about CH_4 emissions from tropical tree stems on upland soils and we do not know whether they are also capable of emitting N_2O.

Although tropical forests on upland soils cover a larger land-surface area than tropical wetlands (Pan et al., 2013), they are generally not considered to be a major source of CH_4 and N_2O emissions. However, the role of tree stems as conduits of trace GHGs in tropical forests on upland soils warrants further attention because many tropical tree species have large buttress

roots and the greatest stem gas emissions are measured within 0.3-m of the soil surface (Rusch and Rennenberg, 1998; Gauci et al., 2010; Pangala et al., 2013). Hence, even minor trace GHG emissions from tropical trees on upland soils could represent a significant source of CH_4 and N_2O. Indeed, recent work in temperate woodland demonstrated that tree stem emissions diminish the methane sink of upland forests (Pitz & Megonigal, 2017), if the same applies to tropical forests, it would affect global trace GHG budgets.

Regardless of whether soils are waterlogged or well-drained, the production of trace GHGs in soils depends on the availability of suitable substrates (Li et al., 2000). Litter quantity can influence the rates of trace GHG emissions from forest soils as it provides substrate (acetate and hydrogen) for methanogens and the nitrate used in denitrification (Teh et al., 2008). The potential link between litter inputs and trace GHG emissions from soil was explored by a study of soil N_2O emissions from a wet forest in Costa Rica, in which doubling leaf litter inputs increased rates of N_2O emissions by 43% relative to controls, with a corresponding decline of 42% in litter removal plots (Wieder et al., 2011). However, litter manipulation treatments in subtropical forest in Southern China had no significant effect on soil CH_4 uptake or N_2O production, implying that abiotic conditions in the mineral soil may be more important than litter quantity (Tang et al., 2006). The effects of litter manipulation on trace GHG emissions from tree stems is presently unknown, but as changes in mineral soil chemistry from litter were the primary driver of changes in CH_4 and N_2O fluxes (Fender et al., 2013), it is conceivable that litter manipulation could also affect tree stem emissions.

Hence, although trees can be a major conduit for CH_4 in tropical floodplains and peat forests, we know very little about tree stem fluxes of CH_4 in tropical forests on upland soils, and there are no field data on tree stem N_2O emissions in the tropics. We aimed to address these gaps in our knowledge of tropical GHG emissions by measuring CH_4 and N_2O fluxes from the soil and tree stems in a seasonal moist tropical forest on upland soils. We focussed our attention on

quantifying seasonal changes in CH_4 and N_2O fluxes at the base of tree stems, and we assessed the specific role of litter in providing substrate for trace GHG production. Accordingly, we conducted our study in an existing long-term litter manipulation experiment during the transition from the dry season to the wet season to test the following hypotheses:

1) Tree stems in tropical forests on upland soils will act as a conduit for CH_4 and N_2O produced in the soil; patterns in trace GHG emissions from tree stems will therefore mimic those from the soil, increasing in the wet season and decreasing in the dry season.
2) Litter manipulation treatments alter substrate availability to microorganisms and will therefore influence CH_4 and N_2O fluxes from soils and tree stems; hence, trace GHG emissions will be greater in litter addition treatments and lower in litter removal plots relative to controls.

Materials and Methods

Field area and sampling

The study was carried out within the Gigante Litter Manipulation Project, approximately 5 km south of Barro Colorado Island (BCI) in Panama, Central America (Sayer & Tanner, 2010). The 15 plots were set up between 2000 and 2002; each plot measures 45-m × 45-m and the edges of the plots were trenched to a depth of 0.5-m, lined with plastic and then backfilled. Starting in January 2003, the litter is raked up and removed from five plots every month (L-) and added to five plots where it is spread as evenly as possible (L+); five plots were left as controls (CT; see Sayer et al. 2006 and Sayer & Tanner 2010 for a full description). The mean annual temperature at the weather station on nearby Barro Colorado Island (within 2 km of the study site) is 26^{o}C, mean annual rainfall is 2,600 mm and there is a strong dry season from mid-December to mid-April (Leigh, 1999). During the study period, maximum and minimum air temperatures were 32.4^{o}C and 24.3^{o}C respectively, soil temperature ranged from 24.9 – 29.2^{o}C

and soil water content (SWC) was between 14% and 40%. The soil in the plots is characterised as a moderately acidic Oxisol (Cavelier, 1992).

Two tree species were selected for this study: the fast-growing canopy tree *Simarouba amara* (Aubl.) and the shade-tolerant subcanopy tree *Heisteria concinna* (Standl.), which occur frequently throughout the study forest and are among the most abundant tree species in the experimental plots (12% of all trees with dbh >10 cm; Sayer and Tanner, 2010). Both species have relatively smooth bark and straight stems, which facilitated sampling and the species have distinct specific wood densities (0.38 g cm^{-3} for *Simarouba* and 0.64 g cm^{-3} for *Heisteria*; Condit et al., 2013), which is likely to influence trace GHG fluxes from stems (Pangala et al., 2013). Trees were mapped and marked using handheld GPS. One individual per species was chosen per plot but only 13 of the 15 experimental plots contained live mature individuals of *Simarouba*; hence the present study included trees in four plots per treatment, making 12 *Heisteria* and 12 *Simarouba* trees in total.

Greenhouse gas fluxes from the soil were measured using permanently installed soil collars located 2-3 m to the north and south of each tree. The collars were made from 120-mm long sections of polyvinyl chloride pipe (internal diameter: 200 mm), which were embedded into the soil to 30-mm depth. All collars were installed at least two weeks prior to sampling in March 2014 and an appropriate amount of litter was placed into the collars in the CT and L+ plots to achieve consistency with the surrounding forest floor. To determine CH_4 and N_2O emissions from the soil, a PVC lid with an inner seal of gas-tight neoprene foam was placed on top of the collar; a 15-ml air sample was taken by syringe via a septum in the lid immediately after closure and then again after 3, 6 and 10 minutes. Each sample was injected into pre-evacuated 12-ml borosilicate vials (Exetainer™, LabCo Ltd, High Wycombe, UK). The suction when removing the lid after sampling demonstrated the integrity of the seal on the soil chamber. Soil

temperature at 0-6 cm depth was recorded adjacent to the collars using a Thermapen (ETI Ltd, Worthing, UK).

Tree stem gas fluxes were measured using a flexible chamber made from a 450-mm × 300-mm sheet of polycarbonate, lined with neoprene foam (19 mm wide, 25 mm thick; Siegenthaler et al. 2016). The chambers were secured to the tree stems at 0.3-m above the forest floor using cam buckle straps. Gas samples were taken by syringe from a septum in the middle of the chamber at 0, 5, 10 and 15 minutes, and injected into pre-evacuated 12-ml vials as described above.

Air samples from the tree stem and soil chambers were collected every two weeks between 30 March and 20 July 2014. Air pressure and temperature outside the stem chamber were recorded at the start of sampling using a Thermometer-Hygrometer-Barometer probe (Commeter C4141; Comet Systems, Czech Republic). Soil temperature at 0-10-cm depth was measured adjacent to the collars using a soil temperature probe and volumetric soil water content at 0-6 cm depth was measured using a Thetaprobe (Delta-T Devices, Cambridge, UK) calibrated to local soil conditions following the manufacturer's instructions. Collection of soil temperature and soil water content data during gas sampling was limited to 28 May - 14 June 2014 and 2 - 6 July 2014 due to equipment malfunction. We therefore used monthly values measured in the plots as part of a separate study (Sayer et al. unpublished data) and weekly rainfall data measured at the meteorological tower on Barro Colorado Island (courtesy of the Physical Monitoring Program of the Smithsonian Tropical Research Institute).

The CH_4 concentrations of the air samples were analysed within a week of sampling using off-axis Integrated Cavity Output Spectroscopy (FMA-200 Fast Methane Analyser; Los Gatos Research, Mountain View, CA, USA). The N_2O concentrations of the air samples were analysed using gas chromatography (Ai 94 Gas Chromatograph, Cambridge Instruments, Ellutia, Ely, UK). All methods for the measurement of GHGs, including the testing of the

chamber method and sensitivity of measurements are discussed fully in Siegenthaler et al. (2016).

Data analyses

The data were inspected visually before further analysis; we considered extreme outliers that lay outside of the 5^{th} - 95^{th} interquartile range as measurement errors and removed them from the dataset. For soil fluxes, we omitted two data-points for CH_4 and one value for N_2O (out of 188 and 108, respectively) and for tree stem fluxes, we omitted 20 data-points for CH_4 and three data-points for N_2O (out of 201 and 115, respectively).

All data analyses were conducted in R 3.3.2 (R Core Team, 2016) using the lme4 package for mixed effects models (Bates et al., 2015). Gas fluxes were calculated for each chamber following Baird et al. (2010), whereby the least squares linear regression slope of the four sample concentrations is plotted against sampling time and the slope to give the gas flux in µg m^{-2} h^{-1}. Gas flux measurements were only used for further statistical analysis if the R^2 of the regression was >0.7; this cut-off point was chosen following Alm et al. (2007; cited in Cooper et al., 2014), who noted that low fluxes (especially those near to zero) tend to have low R^2 values. Concentration changes in N_2O in dry season samples were too small to estimate non-zero fluxes (i.e. R^2 <0.7); we therefore only present wet season data for soil and tree stem N_2O fluxes.

Soil water content, soil temperature, and air temperature were strongly correlated; however, as is typical of the tropics, temperature only varied within a narrow range. Given that rainfall and soil moisture exhibited far larger variation (and have a fundamental control on soil CH_4 and N_2O production), we investigated the relationships between soil water content and trace GHG fluxes from soils and tree stems using monthly means. Relationships were inspected visually and emerging patterns were then tested using linear models. We then assessed the

influence of tree species, litter treatment, and their interaction on soil and stem trace GHG fluxes using linear mixed effects models (*lmer* function) with plot and time as random effects. The significance of each term was determined by comparing nested models using likelihood ratio tests. Models were simplified by sequentially dropping terms until a minimum adequate model was reached, using AICs and p-values to check for model improvement (Pinheiro and Bates, 2000). The final model fit was inspected using diagnostic plots. Effects of seasonal variation were tested by comparing minimum adequate models with and without time as a random effect. Statistics for mixed effects models are given for the comparison between the best-fit model and the corresponding null model. All results are reported as significant at $p < 0.05$ but due to the low number of replicate plots ($n = 4$), marginally significant trends are also reported at $p < 0.1$.

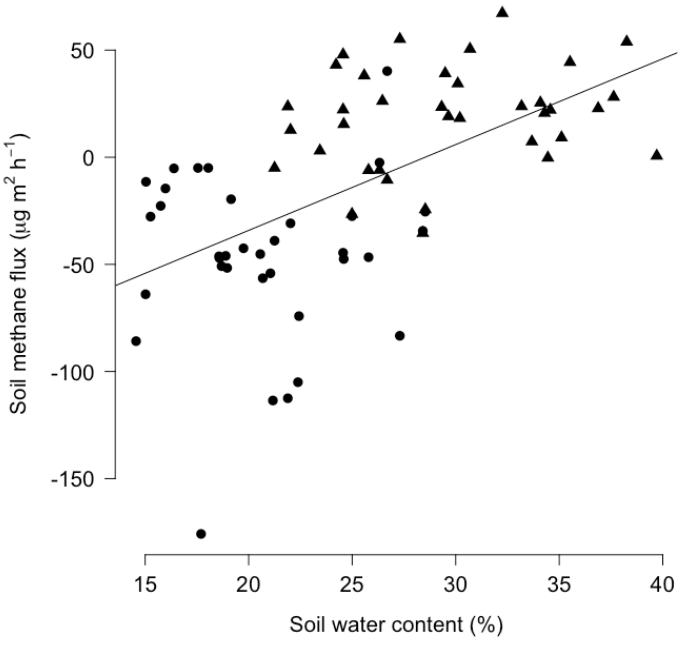

Figure 1. The relationship between methane fluxes from the soil and soil water content at 0-6 cm depth in a lowland tropical forest on upland soil in Panama, Central America, during the transition from the dry season (circles) to the wet season (triangles) from March to July 2014.

Results

Seasonal variation in CH_4 fluxes

Soil water content was strongly related to total rainfall ($R^2 = 0.6$, $p < 0.01$) and CH_4 fluxes increased with soil water content ($R^2 = 0.3$, $p < 0.01$; Fig. 1). Soil CH_4 fluxes therefore varied significantly between the dry and wet season ($p < 0.001$, $\chi^2 = 36.4$), whereby soils acted as a CH_4 sink during the dry season and switched to being a source within two to three weeks of the start of the wet season (Fig. 2).

There was no clear seasonal pattern for tree stem CH_4 fluxes; although stem CH_4 emissions tended to be larger during the wet season, they were not significantly so (Fig. 2) and there were no significant relationships between tree stem fluxes and soil water content.

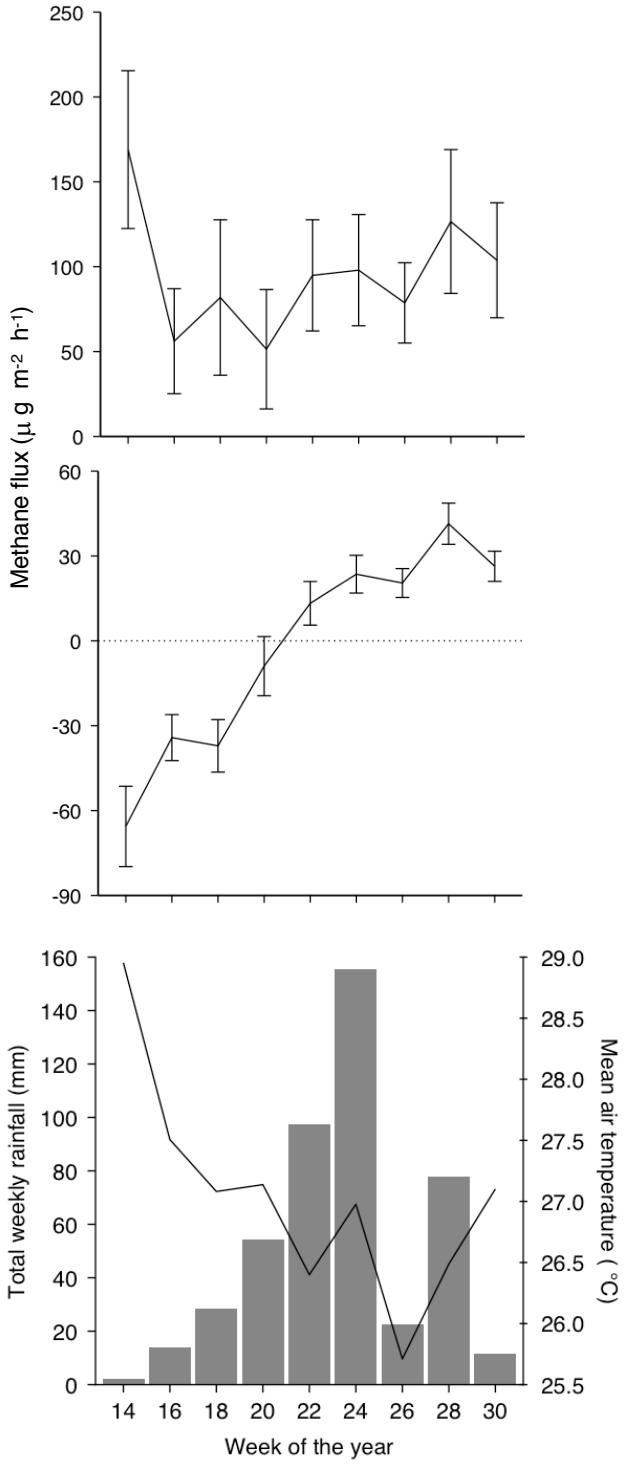

Figure 2 Methane (CH_4) fluxes from tree stems at 0.3-m height (top panel) and soil (centre panel) in a lowland tropical forest on upland soil in Panama, Central America; data shown are pooled across experimental plots with three litter manipulation treatments, means and standard errors are therefore given for n = 12; measurements were made weekly during the transition from the dry season to the wet season (bottom panel, weeks 14-19 and 20-30, respectively), with corresponding changes in total rainfall (bars) and temperature (line).

Species and treatment effects on soil CH_4 fluxes

There were no effects of species, treatment or their interaction on soil CH_4 fluxes. Soil CH_4 fluxes remained predominantly negative until week 24 under individuals of *Heisteria* and until week 21 under individuals of *Simarouba*, indicating dry season uptake of CH_4 before a transition to emissions within two to four weeks after the first heavy rainfall of the year (Figs. 2 and 3). The median flux beneath *Heisteria* was 8.3 µg m^{-2} hr^{-1}, which was slightly higher than the median CH_4 flux of 6.3 µg m^{-2} hr^{-1} from chambers under *Simarouba*.

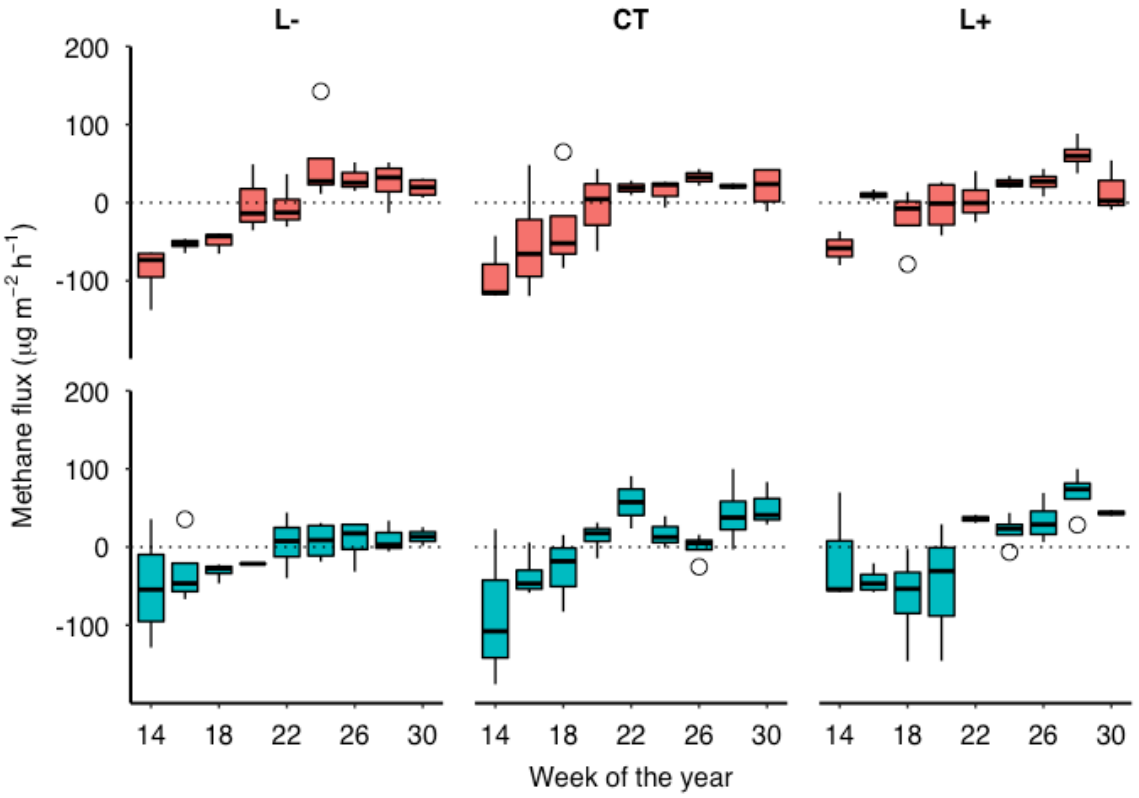

Figure 3. Soil methane (CH_4) fluxes under individuals of two common tree species: *Heisteria concinna* (top panels) and *Simarouba amara* (bottom panels) in experimental litter removal (L-), control (CT) and litter addition (L+) treatments in a lowland tropical forest on upland soil in Panama, Central America, measured weekly during the transition from the dry season (weeks 14-19) to the wet season (weeks 20-30); ranges (boxes and whiskers) and median lines are shown for *n* = 4 individuals per species and treatment.

The range of soil CH_4 fluxes under individuals of *Heisteria* (-190 - 539 μg m^{-2} hr^{-1}) was greater than under individuals of *Simarouba* (-89.4 - 450 μg m^{-2} hr^{-1}). Consequently, the mean soil CH_4 flux beneath *Heisteria* individuals was slightly more negative than that beneath *Simarouba* (-2.8 ±5.1 μg m^{-2} hr^{-1} and -2.3 ±5.5 μg m^{-2} hr^{-1} respectively).

Species and treatment effects on tree stem fluxes of CH_4

Surprisingly, tree stem CH_4 fluxes were mostly positive throughout the study period, even though the upland soils at the study site tended to act as a sink for methane during the dry season (Fig. 2). Accordingly, we found no relationship between soil and stem CH_4 fluxes. There was a significant species × treatment interaction on stem CH_4 fluxes, whereby *Heisteria* stems had higher CH_4 fluxes in L+ plots and lower stem fluxes in L- plots compared to *Simarouba* stems ($p < 0.001$, $\chi^2 = 24.5$; Fig. 4). Overall, the median CH_4 flux was very similar between the two species, with 72.6 μg m^{-2} hr^{-1} and 75.1 μg m^{-2} hr^{-1} for *Heisteria* and *Simarouba* respectively. Tree stem CH_4 fluxes in individuals of *Heisteria* were mostly positive, with a mean flux of 101 ±14.9 μg m^{-2} hr^{-1} over the dry-wet season transition, whereas the mean flux for *Simarouba* was lower at 87.7 ±18.5 μg m^{-2} hr^{-1}.

Stem CH_4 fluxes in *Simarouba* displayed greater inter-week variability across all treatments (Fig. 4) and had a greater range throughout the study (-276 μg m^{-2} hr^{-1} to 678 μg m^{-2} hr^{-1}) than those from *Heisteria* stems. CH_4 stem fluxes from *Heisteria* ranged from -156 to 598 μg m^{-2} hr^{-1} and remained relatively constant throughout the study in CT and L- plots but were much more variable in L+ plots (Fig. 4).

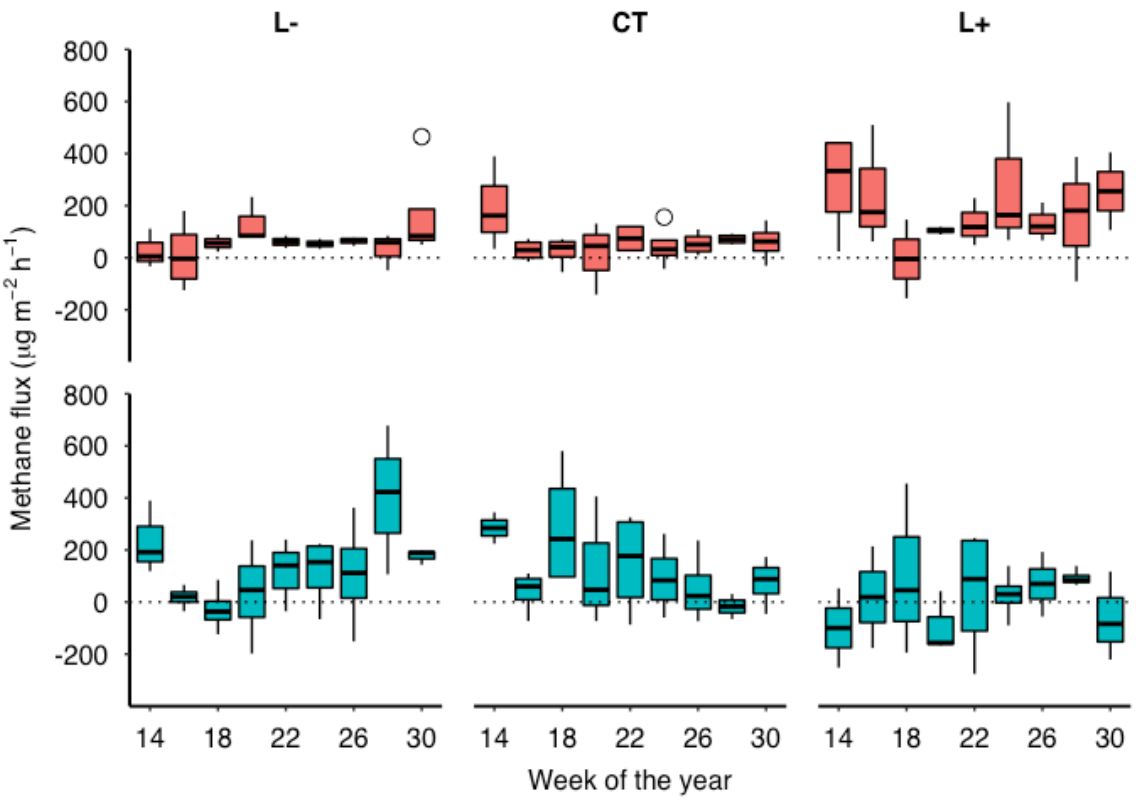

Figure 4. Methane (CH_4) fluxes from tree stems of *Heisteria concinna* (top panels) and *Simarouba amara* (bottom panels) in experimental litter removal (L-), control (CT) and litter addition (L+) treatments in a lowland tropical forest on upland soil in Panama, Central America; fluxes were measured weekly at 0.3-m height during the transition from the dry season (weeks 14-19) to the wet season (weeks 20-30); ranges (boxes and whiskers) and median lines are shown for *n* = 4 individuals per species and treatment.

Seasonal variation in N_2O fluxes

There was no clear seasonal pattern in soil or tree stem N_2O fluxes during the wet season (Fig. 5) and no effect of soil water content. However, we were unable to quantify N_2O fluxes during weeks 14-19, indicating very limited N_2O production during the dry season.

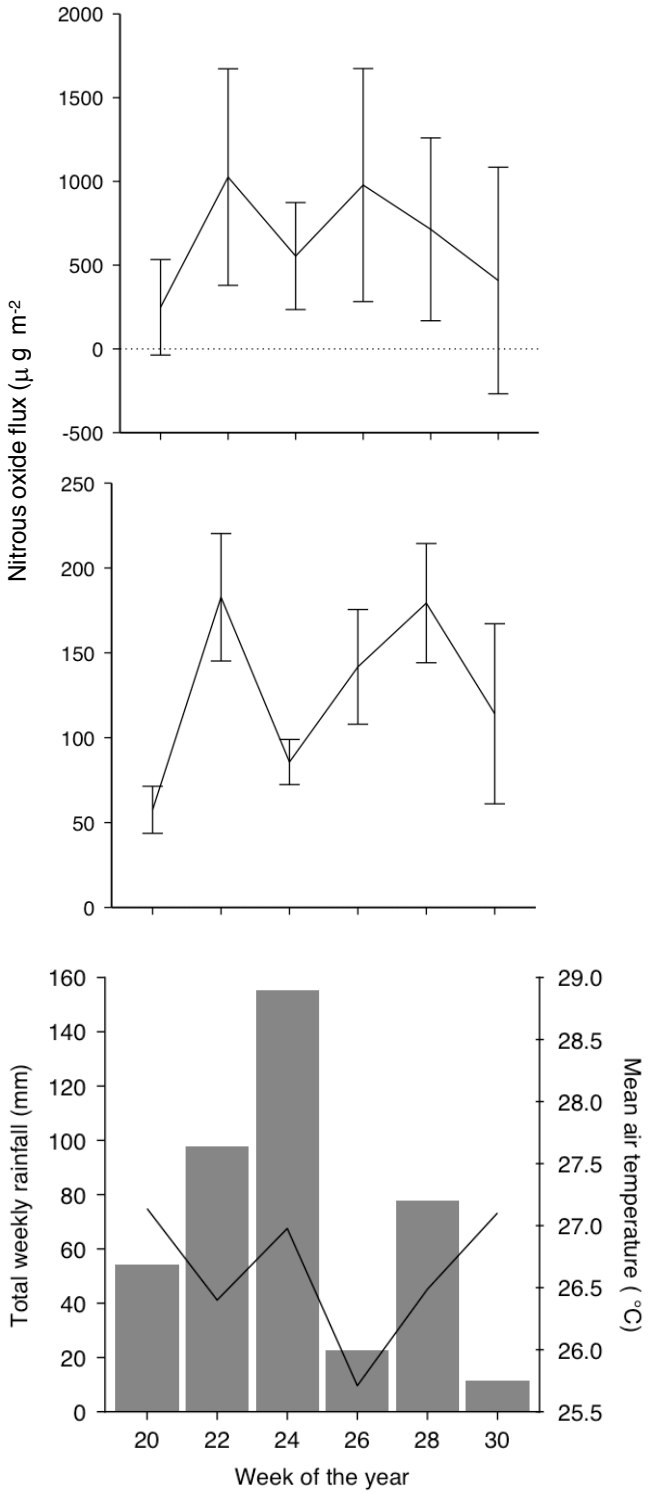

Figure 5 Nitrous oxide (N_2O) fluxes from tree stems at 0.3-m height (top panel) and soil (centre panel) in a lowland tropical forest on upland soil in Panama, Central America; means and standard errors are given for *n* = 4; measurements were made weekly during wet season (bottom panel) showing total rainfall (bars) and temperature (line).

Species and treatment effects on soil N_2O fluxes

There was a marginally significant additive effect of species and litter treatment for soil N_2O fluxes ($p = 0.092$, $\chi^2 = 6.45$), whereby soil N_2O fluxes measured beneath *Heisteria* individuals were greater in L+ plots compared to L- plots and tended to be higher than soil N_2O fluxes measured beneath *Simarouba* (means of 138 ±21.7 µg m^{-2} h^{-1} and 114 ±15.7 µg m^{-2} h^{-1}, respectively; Fig. 6). Wet season soil N_2O fluxes beneath individuals of *Heisteria* ranged from -190 to 539 µg m^{-2} h^{-1} (median: 110 µg m^{-2} h^{-1}) and N_2O fluxes under *Simarouba* trees ranged from -89.4 to 450 µg m^{-2} h^{-1} (median: 87.9 µg m^{-2} h^{-1}).

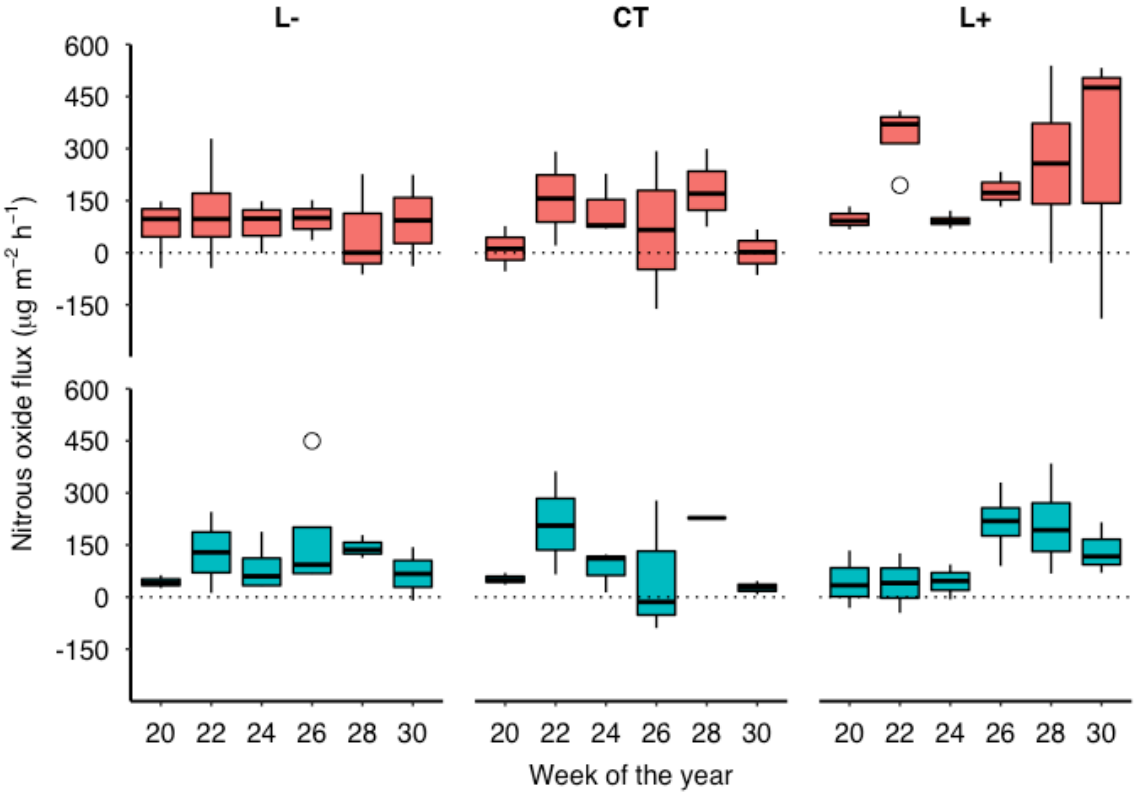

Figure 6. Soil nitrous oxide (N_2O) fluxes under individuals of *Heisteria concinna* (top panels) and *Simarouba amara* (bottom panels) in experimental litter removal (L-), control (CT) and litter addition (L+) treatments in a lowland tropical forest on upland soil in Panama, Central America, measured weekly during the wet season; ranges (boxes and whiskers) and median lines are shown for $n = 4$ individuals per species and treatment.

Species and treatment effects on tree stem fluxes of N_2O

There was a significant additive effect of species and litter treatment on stem N_2O fluxes (χ^2 = 9.66, p = 0.022), whereby fluxes from *Simarouba* stems were greater than those from *Heisteria* in L+ and CT plots, but not in L- plots (Fig. 7). Overall, median N_2O fluxes from *Heisteria* were much lower than those from *Simarouba* (101 µg m^{-2} h^{-1} and 1001 µg m^{-2} h^{-1}, respectively) over the course of the study. N_2O fluxes from *Heisteria* stems were less variable (range: -2857 to 4270 µg m^{-2} h^{-1}) than *Simarouba* (range: -3770 to 8361 µg m^{-2} h^{1}). Overall, a greater proportion of stem fluxes in *Simarouba* were positive and the mean stem flux from *Heisteria* was 80 ±234 µg m^{-2} h^{-1} compared to 1193 ±361 µg m^{-2} h^{-1} for *Simarouba* (Fig. 7).

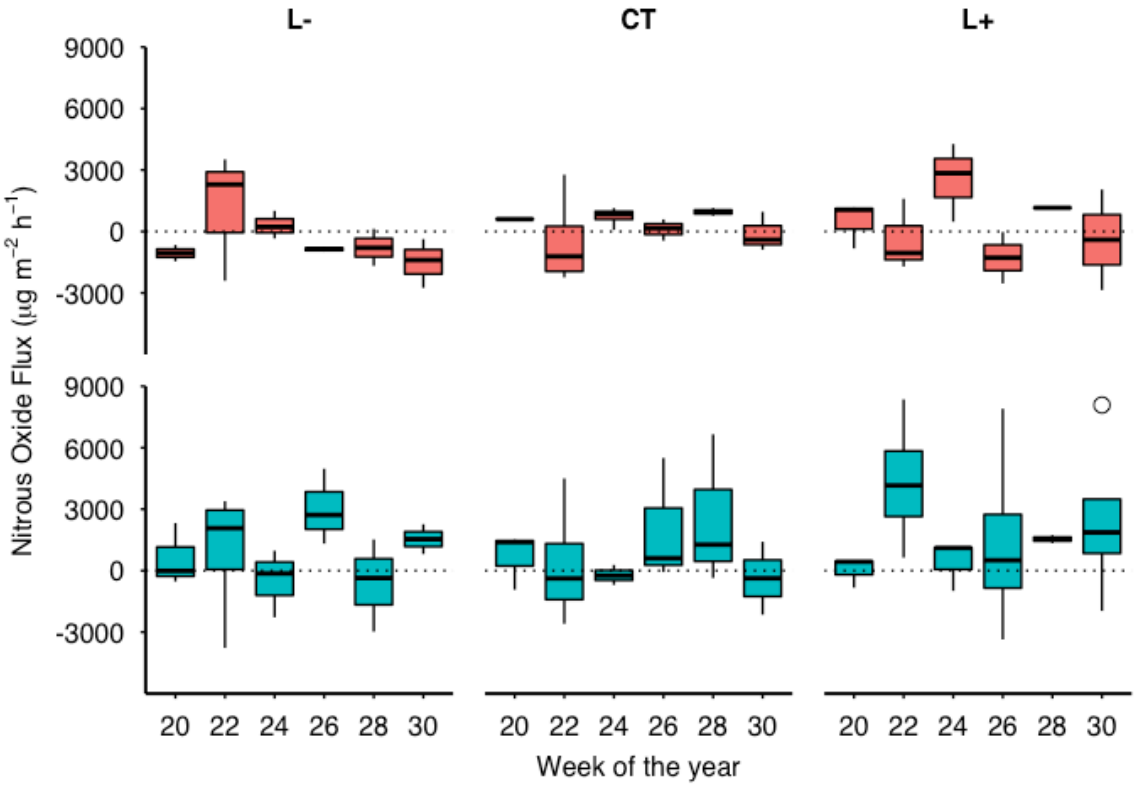

Figure 7. Nitrous oxide (N_2O) fluxes from tree stems of *Heisteria concinna* (top panels) and *Simarouba amara* (bottom panels) in experimental litter removal (L-), control (CT) and litter addition (L+) treatments in a lowland tropical forest on upland soil in Panama, Central America; fluxes were measured weekly at 0.3-m height during the wet season (weeks 20-30); ranges (boxes and whiskers) and median lines are shown for n = 4 individuals per species and treatment.

Discussion

We demonstrate that upland soils in this seasonal tropical forest represented a sink for CH_4 during the dry season but became a source of CH_4 and N_2O during the transition to the wet season. Importantly, tree stems consistently emitted CH_4 during both the wet and dry seasons, which may offset the dry season soil sink. Tree stem fluxes of N_2O were only detectable in the wet season but were also mostly positive, indicating that tropical tree stems on upland soils could be a hitherto unaccounted for source of N_2O.

Seasonal patterns of soil CH_4 and N_2O fluxes

Soil trace GHG fluxes were strongly seasonal. The soil acted as a CH_4 sink during the dry season, when upper horizons of the soil profile have low soil water content and are well aerated and methanogenic archaea are probably dormant. With the onset of the wet season at the beginning of May (week 20; Fig. 2), soil CH_4 fluxes shifted from strongly negative towards positive values, i.e. net CH_4 emissions. The linear relationship between soil CH_4 emissions and soil water content (Fig. 1) is typical of tropical and subtropical swamp forest and rainforest sites (Yu et al., 2008; Rowlings et al., 2012; Hall et al., 2013), and indicates that the higher soil water content during the wet season at our site created conditions that were more favourable for methanogenesis but less so for methanotrophy.

N_2O emissions usually increase with soil water content as the more productive anaerobic process of denitrification becomes dominant (Keller and Reiners, 1994) but we observed no relationship between soil water content and soil N_2O emissions in our study. However, we were unable to statistically assess seasonal patterns in N_2O fluxes because fluxes were not quantifiable for the majority of dry season measurements from the soil or tree stem bases. The lack of measurable N_2O production during the dry season at our study site is nonetheless consistent with strong seasonality in N_2O fluxes, as the low variability in soil water content

during the wet season explains why there was no relationship with N_2O. Alternatively, the timing and frequency of measurements may have been insufficient to detect relationships between soil water content and N_2O fluxes, as soil water saturation at our study site occurred as a result of heavy rainfall, rather than rising water table depth or flooding, and mesocosm studies have demonstrated that N_2O emissions were greatest 24 hours (Machacova et al. 2013) or ~45 hours (Liengaard et al. 2014) after rewetting but then declined rapidly.

We focussed primarily on soil water content as a control of trace GHG fluxes because temperature differences have a more profound effect on trace GHG fluxes when temperatures drop below 15ºC (Castro *et al*., 1995), and soil temperature was consistently >24ºC in our study. Other factors such as diffusion rate (affected by e.g. soil density; Le Mer and Roger, 2001; Liu et al., 2007) and drought effects (Davidson et al., 2008; Itoh et al., 2010) become relatively more important at higher temperatures. It is also worth noting that the 2014 El Niño event resulted in a strong dry season in Panama, with lower rainfall than average, and seasonal effects in the present study may therefore have been exaggerated by the more severe dry season compared with other years.

Trace GHG fluxes from tree stems

Despite substantial changes in soil trace GHG fluxes between the dry and the wet season, there was no clear seasonal pattern in trace GHG fluxes from tree stems and therefore no support for our hypothesis of a relationship between CH_4 and N_2O fluxes from the soil and adjacent tree stems. Emissions of CH_4 and N_2O from tree stems in floodplain and wetland systems reflect the composition of soil trace GHG concentrations (Terazawa et al., 2007; Purvaja et al., 2004; Pangala et al., 2013) because the majority of CH_4 and N_2O emitted via the plant pathway originates from methanogenic consortia and denitrifying communities in the soil. However, variation in tree water uptake and trace GHG production with soil depth could explain why we

found no relationship between soil and tree stem CH_4 or N_2O fluxes. Previous work at the study site demonstrated that soil water content and N_2O concentrations increase with depth, whereas CH_4 concentrations were highest at *c.* 20-cm depth and then decreased with soil depth to *c.* 1.25-m (Koehler et al., 2012). Accordingly, we would expect higher CH_4 fluxes from stems when trees source water from shallower soil horizons, and higher N_2O fluxes when trees access water from deeper in the soil profile. Hence, the relationship between soil and tree stem GHG fluxes is likely to be influenced by the location of CH_4 or N_2O production in the soil profile, the rooting architecture of the tree species, and the preferential water uptake patterns of individual trees. Further, there is increasing evidence that CH_4 is also produced within tree stems (Wang et al., 2016) and methanogens can predominate in heartwood microbial communities (Yip et al., 2018), which could also contribute to CH_4 emissions from tree stems even when the soils were acting as a sink.

The majority of CH_4 and N_2O fluxes from tree stems were positive throughout the study (Figs. 4 & 7) and, unlike soil trace GHG fluxes, the rates did not change significantly between seasons. Consistent trace GHG emissions from tree stem bases has also been observed in temperate upland forests (Wang et al. 2016; Pitz & Megonigal, 2017; Warner et al., 2017) and suggests that GHGs may be produced within the tree stem (Covey et al. 2012; Wang et al. 2016), or that the transport of trace GHGs through tree stems bypassed the oxygenated surface horizons, where the majority of CH_4 oxidation (Teh et al., 2005; Wolf et al., 2012) and more complete denitrification (Koehler et al., 2012; Wieder et al., 2011) occurs. Hence, the production or transport of trace GHGs in tree stems could represent a large and currently unaccounted for source of N_2O and CH_4 emissions from tropical forests on upland soils. The median tree stem fluxes of CH_4 (~ 74 $\mu g\ m^{-2}\ h^{-1}$) and N_2O (~99 $\mu g\ m^{-2}\ h^{-1}$) we measured during the transition from the dry to the rainy season are comparable to fluxes measured in temperate upland trees (Machacova et al., 2013; Wang et al., 2016; Wen et al., 2017; Pitz and Megonigal

2018) and our tree stem CH_4 fluxes also lie within the range of tropical peatland forests (17-185 μg m^{-2} h^{-1}; Pangala et al., 2013).

We measured trace GHG fluxes from the stems of two common tree species with distinct life history strategies and wood densities because stem GHG fluxes are also likely to vary by species' physiological traits (Pangala et al., 2013). In our study, both CH_4 and N_2O fluxes were generally higher from stems of the fast-growing pioneer *Simarouba* (Fig. 4 & 7) except in the litter addition plots, where stem CH_4 fluxes were greater from the slow-growing shade-tolerant tree *Heisteria*. Higher stem emissions from the canopy species *Simarouba* could possibly be explained by greater rates of evapotranspiration and lower wood density compared to the subcanopy species *Heisteria*. Mesocosm studies of two temperate tree species common to forests on upland soils found that fast-growing species created channels of greater gas diffusivity because they had higher fine root density and greater maximum root depth (Fender et al., 2013). Further, higher rates of net primary productivity in canopy species may result in greater root exudation, which could stimulate CH_4 and N_2O production (Butterbach-Bahl et al., 2002). The potential influence of different tree species traits on stem trace GHG fluxes makes it challenging to assess ecosystem-level fluxes in highly diverse tropical forests, especially as CH_4 and N_2O concentrations within soil pore gas and water are also influenced tree diversity (Machacova et al., 2013; Warner et al., 2017). However, we demonstrate that tree species with distinct life history strategies and ecological niches emit CH_4 and N_2O, from their stems, which suggests that trace GHG fluxes from tree stems could be widespread in tropical forests on upland soils.

Interestingly, tree stems also acted as a sink for trace GHG gases in this study (Figs. 4 and 7). It is conceivable that changes in CH_4 and N_2O concentrations in soil water at different depths could generate a diffusion gradient from the atmosphere into tree stems, thus resulting in tree

stem uptake of trace GHGs, possibly as a result of active consumption by epiphytic and endophytic methanotrophs. This intriguing possibility merits further attention.

Links between trace GHG fluxes, seasonality, and decomposition processes

The decomposition of plant litter plays a role in methanogenesis and nitrous oxide emissions because it releases the labile carbon that supplies electron donors for methanogens (Megonigal and Guenther 2008) and the nitrate for denitrification (Teh et al., 2008). In upland tropical forest soils, the combined spatial variability in soil water content, decomposition processes, and electron donors may represent a greater control on trace GHG uptake or emission than any single factor. At our study site, a large proportion of the annual litterfall occurs during the dry season (Sayer & Tanner 2010), and the rapid increase in soil fluxes of CH_4 and N_2O at the start of the wet season are likely to result from a combination of increased water-filled pore space and the decomposition of the thick litter that accumulates during the dry season (Wieder and Wright, 1995). Enhanced decomposition immediately after wetting (Vasconcelos *et al*., 2007) could lead to spikes in N_2O fluxes that coincide with rainfall (e.g. weeks 24 and 28 in Fig. 5). Correspondingly, the low rates of decomposition could also partly explain why we were unable to detect N_2O fluxes in the majority of dry season measurements.

Given the influence of decomposition processes on trace GHG production, we hypothesised that both CH_4 and N_2O emissions would be higher in litter addition plots as a result of greater availability in substrate for soil microorganisms. Although there were no consistent effects of the litter treatments on trace GHG emissions, higher N_2O emissions in litter addition plots towards the end of the study period (weeks 24-30; Fig. 6 & 7) and the additive or interactive effect of litter addition and species on tree stem N_2O and CH_4 fluxes (Fig. 4) suggest that there is a connection between trace GHG fluxes and litter quantity. However, increased litter inputs are only likely to result in increased N_2O emissions where there are sufficiently large

communities of denitrifying bacteria that can respond quickly to wetting events, creating hotspots and 'hot moments' (McClain et al. 2003). The high inter-week variation in tree stem N_2O fluxes in the present study (Fig. 7) could therefore also be explained by the timing and presence of such hotspots within the rooting zone.

Overall, the discrepancies between soil and stem trace GHG fluxes, and the apparent stronger effect of litter manipulation on fluxes of CH_4 and N_2O from *Heisteria* tree stems compared to *Simarouba* stems (Fig. 4 and 7) may be attributed to differences in species' rooting depths and the gradients of trace GHG production with soil depth. The possible role of rooting depth as a control of trace GHG fluxes from tree stems on upland soils is another avenue of investigation that requires further attention.

Our results suggest that tropical tree stems on upland soils may represent a hitherto unaccounted for conduit of trace GHG emissions, which likely originate from deeper soil horizons. Together, litter addition and tree species identity influenced stem CH_4 and N_2O fluxes, which suggests that tree uptake and emissions of trace GHGs is influenced both by decomposition processes and species traits. Given that tropical forests on upland soils cover a larger area than tropical wetland forests, the mechanisms underlying the fluxes of CH_4 and N_2O from tree stems, and their contribution to global trace GHG budgets, merits further examination.

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