

The role of termite CH₄ emissions on ecosystem scale: a case study in the Amazon rain forest

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Abstract. The magnitude of termite methane (CH₄) emissions is still an uncertain part of the global CH₄ budget and current emission estimates are based on limited field studies. We present in-situ CH₄ emission measurements of termite mounds and termite mound sub samples, performed in the Amazon rain forest. Emissions of five termite mounds of the species *Neocapritermes brasiliensis* were measured by use of a large flux chamber connected to a portable gas analyser, measuring CH₄ and CO₂.

5 In addition, the emission of mound sub samples was measured, after which termites were counted, so that a termite CH₄ and CO₂ emission factor could be determined.

Mound emissions were found to range between 17.0 ~~34.8~~ and 34.8 nmol mound⁻¹ s⁻¹ for CH₄ and between ~~1.6-13.5~~ 1.1 and 13.0 μmol mound⁻¹ s⁻¹ for CO₂. A termite emission factor of ~~0.32~~ 0.35 μmol CH₄ g_{termite}⁻¹ h⁻¹ was found, which is almost twice as high as the only other reported ~~average~~ value for the Amazon. By combining mound emission measurements with

10 the termite emission factor, colony sizes could be estimated, which were found to range between 55-125 thousand individuals. Estimates were similar to literature values, and we therefore propose that this method can be used as a quick non-intrusive method to estimate termite colony size in the field.

The role of termites in the ecosystems CH₄ budget was evaluated by use of two approaches. Termite mound emission values were combined with local ~~termite~~ mound density numbers, leading to an estimate of 0.15-0.71 nmol CH₄ m⁻² s⁻¹ on average
15 emitted by termite mounds. In addition, the termite CH₄ emission factor from this study was combined with termite ~~density~~ biomass numbers, resulting in an estimate of ~~termite-emitted~~ termite-emitted CH₄ of ~1.0 nmol m⁻² s⁻¹. Considering the relatively low net CH₄ emissions previously measured at this ecosystem, we expect that termites play an important role in the CH₄ budget of this Terra Firme ecosystem.

20 1 Introduction

Methane (CH₄) is ~~the second most important long-lived anthropogenic greenhouse gas~~ one of the most important greenhouse gases, but its natural sources are still not well understood. Anaerobic decomposition processes in wetlands are expected to represent the largest natural CH₄ source, but estimates remain a large source of uncertainty (Kirschke et al., 2013; Saunio et al., 2020). Recently, alternative CH₄ production mechanisms and their possible important role on ecosystem scale have been
25 proposed, such as the CH₄ production by living vegetation (Bruhn et al., 2012; Wang et al., 2014), the CH₄ emission due to photo and thermal degradation (Lee et al., 2012), or the transport of anaerobic soil-produced CH₄ through wetland trees (Pangala et al., 2015; Rice et al., 2010). An additional known CH₄ source in tropical ecosystems is the emission by termites. Termites (isoptera) can mostly be found between 45°N and 45°S, and are especially abundant in warm ecosystems (Bignell, 2006; Brian and Brian, 1978; Gomati et al., 2011; Wood, 1988). They are highly socialised insects, living in large commu-
30 nities of up to several million individuals (Wood, 1988). Termites are considered ‘ecosystem engineers’: they are known for decomposing organic substances, and moving and mixing organic and mineral materials, thereby enhancing humus formation, modifying soil structure, and improving soil fertility (Bignell, 2006; Brian and Brian, 1978; Bignell and Eggleton, 2000; Mishra et al., 1980; De Bruyn and Conacher, 1990; Wood, 1988). In addition, they are able to modify their environment to their needs: most termite species live in complex above or (partly) below-ground nests where temperature and moisture remain
35 stable (Bignell, 2019; Noirot and Darlington, 2000; Wood, 1988). Recently, it was shown that termites ~~have increase their activity during droughts, resulting in, among others, enhanced litter decomposition, elevated soil moisture and higher seedling survival rates, thereby demonstrating~~ a mitigating effect during droughts in tropical rain forests (Ashton et al., 2019).

Three main groups of termites can be distinguished, based on their main feeding habits: soil-feeding (humiverous) termites, who can mainly be found in and on the soil, decomposing decayed organic soil material, xylophagous termites, feeding on (de-
40 composed) wood, which can also be found in living trees, and ~~fungus-eating~~ fungus-feeding termites, which live in a symbiotic relationship with fungus (Eggleton, 2000; Sanderson, 1996).

CH₄ production by termites was first described and measured by Cook (1932). Follow up studies found that methane is produced by almost all termite species, and that its production takes place in the termite gut: in higher termites (dominant in
45 tropical forests, more evolved species with respect to diet and community complexity) CH₄ production is caused by symbiotic bacteria, and in lower termites the production is caused by flagellate protozoa (Bignell et al., 1997; Brune, 2018; Lee et al., 1971). In a laboratory experiment Zimmerman et al. (1982) measured the emission strength of individual termites and, by use of termite biomass ~~estimates numbers~~, presented a global termite emission estimate of 150 Tg CH₄ yr⁻¹, which was estimated to be 40% of the global natural CH₄ emissions. Different estimates followed, resulting in lower ~~estimates values~~, such as by
50 Seiler et al. (1984) of 2-5 Tg yr⁻¹, by Fraser et al. (1986) of ~~<15-14~~ Tg yr⁻¹, by Khalil et al. (1990) of 12 Tg yr⁻¹, and by Martius et al. (1993) of 26 Tg yr⁻¹. More recent literature uses estimates in the range of 2-15 Tg CH₄ per year (Ciais et al.,

2014; Kirschke et al., 2013; Sanderson, 1996; Saunois et al., 2020), which is ~~around 2.5~~approximately 0.5-4% of the total estimated natural source CH₄ emission (Saunois et al., 2020). While on global scale termite emissions can be considered small in comparison to natural sources like wetland emissions (~147 Tg yr⁻¹) or fresh water emissions (~159 Tg yr⁻¹) (Saunois et al., 2020), the question remains what their role can be in the CH₄ budget of a local tropical ecosystem.

Estimates of global termite CH₄ emissions are based on field and laboratory measurements. To estimate global CH₄ termite emissions, most commonly the CH₄ emission per termite (mg CH₄ termite⁻¹ h⁻¹) or termite mass (mg CH₄ g_{termite}⁻¹ h⁻¹) is measured, whereby termite mass can either be measured directly or be taken from literature (Sanderson, 1996). The disadvantage of this approach is that termites are removed from their natural environment, thereby possibly changing their emission and behaviour. Another approach is to measure termite nest CH₄ emissions in-situ in the field. In this case, emissions are expressed per mound or nest (mg CH₄ mound⁻¹ h⁻¹). While this method does not disturb the natural environment, correct estimation of termite nest colony size is challenging, wherefore values are hard to convert to emission-per-termite values (Jones et al., 2005). Besides CH₄, termite emissions of other gases have also been investigated, such as for CO₂, O₂, CO, H₂, CHCl₃, N₂O and different hydrocarbons (Cook, 1932; Khalil et al., 1990; Zimmerman et al., 1982). In previous studies, measurements of termite CO₂ ~~measurements-emissions~~ were often performed alongside CH₄ emission measurements, and ~~often-generally~~ a clear relationship between CH₄ and CO₂ emissions was found, of which the ratio is expected to be species dependent (Seiler et al., 1984; Jamali et al., 2013). For ~~termite-emitted~~termite-emitted CO₂, reported global estimates are 50 ~~GtPg~~ yr⁻¹ (Zimmerman et al., 1982), 4 ~~GtPg~~ yr⁻¹ (Khalil et al., 1990), and 3.5 ~~GtPg~~ yr⁻¹ (Sanderson, 1996) (1 ~~GtPg~~ = 1000 Tg). In addition, Khalil et al. (1990) observed mound CO uptake and emissions, but reported them to be irregular and small. Strong termite mound N₂O emissions have also been detected (Brümmer et al., 2009b; Brauman et al., 2015), although they were also found to be very irregular or undetectable (Khalil et al., 1990; Zimmerman et al., 1982). Brauman et al. (2015) suggested that termite mound N₂O emissions occur if N-rich organic matter is available.

Current global ~~termite-termite~~ CH₄ emission estimates are based on relatively few studies, and there is still a lack of data on termite CH₄ emission rates (Brune, 2018). In addition, existing studies have mostly focused on Australian or Asian species (~~Eggleton et al., 1999; Fraser et al., 1986; Jamali et al., 2011a, b, 2013; Khalil et al., 1990; Macdonald et al., 1998; Sugimoto et al., 1998b~~) (Eggleton et al., 1999; Fraser et al., 1986; Jamali et al., 2011a, b, 2013; Khalil et al., 1990; Macdonald et al., 1998; Sugimoto et al., 1998a) or African species (~~Brauman et al., 1992; Brümmer et al., 2009a; Macdonald et al., 1998; Rouland et al., 1993; Sawadogo et al., 2012, 2013~~) (Brauman et al., 1992; Brümmer et al., 2009a; Macdonald et al., 1998; Rouland et al., 1993; Sawadogo et al., 2011, 2012; Seiler et al., 1993). To our knowledge, only two studies focused on CH₄ ~~emissions-emission~~ of termites in the Amazon (Martius et al., 1993; Queiroz, 2004), and only one study reported CH₄ emission values for Amazonian termites (Martius et al., 1993). Martius et al. (1993) performed field measurements on wood-feeding termites by semi-field and laboratory measurements, and suggested that Amazonian termites release more methane than species in other regions. In addition, for the Amazon, it is expected that most termites are soil-feeding (Jones and Eggleton, 2010), a group which are expected to be the strongest emitters of CH₄

(Bignell and Eggleton, 2000; Brauman et al., 1992).

In this paper, we are presenting a case study performed in a tropical rain forest in the Amazon, where we measured the emission of CH₄ and other gases of epigeal (above-ground) termite nests of the species *Neocapritermes brasiliensis*, a soil-feeding species¹ abundant in the Amazon (Constantino, 1992; Pequeno et al., 2013), and one of the most common species in the region (Dambros et al., 2016). In addition we measured the CH₄ emission of countable groups of termites. The goal of our research was twofold. Firstly, we are providing the first CH₄ and other gas emission measurements of the species *N. brasiliensis*, thereby expanding the limited literature on CH₄ emissions from Amazonian termites. Secondly, we are aiming to quantify the role of termite emissions in the CH₄ budget of this specific ecosystem, as part of a larger ecosystem CH₄ budget study (van Asperen et al., in preparation). In addition, we are presenting a possible quick non-intrusive field method to estimate termite colony size in-situ.

2 Material and methods

2.1 Study site

The study was conducted at the experimental field site Reserva Biológica do Cuieiras – ZF2 (2 °36" 32.67 S, 60 °12"33.48 W, 40-110 m above sea level (a.s.l.), managed by the *Instituto Nacional de Pesquisas da Amazônia* (INPA), located ~50 km northwest of Manaus (Brazil). Field site ZF2 consists of plateaus and valleys with typical terra firme forest with tree heights of 35-40 m on the plateaus and 20-35 m in the valleys. Soils on the plateau are clayey and can be classified as Oxisols and Ultisols. Soils in the valleys contain more sand and can be classified as Spodosols (Luizão et al., 2004; Zanchi et al., 2014). The field site has a strong seasonality, with a wet season from December to April, and a dry season from June to September. Annual average temperatures range between 26-28 °C, and annual average precipitation is around 2400 mm. More information about the field site can be found in Araújo et al. (2002); Chambers et al. (2004); Luizão et al. (2004); Quesada et al. (2010); Zanchi et al. (2014). Measurements took place at the end of the wet season (March 2020).

2.2 Selection of termite mounds

In the study area, two main trails exist, following the topography from valley to plateau, and termite nests in vicinity of these trails were inventoried. For practical reasons, only free-standing epigeal (above-ground) nests were considered, from here on called mounds. Twenty termite mounds were selected for further research, and of each mound the termite species was determined. For flux chamber measurements, five mounds with the same termite species were selected ~~For~~ (nr. 13, nr. 14,

¹The species *Neocapritermes brasiliensis* is a wood/soil interface feeding species. Species feeding on extremely decomposed wood are in the centre of the 'wood-soil decomposition gradient' termite classification (Bourguignon et al., 2011), but are classified as soil-feeders according to Eggleton and Tayasu (2001).

115 [nr. 15](#), [nr. 16](#), and [nr. 19](#)); for practical reasons, chosen mounds were in close proximity of each other, and all located in the valley. ~~For comparison~~[As an exploratory measurement](#), an additional mound was selected of a different species on the plateau ~~(nr. 6)~~. Of each mound, height and perimeter were measured. Termite mound volumes were estimated by use of the following formula, as also used in Ribeiro (1997) and in Pequeno et al. (2013):

$$V = \frac{\pi HWT}{6} \quad (1)$$

120 wherein V is the mound volume (cm³), H is the height (cm), W is the width (cm), and T is the thickness (cm) of the mound. Termite mound surface was estimated by mathematically considering the lower part of the mound as a column, and the upper part as half a sphere. Details of each mound (dimensions, species, location) are given in Table 1.

2.3 Mound flux chamber set up

125 Collars (stainless steel, 15 cm height, 56.5 cm diameter) were placed around the five selected termite mounds a week before the start of the measurements. Collars were inserted for approximately 5 cm into the soil/litter layer. ~~In addition, one collar was placed at some distance from mound 15, containing only soil and litter, representing a blank (non-termite) measurement. From here on, this collar will be referred to as 'blank measurement'~~. A flux chamber was created by use of a 220 L slightly cone-shaped [polyethylene](#) bucket, with a diameter of 57.5 cm. A strip of closed-pore foam (1 cm x 1 cm x 57.5 cm) was attached over the whole inner perimeter, so that if the bucket was placed on the collar, the foam strip would seal the part between the bucket and the collar. Two one-touch fittings (1/4 inch, SMC Pneumatics) were installed on each side of the bucket. [On the inside of the bucket, a 4 inlet vertical sampling tube was placed, so that air was sampled from different heights \(~10, ~25, ~35 and ~50 cm\) in the headspace \(Clough et al., 2020\)](#). The set up (chamber and tubing) ~~were was~~ tested for internal emissions of all measured gases. For CO (see Appendix), an internal emission of <0.014 nmol s⁻¹ was found: presented CO ~~flux values~~ [fluxes](#) are not corrected for this possible internal emission.

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CH₄ and CO₂ concentrations were measured with a Los Gatos Ultraportable Greenhouse Gas Analyser. The instrument was connected in a closed loop with the flux chamber (2 x 2 meter PTFE tubing, 1/4 inch). For air circulation, the internal pump of the Los Gatos was used, with a flow of ~~~0.3~~[~0.35](#) L min⁻¹. The instrument measures concentrations every second; 10-sec averaged concentrations were saved and used for flux calculations. For each measurement, the flux chamber was closed for ~~25-20~~ minutes, during which time concentrations were measured continuously. All five mounds were always measured on the same day and in the same order. Over one week, each mound was measured three times, each time at approximately the same hour of the day.

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145 2.4 Flux calculations

Fluxes were calculated as follows. By use of the ideal gas law, mole fractions (~~ppb nmol/ppm $\mu\text{mol mol}^{-1}$~~) were converted to ~~molar densities~~ concentrations ($\text{nmol}/\mu\text{mol m}^{-3}$). For chamber temperature, a standard temperature of 25 °C was assumed. For chamber volume (CV), the termite mound volume (Table 1) was deducted from the bucket volume (220 L).

150 Fluxes could be calculated as follows:

$$F = \frac{dC}{dt} * \frac{CV}{A} \quad (2)$$

wherein $\frac{dC}{dt}$ is the concentration ~~increase (nmol change (nmol/ $\mu\text{mol m}^{-3} \text{ s}^{-1}$), CV the corrected chamber volume (m^3),~~
155 and A the collar area (0.25 m^2). Linear regression was used to derive the concentration ~~increase. Given change, and given~~
error bars are the propagated standard error of the linear regression slope. ~~All reported fluxes showed an overall $\frac{dC}{dt}$ increase~~
~~with~~ Concentration increases were calculated over the last 10 minutes of the chamber closure, to avoid possible effects of the
bag filling (see Appendix). If clear headspace concentration fluctuations were observed in the beginning of this time window,
possibly by a remaining effect of the bag filling, the window was shortened by a maximum of 2 minutes (leaving a time
160 window of 8 minutes). All calculated dC/dt increases showed a $R^2 > 0.95$. In addition, all fluxes were corrected for dilution
effects caused by the filling of Unless mentioned otherwise, given mound CO_2 emissions are corrected for the sampling bags
(see Appendix). Fluxes are expressed in $\text{nmol}/\mu\text{mol collar}^{-1} \text{ s}^{-1}$ or $\text{nmol}/\mu\text{mol mound}^{-1} \text{ s}^{-1}$, depending on whether a termite
mound is present in the collar. estimated contribution of soil respiration, by subtracting the average valley soil emission (see
§2.5). For mound nr. 6, the average plateau soil emission was subtracted.

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2.5 ~~Soil flux measurements around termite~~ Valley and mound adjacent soil fluxes

To quantify the CH_4 and CO_2 emissions of the soils ~~surrounding adjacent to~~ the termite mounds, four soil collars were installed around each mound: two soil collars were placed at 20 and 45 cm distance from the mound (distance between mound collar and middle of soil collar), and two additional soil collars were placed on the opposite side of the mound at the same
170 distances. The soil collars were of 20 cm diameter, with a height of 10 cm, and were inserted for 5 cm into the soil. The flux chamber height was 15 cm, so that the soil chamber volume was 4.7 L. ~~The soil chamber had two one-touch fittings on top, to~~
To be able to connect the Los Gatos instrument in the same way as to the 220 L flux chamber. Every, the soil chamber had
two one-touch fittings on top. The chamber and collars were created from a common PVC sewage pipe. Every mound adjacent
soil flux measurement was 4 minutes, and the set of 4 collar measurements was performed once per mound ~~-, with exception~~
175 of mound nr. 19. For mound nr. 13 and nr. 14, the measurements were performed on the 2nd measurement day, for mound nr.

15 and nr. 16, the measurements were done on the 3rd measurement day. Mound adjacent soil fluxes will be expressed per mound-collar area (0.25 m²), to be better comparable to mound emissions. The same chamber set up was used in a sub study at a close by transect (~500 m from termite mounds) where, among others, valley soil (10 collars) and plateau soil (10 collars) fluxes were measured (3 repetitions). Measured soil fluxes from the valley will be shown for comparison.

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2.6 Termite mound sub sample emission measurements

After each last mound flux measurement, a mound sample was taken of approximately 1 L volume. From this, three small sub samples were taken (volume not determined). When selecting a piece, we tried to look for solid not crumbling pieces, so that the inside of the sub sample was undisturbed. From the sample from mound nr. 19, only one suitable sub sample was found. 185 Each sub sample was placed in a small closed box (12.6 cm x 19.2 cm x 6.8 cm), with two one-touch fittings, functioning as a small closed flux chamber. A blank measurement was made with the small box, and no internal emissions were found. Each mound sub sample was measured with the Los Gatos instrument for 5 minutes, to determine the CH₄ and CO₂ production in the chamber over time. After each measurement, the mound sample was carefully broken open and termites were counted, so that the CH₄ and CO₂ emission per termite could be calculated. The measurements took place next to the mound, 190 and time between sampling and measuring was always less than 15 min. To verify whether the termite emission factor was stable between seasons and mounds, additional measurements were performed. In October 2020 (dry season), the same type of measurements were performed on 15 subsamples of the same termite mounds, and in December 2020 (transition dry-wet season), measurements were performed on 5 subsamples of a different mound of the same species.

195 2.7 Termite mass measurement

Termite mass was measured in the Laboratory of Systematics and Ecology of Soil Invertebrates at INPA. ~~80-480~~ living workers of the species *N. brasiliensis* were weighted in 5 subgroups (4x n=100, 1 x n=80) by use of a precision scale (FA2104N). Reported individual termite mass is fresh weight per termite (mg termite⁻¹).

3 Results

200 3.1 Mound CH₄ and CO₂ emissions

~~Mound~~ Headspace concentrations increased strongly during chamber closure, and chamber concentrations climbed up to 5750 nmol CH₄ emissions mol⁻¹ and up to 1950 μmol CO₂ mol⁻¹. CH₄ emissions of mounds nr. 13-19 ranged between 17.0 -34.8 and 34.8 nmol mound⁻¹ s⁻¹ (Fig. 1), with an average emission of 25.2 nmol mound⁻¹ s⁻¹. The blank measurements (collar with only soil and litter) showed an average Additional valley measurements showed heterogeneous soil CH₄ emission of 1.15 nmol collar fluxes with small uptake and emission taking place alongside, ranging between -0.1 and 2.9 nmol m⁻² s⁻¹ 205

(med=-0.02, avg=0.15, sd=0.54). Mound adjacent soil CH₄ fluxes, measured at 20 and 45 cm from the mound, ranged between 0.4 and 8.9 nmol CH₄ m⁻² s⁻¹. Mound (avg=2.14, sd=2.00), and were on average enhanced in comparison to valley soils (Fig. 2). Soil valley CO₂ emissions were between 1.6-13.5 fluxes were found to range between 0.9 and 3.7 μmol mound⁻² s⁻¹ (avg=2.14, sd=0.74) (Fig. 2), and the average plateau soil CO₂ emission was 4.03 μmol m⁻² s⁻¹, with (sd=1.36). Mound adjacent soil CO₂ fluxes showed an average emission of 8.7-4.81 μmol CO₂ m⁻² s⁻¹ (range=2.0-10.1, sd=2.04), thereby being enhanced with respect to the surrounding valley soils (Fig. 2). Mound CO₂ emissions, corrected for the average valley and plateau soil respiration, were ranging between 1.1 and 13.0 μmol mound⁻¹ s⁻¹. The blank measurements showed smaller fluxes, with an average emission of 0.47-8.14 μmol collar mound⁻¹ s⁻¹ (Fig. 1 average of mounds nr. 13-19).

The

During chamber closure, the concentration changes in CH₄ and CO₂ concentration increases inside the closed flux chamber were strongly correlated ($R^2 > 0.95$ for each chamber closure). The mound emission ratio between the mound CH₄ and CO₂ emission (CH₄/CO₂ ratios, shown in Fig. 3, varied between 2.0 and 11.6 * 10⁻³) ranged between 2.1 and 17.1 * 10⁻³ (average ratio: 3.9 * 10⁻³), but showed little variation Fig. 3), and showed a constant ratio when data from the blank measurements and data from mound mound nr. 19 (furthest away from other mounds) and mound nr. 6 (different species and location) were excluded (average ratio: 2.6 * 10⁻³ to 2.8 * 10⁻³, sd=0.4). The smallest mound (mound nr. 19) clearly showed smaller emissions than the other four mounds of the same species smaller than average emissions, but in general no strong correlation was found between measured mound CH₄ emissions, and mound height ($R^2=0.08$) or volume ($R^2=0.08$), and a small correlation was found between mound CO₂ emissions and mound volume height ($R^2=0.44$) and mound height volume ($R^2=0.54$) (Fig. 2) 0.44).

225

Mound adjacent soil and emissions Mound adjacent and soil emissions were measured around each mound once. For mound 13 and 14, this was done on the 2nd measurement day, for mound 15 and 16, this was done on the 3rd measurement day. Due to some practical issues, the measurements performed around mound 19 could not be used. Figure 2 shows the soil and emissions around each mound, expressed in emission per 0.25 m²: this unit was chosen to be able to compare soil flux measurements to mound (and blank) flux measurements, measured by the larger collar of 0.25 m². The small set in figure in the figures left corner shows the soil emissions in comparison to the day-specific mound emission. Average soil and emissions were respectively 0.5 nmol 'collar'⁻¹ s⁻¹ and 1.3 μmol 'collar'⁻¹ s⁻¹ (wherein collar stands for 0.25 m²). The measurements show that there is no clear emission pattern with increasing distance from the mound, and that mound adjacent soil fluxes are not strongly enhanced in comparison to the blank measurements (average blank flux measurements: 1.15 nmol and 0.47 μmol collar⁻¹ s⁻¹ for resp. and).

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3.2 Termite weight, individual termite emission, and colony size estimation

The living weight of 80 workers was measured to be 0.264 g. The average weight of 5 subsets of living workers of the species *N. brasiliensis* was determined, and was found to range between 2.83 and 3.33 mg, with an average weight of 3.07 mg (sd=0.18), which is 3.3 mg per worker. This value is similar to what was found by Pequeno et al. (2017), who measured

240 Pequeno et al. (2013), who reported 3.0 (\pm mg (sd=0.4)mg for workers and 6.6 (\pm 0.3) mg for soldiers. The . Since the species
N. brasiliensis has a relatively low soldiers:workers ratio of 1:100 (Krishna and Araujo, 1968). ~~For our calculations~~, we will
use ~~an average fresh weight of 3.33 mg termite⁻¹~~ the worker weight 3.07 mg (sd=0.18) as an average termite weight for the
species *N. brasiliensis*.

245 CH₄ and CO₂ emissions of 13 mound sub samples were measured. For each sub sample, the measured gas production was
plotted over the counted termites (Fig. 4). The fitted line has a forced intercept at y=0. For CH₄, an emission of 0.0002985
nmol termite⁻¹ s⁻¹ was found (se=1.77*10⁻⁵), fitted with an R² of 0.95 (n=13). The set of additional measurements resulted in
similar termite CH₄ emission factors, namely 0.0002976 nmol termite⁻¹ s⁻¹ (se=1.32*10⁻⁵) and 0.0003043 nmol termite⁻¹
s⁻¹ (se=1.41*10⁻⁵), for respectively the measurements of October and December 2020. Given estimates in this paper will be
250 based on the termite emission factor of 0.0002985 nmol CH₄ termite⁻¹ s⁻¹. For CO₂, an emission of ~~0.0001316 μ mol~~ 0.1316
nmol termite⁻¹ s⁻¹ was found (se=2.59*10⁻⁵⁻²), with an R² of 0.68 (n=13). Excluding the out ~~liers (32, 14.9 nmol s⁻¹~~
and 313, 0.81 μ mol ~~80.9 nmol s⁻¹) gives an R² of 0.80~~ gave an R² of 0.88 (n=1211), with a CO₂ emission of 0.000076 μ mol
0.074 nmol termite⁻¹ s⁻¹ (se=1.148.5*10⁻⁵⁻³). Converting the emission rates from termite to termite-mass (fresh weight),
and from seconds to hourly rates gives a termite emission factor of ~~0.32~~ 0.35 μ mol g_{termite}⁻¹ h⁻¹ (se=0.02) for CH₄ and of ~~82.2~~
255 86.8 μ mol g_{termite}⁻¹ h⁻¹ (se=~~0.04~~ 10.0) for CO₂ (Table 2).

By combining the termite ~~emission factors~~ CH₄ emission factor with the termite mound CH₄ emissions, colony sizes were
estimated. Colony size estimates were based on highest measured emissions and were found to range between ~~50-120~~ 55-125
thousand individuals (Table 3). ~~Population~~ Colony size can also be estimated by use of mound volume or mound external
260 surface. Table 3 shows the ~~population-colony size~~ estimates, based on values as given by Lepage and Darlington (2000) for
termites in general, and also ~~reports the population estimate based on the work of Pequeno et al. (2013)~~ shows the estimates
based the 'mound volume-termite biomass' relation found by Pequeno et al. (2013), specifically for the species *N. brasiliensis*.

4 Discussion

265 4.1 CH₄ and CO₂ emissions

~~Termite-Measured mound~~ CH₄ emissions ~~of were of similar magnitude to emissions found by previous studies (Table 2, middle and lower part). The termite emission factor, determined for the soil-feeding species *N. brasiliensis* were, was found to be 0.32~~ 0.35 $\mu\text{mol g}_{\text{termite}}^{-1} \text{h}^{-1}$ (sd=0.02), which is similar to most values found in literature-values found for other species (Table 2, upper part), but almost two times higher than the average value reported by Martius et al. (1993) for a wood-feeding species in
270 the Amazon (~~2.5-0.19 $\mu\text{mol g}_{\text{termite}}^{-1} \text{h}^{-1}$ = 0.16 $\mu\text{mol g}_{\text{termite}}^{-1} \text{h}^{-1}$~~). Our emission rate is within the reported range of 0.1-0.4 $\mu\text{mol g}_{\text{termite}}^{-1} \text{h}^{-1}$ for soil feeders (Sugimoto et al., 2000). ~~Measured mound emissions-Mound CO₂ emissions and the termite CO₂ emission factor were similar to a little higher in comparison to the few values found in literature (61-125 $\mu\text{mol mound}^{-1} \text{h}^{-1}$) are in the same range as mound emissions found by previous studies (Table 2). Nevertheless, since mound material and termites were measured together, the contribution of indirect termite emissions, i.e. mound respiration, cannot be quantified,~~
275 so that the direct termite-produced CO₂ emission is presumably lower.

There is a large variety in type of termite mounds (shape and size are dependent on ~~e.a., among others,~~ species, ecosystem, climate (Noirot and Darlington, 2000)), explaining the wide range of reported termite mound CH₄ emissions (Table 2, middle and lower part). In-situ measurement of termite ~~mound emissions-mounds~~ gives information about ~~termite-the net~~
280 CH₄ ~~production-emission~~ under natural conditions, but ~~are-is~~ unable to distinguish sources and sinks inside the mound. ~~Methanotrophic bacteria are~~ One known CH₄ sink in termite mounds is the uptake by methanotrophic bacteria, which are also responsible for the CH₄ uptake in aerobic soils, ~~and their possible presence in termite mounds was already suggested by Seiler et al. (1984). Other studies have confirmed their presence (Chiri et al., 2019; Ho et al., 2013), and recent studies have been focusing on whether methanotrophic bacteria are also present in the termite guts, a topic still under discussion~~
285 ~~(Ho et al., 2013; Pester et al., 2007; Reuß et al., 2015). Different estimates exist on the effect of these bacteria on the net mound flux. Sugimoto et al. (1998a) compared the $\delta^{13}\text{C}$ of emitted by mounds to the $\delta^{13}\text{C}$ of emitted by termites, and found a fractionation of 0.987 (emitted by mound/produced by termites). Other estimates range widely between no observable uptake to very strong uptake rates (up to 80%) (Khalil et al., 1990; Macdonald et al., 1998; Nauer et al., 2018; Sugimoto et al., 1998a) —A more elaborate overview of recent findings on termite mound uptake processes can be found in Nauer et al. (2018) and Chiri et al. (2019).~~ The presence and magnitude of this process have been discussed and reviewed by different studies
290 (Ho et al., 2013; Khalil et al., 1990; Macdonald et al., 1998; Nauer et al., 2018; Seiler et al., 1984; Sugimoto et al., 1998a; Pester et al., 2018). The role of possible mound CH₄ uptake should also be acknowledged for the measurement of individual termite emissions (Table 2, upper part): most literature values, including values from this study, are based on termite incubation in presence of mound material, with ongoing CH₄ uptake, wherefore actual termite CH₄ emission values might be higher.

295

~~Mound emissions ranged between 6-49 $\text{mmol mound}^{-1} \text{h}^{-1}$, which fits in the wide range of reported values (Table ??). The relation between the amount of termites and emitted was found to be 82.2 $\mu\text{mol g}_{\text{termite}}^{-1} \text{h}^{-1}$, which is higher than~~

most reported values before. Also here it should be considered that mound material and termites were measured together. Considering the presumably ongoing soil and mound material decomposition processes, the termite produced emission rates are likely lower.

The measured emissions of individual mounds showed small variation, such as an emission increase of 25.3 to 29.5 $\text{nmol mound}^{-1} \text{s}^{-1}$ at mound 15. One explanation is Small variation in mound emission magnitudes was observed between measurement days. This can be caused by a variation in colony size (due to foraging activities) or termite activity, driven by fluctuations in temperature or radiation ~~fluctuations~~ (Jamali et al., 2011a; Ohiagu and Wood, 1976; Sands, 1965; Seiler et al., 1984). However, as our ~~measured~~ termite mounds are on the forest floor of a tropical rain in a tropical forest with relatively constant temperatures and ~~with~~ only indirect daylight, strong diurnal temperature and radiation patterns are not expected. ~~In addition, since each mound measurement was performed at the same time of the day (± 1 hour), it is unlikely that this variation is caused by a diurnal cycle. Another possibility is that the variation can be explained by the degree of air flow~~ Small variation can also be caused by minimal air transport below the soil collar. ~~Preliminary test measurements, through the porous upper soil layer; during preliminary tests~~ without a collar revealed that the lightest forest breeze already caused strong chamber concentration drops. It is likely that even with a collar not all below collar air flow was prevented, especially considering the depth and the porosity of the valley litter layer. This theory is supported by the overall coherent and concentrations during chamber closure, which followed the same pattern at all times ($R^2 > 0.99$). ~~we observed that even a light forest breeze can cause chamber headspace variations.~~ In case our set up was subject to minor air transport ~~around below~~ the collar, the given mound estimates will be ~~an underestimation of~~ slightly underestimated with respect to the actual mound fluxes. ~~An additional~~ Another possible underestimation is caused by the estimated corrected chamber volume CV, as used in Eq. (2). In this study, we considered the mound volume as a solid body. A previous study considered the solid nest volume as ~~10%~~ 10% of the actual mound volume (Martius et al., 1993), leading to a larger corrected chamber volume, and therefore to larger calculated mound emissions. By use of this approach, average ~~measured emissions would~~ calculated mound emissions would increase by almost 30% to be 32.7 $\text{nmol mound}^{-1} \text{s}^{-1}$ instead of 25.2 $\text{nmol CH}_4 \text{ mound}^{-1} \text{s}^{-1}$.

The mound emission CH_4/CO_2 ratio was found to be relatively constant over 4 of the 5 mounds, ~~with an average ratio of $2.6 \cdot 10^{-3}$. Mound 19, the furthest located from the other mounds, showed relatively low emissions in comparison to its emissions, and showed an average /ratio of $8.4 \cdot 10^{-3}$. Values in~~ While values in literature indicate a wide range of ~~reported~~ CH_4/CO_2 ratios (Table ~~??~~). ~~However~~ 2, both Seiler et al. (1984) ~~and as~~ Jamali et al. (2013) found little variation between mounds of the same species, and concluded that the ~~emission~~ ratio is species-specific. Our average variation of a factor of ~~of ~ 3 for the /ratio of mound emissions of 4 between mounds of~~ the same species is of the same magnitude as what was observed in earlier studies (Seiler et al., 1984; Jamali et al., 2013). ~~Since mound 19 was located in a different part of the valley, it is likely that the characteristics of the surrounding organic matter were slightly different, affecting the /ratio, as also suggested by~~ Seiler et al. (1984).

4.2 Colony size estimate

To estimate colony sizes of (epigeal) nest building termites, different methods ~~exists. Excavation of a termite nest causes a strong disturbance, initiating an evacuation of the nest. To prevent this, fumigation with methyl bromide is usually applied, exist. One method is by fumigation of the nest (to prevent colony evacuation) followed by excavation,~~ after which termites
335 can be removed from the nest debris by flotation in water, ~~and can be counted.~~ This process is labour intensive, and can take five persons up to three weeks to finish one nest (Darlington, 1984; Jones et al., 2005). A faster method is by sub sampling known volumes of the mound, counting the termites in the sub sample, and extrapolating this to the total mound volume. Termite mounds can have irregular shapes, wherefore volume estimates strongly depend on which volume estimation approach ~~(hemisphere, cone, column)~~ is used (Jones et al., 2005). ~~So while this method is faster and less intrusive, it depends strongly on~~
340 ~~correct volume estimation and it still takes several hours per mound to estimate a colony size.~~

The population estimation method we tested combined CH₄ mound emissions with ~~an in-situ measured a~~ termite emission factor, measured in-situ at the field site. We estimated colony sizes ranging between ~~54.6-116.6 *10³~~ 57.6 and 124.0 thousand termites per mound. For all mounds, our population estimate was in the estimated range based on mound volume or external
345 surface area, as taken from literature equations (Table 3). Comparison to estimates based on a *N. brasiliensis* species-specific equation ~~showed differences of maximum 33~~ shows an average difference of 20% (Pequeno et al., 2013); it should be noted that the relation found between mound volume and ~~termite population colony biomass~~ by Pequeno et al. (2013) was quite weak ($R^2=0.41$), and our estimates would fit in the general spread they observed in their data (~~Pequeno et al., 2013~~). Interestingly, Pequeno et al. (2013) concluded that mound volume is a weak indicator for population size for nests of the species *N. brasiliensis*, as also indicated by the weak correlation we found between mound volume and mound CH₄ emissions (~~Fig.??~~).
350 The influence of mound CH₄ uptake on our population estimate method should be ~~contemplated~~ considered: mound methanotrophic CH₄ uptake ~~likely probably~~ decreases the net mound CH₄ emission, resulting in an underestimation of the colony size when linking it to termite emission factors, as also suggested by Nauer et al. (2018). However, our termite emission factor was determined inside small pieces of undisturbed mound material, ~~wherefore so that~~ the materials CH₄ uptake rate was ~~likely~~
355 presumably only little affected. ~~We hypothesise therefore It is therefore likely~~ that our termite emission factor is underestimated to the same degree as our mound emissions, wherefore both values can still be combined.

Overall, our colony size estimation approach can be considered as a test case for a quick population estimation method. The combination of one mound flux measurement (15 minutes) in combination with 5 sub sample measurements (5x5 minutes) can
360 be performed within 1 hour, ~~including the counting of the termites, being thereby thereby being~~ faster than the original methods. Also, the method is applicable to epigeal mounds of all species, independent of internal mound structure (Josens and Soki, 2010) or species characteristics (Pequeno et al., 2013). In addition, the ~~population estimation method we present~~ method is not strongly dependent on a correct mound volume estimate, which remains a source of uncertainty (Jones et al., 2005), and which has been shown to be a weak indicator of population size for some species (Pequeno et al., 2013; Josens and Soki, 2010).

365 ~~Furthermore~~Moreover, mounds can also be measured several times in a row before sub sample measurement, so that colony size dynamics over time can be studied noninvasively. A ~~drawback~~disadvantage of this method is that it is only applicable ~~for to~~ freestanding epigeal mounds, at least with the current type of chamber set up. For a possible follow up study, ~~a direct comparison of population estimation methods is proposed~~we propose a set up wherein the different methods are compared.

370 4.3 Role of termites on ecosystem scale

~~Mound adjacent soil flux measurements showed no enhanced~~Valley soil CH₄ and CO₂ fluxes ~~in comparison to soils in the blank collar. Additional measurements in the valley showed lower~~were similar to what was found by earlier studies (Souza, 2005; Moura, 2012; Chambers et al., 2004; Zanchi et al., 2014). On average, mound adjacent soil CH₄ and CO₂ fluxes than our blank collar soil fluxes, as also shown by Moura (2012), possibly indicating that our blank collar location might show
375 ~~unrepresentatively high and fluxes. However,~~were enhanced with respect to valley soils, although differences were small, and no clear emission pattern with 'distance to mound' was observed. While mound adjacent soil fluxes are possibly enhanced, we preferred to avoid overestimation, ~~it was and~~ decided to treat termite mounds as very local hot spots, with measured fluxes only representative for the collar area of 0.25 m². On average, CH₄ and CO₂ fluxes per collar area were found to be a factor ~630 and ~16 higher when an active termite mound was present.

380

To estimate the role of termites on ecosystem scale, one approach is to combine mound emission values with termite mound density numbers. A local study reported a density value of 21.6 mounds ha⁻¹ for the species *N. brasiliensis* specifically (Pequeno, 2014), which deducts to an average CH₄ emission of 0.05 nmol m⁻² s⁻¹ caused by mounds of this species alone. Non-species specific mound densities are known to vary strongly between and within ecosystems (Ackerman (2006), Appendix B8). We found five ~~local~~local studies reporting mound (epigeal nest) density values, which were ~100 mounds ha⁻¹ (Queiroz, 2004), 193 mounds ha⁻¹ (Oliveira et al., 2016), 250 mounds ha⁻¹ (Dambros et al., 2016), 60 and 280 mounds ha⁻¹ (de Souza and Brown, 1994), and even 760 mounds ha⁻¹ (Ackerman et al., 2007). When excluding the strong outlier of 760 mound ha⁻¹, the emission of termite mounds on ecosystem scale was estimated to range between 0.15-0.71 nmol m⁻² s⁻¹ for CH₄ and between 0.05-~~0.24~~0.23 μmol m⁻² s⁻¹ for CO₂. Since (epigeal) mounds only represent a part of the total termite
390 community, and not the termites located in the subsoil, in dead wood or on trees (arboreal nests), this emission value ~~likely~~ underestimates the actual role of termites on ecosystem scale. ~~Different studies reported ratios of epigeal nest-building colonies in relation to total amount of colonies, such as Constantino (1992) (0.05-0.13), de Souza and Brown (1994) (0.02-0.09), and Martius et al. (1996) (~0.1). However, since colony size can differ strongly between species, these ratios cannot be used to correctly upscale mound emissions to ecosystem scale.~~ To our knowledge, only Bandeira and Torres (1985) (as given in
395 Martius et al. (1996)) assessed the ratio between nest-building ~~termite biomass~~ vs total termite biomass, and estimated it to be ~0.16. Considering the limited literature on this subject, we prefer not too further extrapolate our mound emission measurements.

A ~~different~~ more comprehensive approach is to use termite biomass estimates and combine them with termite emission factors, a method which is commonly used for global CH₄ budget studies (Kirschke et al., 2013; Saunio et al., 2020). For active 400 tropical ecosystems, generally a termite biomass of ~11 g termite m⁻² is assumed (Bignell and Eggleton, 2000; Kirschke et al., 2013; Sanderson, 1996; Saunio et al., 2020). Considering the previously found value of ~~0.175-0.19~~ 0.175-0.19 μmol CH₄ g_{termite}⁻¹ h⁻¹ for wood-feeding termites in the Amazon (Martius et al., 1993), and our newly found termite emission factor of ~~0.32-0.35~~ 0.32-0.35 μmol CH₄ g_{termite}⁻¹ h⁻¹ for a soil-feeding termite, a termite-derived ecosystem CH₄ emission range of ~~0.5-1.0-0.6-1.1~~ 0.5-1.0-0.6-1.1 nmol m⁻² 405 s⁻¹ can be calculated. For CO₂, our termite emission factor of ~~82.2-86.8~~ 82.2-86.8 μmol CO₂ g_{termite}⁻¹ h⁻¹ leads to a ~~termite-derived~~ termite-induced ecosystem CO₂ emission of ~~0.25-~0.27~~ 0.25-~0.27 μmol CO₂ m⁻² s⁻¹.

An overview of the different estimates is given in Table 4. ~~For each~~ Each of these estimates ~~, it should be considered that our~~ values are based on measurements from mounds and termites ~~which were all~~ found in the valley, ~~and~~ which were only measured during the wet season. Nevertheless, an exploratory measurement of a small mound of a different species on the plateau 410 (mound nr. 6) indicated CH₄ fluxes of a similar magnitude in comparison to a similar-sized mound in the valley (mound nr. 19). Furthermore, ~~additional exploratory dry season~~ additional exploratory dry season measurements of the same mounds ~~(and of mound sub-samples) during the dry season (September 2020) revealed emission values of the~~ showed emissions of the same magnitude (not shown), ~~and~~ additional dry season mound subsample measurements revealed very consistent termite CH₄ emission factors (Fig. 4). We 415 therefore do not expect that mound CH₄ emissions are only of importance in the valleys, or only present in the wet season.

~~The emission estimate based on mound density, accounting only for epigeal nest building species, is likely underestimating the actual role of termites on ecosystem scale. It therefore makes sense that the other emission estimate (based on termite density) is higher for as well as for (Table 4). To put both~~ To put the estimates in perspective, not-termite specific ecosystem 420 CH₄ and CO₂ fluxes, measured at this field site during earlier studies, are given. Ecosystem termite CO₂ emissions ~~are were~~ estimated to range between 0.05-~~0.25-0.27~~ 0.25-0.27 μmol m⁻² s⁻¹, which is ~~around approximately~~ ~1-3% of the estimated total ecosystem respiration (7.8 μmol m⁻² s⁻¹ ~~;(Chambers et al., 2004)).~~ However, as discussed before, for as well Nevertheless, since the ‘emission per mound’ as well as the ‘termite emission factor’ are ~~likely overestimated, wherefore the actual role of both affected by indirect effects of termite activity (mound respiration), the contribution of direct~~ termite-emitted CO₂ ~~on~~ 425 ecosystem scale is probably into the ecosystem is presumably smaller. For CH₄, ~~termite-derived fluxes are estimated to be between 0.15-1.0 nmol m⁻² s⁻¹.~~ For, ~~as earlier discussed,~~ we rather expect an underestimation than an overestimation of our termite and mound emission values, wherefore we expect that these ecosystem estimates are conservative lower bound. For CH₄, it is difficult to judge the role on ecosystem scale, since the earlier measured CH₄ flux (above canopy EC measurements, ~2.0 nmol m⁻² s⁻¹ (Querino et al., 2011)), is a net flux of uptake and emission processes with relatively unknown individual magnitudes. Nevertheless, considering the magnitude of our estimated ~~termite-derived termite-emitted~~ termite-derived termite-emitted CH₄ emissions 430 (0.15-~~1.0-1.1~~ 1.1 nmol m⁻² s⁻¹), it is expected that termites play a significant role in this Terra Firme ecosystem.

4.4 Implications for global termite emission estimate

~~As described before, Termites contribution to tropical South America CH₄ budget~~

435 ~~In current CH₄ budget studies combine termite density values with termite emission factors to estimate global termite emissions. In current budget studies, an a termite emission factor of $0.175 \mu\text{mol g}_{\text{termite}}^{-1} \text{h}^{-1}$ ($2.8 \mu\text{g CH}_4 \text{g}_{\text{termite}}^{-1} \text{h}^{-1}$)² is used for ‘Tropical ecosystems and Mediterranean shrub lands’² (Kirschke et al., 2013; Saunois et al., 2020), which is mainly based on field studies in Africa and Australia (~~Brümmer et al., 2009a; Jamali et al., 2011a, b; Macdonald et al., 1998; MacDonald et al., 1999; Sanderson, 1996~~). The only termite emission factor measured ~~in for~~ the Amazon rain forest is by Martius et al. (1993) (~~2.5–3.0~~ $\mu\text{g g}_{\text{termite}}^{-1} \text{h}^{-1}$) for a wood-feeding termite species, which are expected to emit less CH₄ than soil-feeding termites (Bignell and Eggleton, 2000; Brauman et al., 1992). ~~Based on our measurements, we report an emission factor of $0.32 \mu\text{mol g}_{\text{termite}}^{-1} \text{h}^{-1}$ species (Bignell and Eggleton, 2000; Brauman et al., 1992). As a back-of-the-envelope calculation, based on Kirschke et al. (2013): 36% of global termite emission (~~~5.1–11~~ Tg) is expected to come from the region of ‘tropical South America’ ($0.36 * 11 = 3.96$ Tg). Substituting the emission factor of 2.8 with ~~the newly found $5.6 \mu\text{g CH}_4 \text{g}_{\text{termite}}^{-1} \text{h}^{-1}$), which is ~2 times higher than the ecosystem emission factor which is currently used in budget studies would increase this regions estimate to 7.92 Tg, and thereby the global estimate to 14.96 Tg.~~~~~~

Our study points out that termite emissions are still an uncertain source in the CH₄ budget, and are especially poorly quantified for the Amazon rain forest. Measurement of CH₄ emissions from different termite species, preferably covering species of different feeding or nesting habits, ~~such as wood-feeders or arboreal nest builders, allied in combination~~ with more precise termite distribution and abundance data, would allow more precise estimates and a better understanding of the role of ~~each micro-habitat on termite termites in the CH₄ emission budget.~~

5 Conclusions

455 In-situ measurement of termite mound CH₄ and CO₂ emissions confirmed that mounds ~~can be considered as are~~ important local hot spots, playing a considerable role on ecosystem scale. Measured ~~termite mound emissions of the species *N. brasiliensis* were of similar magnitude of what has been observed before for different soil-feeding to observed emissions for different soil and wood-feeding species, and emissions mounds showed a relatively constant CH₄/CO₂ emission ratio. By performing emission measurements on small groups of termites, we derived a termite CH₄ emission factor, so far only the second value reported for the Amazon rain forest. The newly found termite emission factor, measured for a soil-feeding species, is almost twice as high as the previously reported average value for the Amazon, which was determined for a wood-feeding species. By~~

²~~Kirschke et al. (2013) and Saunois et al. (2020) stated a termite emission factor $2.8 (1.0) \text{mg (g}_{\text{termite}}^{-1} \text{h}^{-1})$. Correspondence with the authors clarified that a termite emission factor of $2.8 (1.0) \mu\text{g (g}_{\text{termite}}^{-1} \text{h}^{-1})$ was meant.~~

²Kirschke et al. (2013) and Saunois et al. (2020) stated a termite emission factor $2.8 (\pm 1.0) \text{mg CH}_4 (\text{g}_{\text{termite}}^{-1} \text{h}^{-1})$. Correspondence with the authors clarified that a termite emission factor of $2.8 (\pm 1.0) \mu\text{g CH}_4 (\text{g}_{\text{termite}}^{-1} \text{h}^{-1})$ was meant.

combining mound emissions and termite emission valuesfactors, mound colony sizes were estimated, and values were similar to estimates based on literature review. Considering the quick, wide applicable and non-intrusive non-destructive nature of this method, we hypothesise approach, we propose that it can be used as a better population estimate approach than an alternative to the traditional methods, that are either destructive or too specificintrusive and time-consuming.
465 Assessment of the magnitude of termite-emitted termite-emitted CH₄ on ecosystem scale was attempted by two approaches. Mound emission values were combined with mound density numbers, leading to an estimate of 0.15-0.71 nmol CH₄ m⁻² s⁻¹ emitted by mounds on average; since this estimate neglects emission from termite activity outside mounds, the number is likely an underestimation. Termite-The CH₄ emission valuestermite emission factor from this study, and from the only other Amazon
470 field study, were combined with termite density biomass numbers, resulting in an estimate of termite-emitted termite-emitted CH₄ of 0.5-1.0 0.6-1.1 nmol m⁻² s⁻¹. Considering the relatively low CH₄ emissions previously measured at this ecosystem, we expect that termites play an important role in the CH₄ budget of this Terra Firme ecosystem.

Appendix A: Termite mounds: N₂O, CO, and δ¹³C of CO₂

A1 Methodology

475 In addition to the direct mound CH₄ and CO₂ emission measurements (performed with the Los Gatos instrument), mound N₂O and CO fluxes and the δ¹³C of the mound CO₂ flux were determined by the following method. Three bags (5L inert foil, Sigma-Aldrich) were sampled consecutively from the closed mound flux chamber (see section 2.4)during chamber closure. The bags were measured on the same or the consecutive day with a Spectronus FTIR analyser, which can quantify concentrations of CO₂, CH₄, N₂O and CO, and can determine the δ¹³C of CO₂. The N₂O and the δ¹³C of CO₂ measurements of
480 the FTIR analyser have a cross sensitivity for CO₂ concentrations, which is well quantified for the CO₂ range 380-800 ppm (Hammer et al., 2013). In order to sample air with CO₂ concentrations << 800 ppmμmol mol⁻¹, air samples were taken in the first minutes after chamber closure (2 min, 5 min, 8 min). Out of the 45 taken bag samples, 2 bag samples could not be used.

Before measurement of the bag sample, sample lines were flushed with bag sample air. Air samples were dried by a Nafion
485 dryer and by a column of magnesium perchlorate. Measurements were corrected for pressure and temperature variations as well as for cross-sensitivities (Hammer et al., 2013). For more information on this instrument, please refer to Griffith et al. (2012). For calibration of the instrument, 2 calibration gases were used: gas 1 with values 381.8 μmol CO₂ mol⁻¹, 2494.9 nmol CH₄ mol⁻¹, 336.6 nmol N₂O mol⁻¹, 431.0 nmol CO mol⁻¹, and a δ¹³C of CO₂ of -7.95 ‰for gas 1, and, and gas 2
with values 501.6 μmol CO₂ mol⁻¹, 2127.0 nmol CH₄ mol⁻¹, 327.8 nmol N₂O mol⁻¹, 256.7 nmol CO mol⁻¹, -14.41 ‰for
490 gas 2, for respectively , , , and and a δ¹³C of CO₂ of -14.41 ‰.

To calculate the fluxes of N₂O and CO, FTIR-measured bag concentrations of N₂O, CO and CO₂ were used. For each chamber closure, the $\frac{dN_2O}{dt}$, $\frac{dCO}{dt}$ and $\frac{dCO_2}{dt}$ were calculated, so that ratios the the ratios $\frac{dN_2O}{dCO_2}$ and $\frac{dCO}{dCO_2}$ could be derived. To calculate the fluxes of N₂O and CO, the ratios were combined with the in-situ measured-determined mound CO₂ flux, as

495 measured by the Los Gatos instrument. This approach was chosen because the intended 3 min bag sampling interval was not always accomplished, so that an exact Δt could not be assumed with certainty. To determine the $\delta^{13}\text{C}$ of the CO_2 emitted by the termite mounds, Keeling plots were used (Pataki et al., 2003).

A2 Mound N_2O and CO fluxes

~~Gas samples taken from the closed flux chamber-~~

500 Gas samples (3 samples per chamber closure) revealed stable N_2O concentrations, and headspace concentrations ranged between 333.7 and 342.4 ppb. No consistent concentration changes (increase or decrease) during chamber closure were observed, indicating no or very low nmol mol^{-1} over the different chamber closures. Since headspace CO_2 concentrations sometimes exceeded $800 \mu\text{mol mol}^{-1}$, and N_2O emissions. Since the ecosystem, CO_2 cross-sensitivity becomes uncertain at higher CO_2 concentrations (Hammer et al., 2013), not all 3 headspace samples per chamber closure could be used, wherefore qualitative
505 N_2O flux estimates cannot be reported. As a back-of-the-envelope calculation, N_2O fluxes were calculated if 2 headspace samples were with $\text{CO}_2 < 800 \mu\text{mol mol}^{-1}$, and if a minimum N_2O concentration difference of $0.18 \text{ nmol mol}^{-1}$ was found (FTIR precision (σ) for 5 min spectra is $0.09 \text{ nmol mol}^{-1}$), which gave us 3 mound flux estimates ranging between 0.03 and especially the valleys, are known to be low on nitrogen (Quesada et al., 2010), this is $0.11 \text{ nmol N}_2\text{O mound}^{-1} \text{ s}^{-1}$. Similarly low fluxes were found during additionally performed soil flux measurements, performed as part of a substudy, which
510 showed valley soil fluxes ranging between $0.008\text{-}0.106 \text{ nmol m}^{-2} \text{ s}^{-1}$. The low mound fluxes would be in agreement with conclusions from a previous study (Brauman et al., 2015) which suggested that termite mound N_2O emissions are dependent on the N-content of the termites diet (Brauman et al., 2015), which is expected to be low in the valleys of this ecosystem (Quesada et al., 2010).

515 Chamber CO concentrations ranged between 120 and 220 ~~ppb~~ nmol mol^{-1} , and showed a clear uptake on all days and for all mounds, ranging between -0.04 to $-0.78 \text{ nmol mound}^{-1} \text{ s}^{-1}$ (Fig. A1). ~~The 'blank' soil location showed emissions between 0.31 and $0.52 \text{ nmol collar}^{-1} \text{ s}^{-1}$.~~ Termite mound uptake has been observed before by Khalil et al. (1990). We expect that the observed uptake is caused by aerobic CO-oxidising bacteria in the mound, which are also responsible for the CO uptake in (tropical) soils (Conrad, 1996; Kisselle et al., 2002; Liu et al., 2018; Potter et al., 1996; Whalen and Reeburgh,
520 2001; Yonemura et al., 2000a). Soil CO uptake is dependent on atmospheric CO and therefore often limited by low soil diffusivity (Sun et al., 2018; Yonemura et al., 2000b). The dry porous mound material (Martius et al., 1993) is therefore a suitable place for CO uptake. ~~The observed emissions of the blank (soil) collar ($0.31\text{-}0.52 \text{ nmol collar}^{-1} \text{ s}^{-1}$) are likely caused by the counteracting abiotic production, driven by temperature and radiation (King et al., 2012; Lee et al., 2012; Pihlatie et al., 2016; Van Asperen
525 ~~or by a lesser studied anaerobic biological process (Moxley and Smith, 1998). While we expect that both soil uptake and emission are taking place in the blank soil collar (Kisselle et al., 2002; Liu et al., 2018; Potter et al., 1996; Van Asperen et al., 2015) ; it is likely that soil uptake is limited due to the low diffusivity of the wet valley soil, wherefore production becomes the dominant process.~~~~

A3 $\delta^{13}\text{C}$ of the ~~mound-emitted~~mound-emitted CO_2

530 ~~Despite our effort to sample air with low concentrations (cross sensitivity corrections are well determined for <800 ppm), only 19 out of 43 samples showed concentrations lower than 800 ppm. Nevertheless, for~~

For each chamber measurement, a mound-specific $\delta^{13}\text{C}$ value of the CO_2 flux was determined. Figure A2 shows the Keeling plot intercepts, wherein error bars represent the standard errors of the intercept. ~~Per mound, an average was calculated, which were -38.1‰ (mound 13, $\text{se}=0.9$), -36.2‰ (mound 14, $\text{se}=1.0$), -35.7‰ (mound 15, $\text{se}=0.1$), -34.7‰ (mound 16, $\text{se}=1.4$), and~~
535 ~~-34.7‰ (mound 19, $\text{se}=1.3$). For calculation of these averages, values with a linear regression of $R^2 < 0.99$, or values based on a linear regression of only two measurements, were excluded (indicated as dark red squares in Fig. A2). The $\delta^{13}\text{C}$ of the blank collar (soil) flux was -33.7‰ ($\text{se}=2.5$). Previous studies have found that mound material can be enriched or depleted in ^{13}C in comparison to surrounding soils, although differences are usually small ($\sim 1\text{‰}$) (Siebers et al., 2015; Spain and Reddell, 1996). Studies reporting values on mound emitted $\delta^{13}\text{C}$ of have not been found. Based on our measurements, no *significant* difference~~
540 ~~in the $\delta^{13}\text{C}$ between mound and soil emitted was found (-33.7‰ ($\text{se}=2.5$) for soil, in comparison to -38.1‰ to -34.7‰ for termite mound emitted).~~ In general, the values were more depleted than values found by De Araujo et al. (2008), who found a $\delta^{13}\text{C}$ of -30.1‰ for valley litter during the dry season (August 2004). ~~To investigate whether our~~ However, for our measurements, at least one sample bag per chamber closure was with $\text{CO}_2 > 800 \mu\text{mol mol}^{-1}$, so that the CO_2 cross sensitivity correction for these samples was less certain. Intercepts based on only the first 2 concentrations points, which were generally
545 lower (or around) $800 \mu\text{mol mol}^{-1}$, resulted on average in less depleted ($\sim 1\text{‰}$) $\delta^{13}\text{C}$ values. To investigate if these values are representative for other mounds ~~or soils in the valley~~, and to investigate whether an isotopic difference exists between mound and ~~soil emitted~~soil-emitted CO_2 , more measurements would be needed.

Author contributions. HA designed and performed the field experiment, and wrote the paper, JA was responsible for the determination of
550 the termite species, and gave input on the entomology part of the research, BF and AA provided access to the logistics and infrastructure of the field site, JA, TW, BF, AA and JN reviewed and commented on the paper.

Competing interests. The authors declare that they have no conflict of interest.

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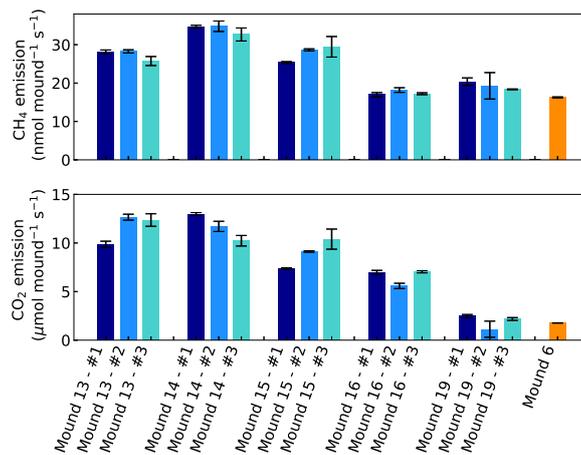


Figure 1. CH₄ and CO₂ emissions of mounds nr. 13 -19 (in valley) ~~and~~ of mound nr. 6 (on plateau), ~~and of a blank collar (in valley),~~ expressed in nmol and μmol mound⁻¹ s⁻¹, which represents a ~~collar-area~~ collar area of 0.25 m². All mounds (except mound nr. 6) were measured 3 times during one week, and each series-nr (#) was measured on the same day and in the same order. Error bars are propagated standard errors of the linear regression slope, as described in ~~section~~ §2.4.

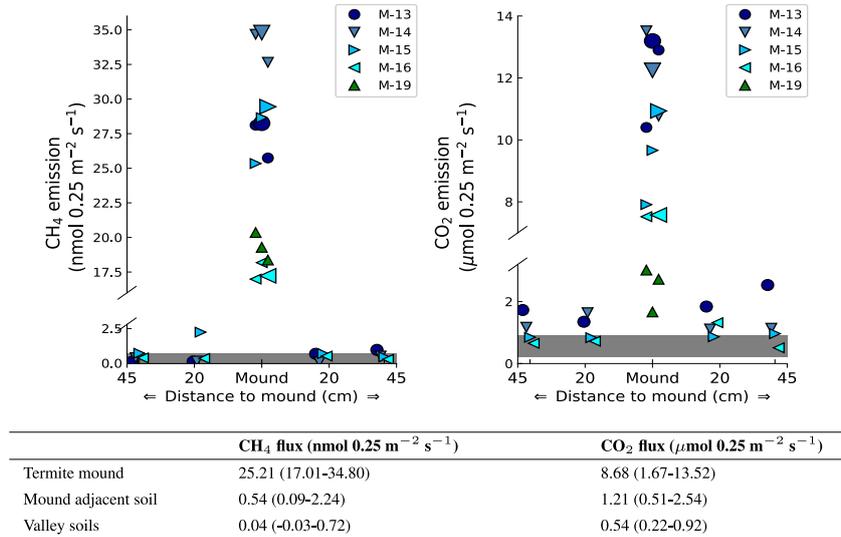


Figure 2. Measured mound emissions and mound adjacent soil fluxes for CH₄ (left) and CO₂ (right) for mound nr. 13, nr. 14, nr. 15 and nr. 16 expressed in nmol 0.25 m⁻² s⁻¹ for CH₄ and μmol 0.25 m⁻² s⁻¹ for CO₂ (collar area is 0.25 m²). Note that for CO₂ here the *net* mound emissions per collar area, not corrected for soil respiration, are shown and stated. The centrally-placed markers are the measured mound emissions (also for mound nr. 19); the larger marker indicates the day-specific mound emission when mound adjacent soil fluxes were measured. The grey bar indicates the range of additionally measured soil valley fluxes. The range and average flux for each group of measurements are given in the table. On average measured mound CH₄ and CO₂ fluxes were a factor 630 and 16 higher in comparison to the surrounding soil valley fluxes.

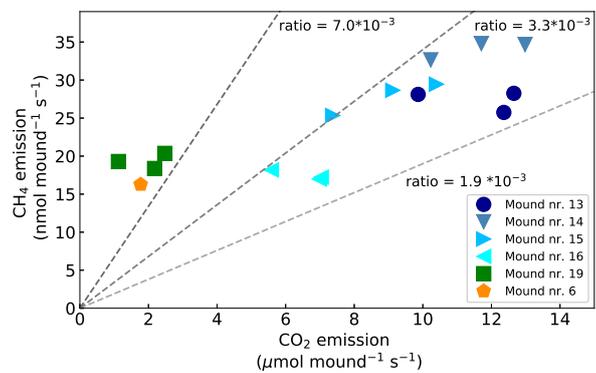


Figure 3. Mound CO₂ emissions ($\mu\text{mol mound}^{-1} \text{s}^{-1}$) versus mound CH₄ emissions ($\text{nmol mound}^{-1} \text{s}^{-1}$). Dotted lines indicate the different $d\text{CH}_4/d\text{CO}_2$ emission ratios.

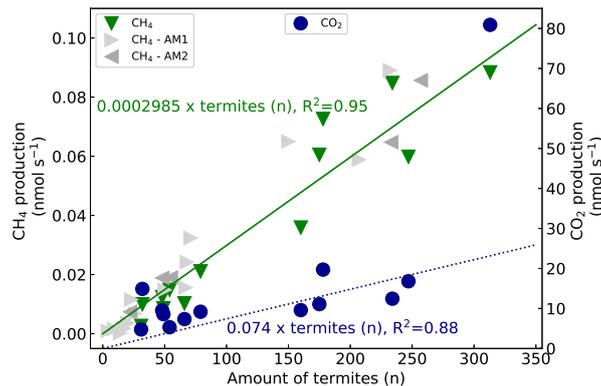


Figure 4. CH₄ production (left axis, green triangles) and CO₂ production (right axis, blue circles), ~~measured in the closed small flux chamber,~~ over counted termites. The lines (green solid for CH₄, blue dashed for CO₂) represent a linear regression fit with forced intercept at y=0. For CH₄, a production of 0.0002985 nmol termite⁻¹ s⁻¹ (se=1.77*10⁻⁵, R²=0.95) was found, and for CO₂, a production of 0.1316 ~~μmol-nmol~~ termite⁻¹ s⁻¹ (se=2.59*10⁻⁵⁻², R²=0.68) was found. Excluding the outliers (32, 14.9 nmol s⁻¹ & 313, 80.9 nmol s⁻¹) gives an R² of 0.88 (n=11), with a CO₂ emission of 0.074 nmol termite⁻¹ s⁻¹ (se=8.5*10⁻³). For comparison, two sets of additional subsample CH₄ emission measurements are shown. The first additional measurements (AM1, light grey triangles) resulted in a termite emission factor of 0.0002976 nmol termite⁻¹ s⁻¹ (se=1.32*10⁻⁵) (one measurement point (599 termites, 0.165 nmol s⁻¹) is not shown in this figure). The second set (AM2, dark grey triangles) gave a termite emission factor of 0.0003043 nmol termite⁻¹ s⁻¹ (se=1.41*10⁻⁵).

~~Measured mound emissions (left axis) and mound emissions (right axis) versus mound height (cm) (upper figure) and estimated mound volume (L) (lower figure). Blue circles indicate emissions, green triangles indicate emissions:~~

760 ~~Mound-adjacent soil fluxes (left) and soil fluxes (right) for mound 13, 14, 15 and 16 expressed in nmol collar⁻¹ s⁻¹ for and μmol collar⁻¹ s⁻¹ for (collar is 0.25 m²). Small inserted figures show mound emission of respective mound on same measurement day.~~

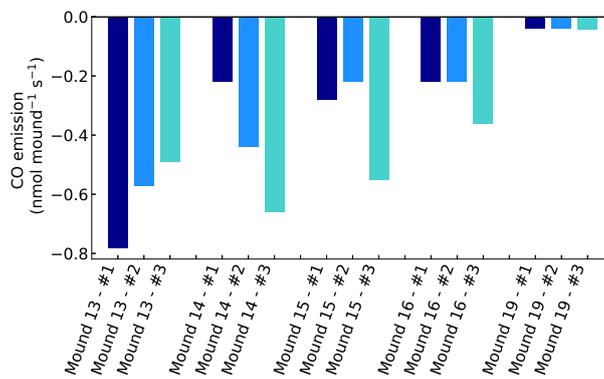


Figure A1. CO emissions of valley mounds nr. 13 -19 (~~in valley~~), mound 6 (~~on plateau~~) and of a blank collar (~~in valley~~), expressed in nmol mound⁻¹ s⁻¹, which represents a ~~collar area~~ collar area of 0.25 m². All mounds (~~except mound 6~~) were measured 3 times during one week, and each series-nr (#) was measured on the same day and in the same order.

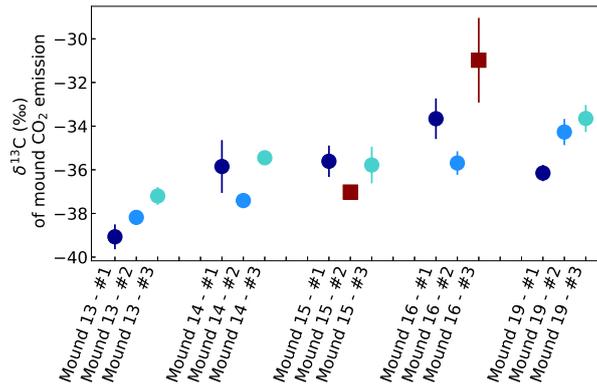


Figure A2. $\delta^{13}\text{C}$ of CO_2 emitted by mounds nr. 13 -19~~and by soil in a blank collar~~, derived by use of Keeling plots. Error bars represent the standard error of the linear regression intercept. Red squares indicate intercepts based on linear regression fits with $R^2 < 0.99$, or based on linear regression with only 2 instead of 3 sample points. All mounds were measured 3 times during one week, and each series-nr was measured on the same day and in the same order. Per mound, an average was calculated, which were -38.1‰ (mound nr. 13, se=0.9), -36.2‰ (mound nr. 14, se=1.0), -35.7‰ (mound nr. 15, se=0.1), -34.7‰ (mound nr. 16, se=1.4), and -34.7‰ (mound nr. 19, se=1.3). For calculation of these averages, values with a linear regression of $R^2 < 0.99$ or values based on a linear regression of only two measurements (indicated as dark red squares), were excluded.

Table 1. Termite mounds: location, dimensions, and observed species. ~~Termite mound volumes were~~ Volume is estimated mound volume as calculated by Eq. (1), and ~~mound surfaces were~~ surface is estimated mound surface by mathematically considering the lower part of the mound as a column, and the upper part as half a sphere. In mound 1, two different termite species were found. ~~Mounds-~~ N. bra stands for Neocapritermes brasiliensis, H. ten for Heterotermes tenuis, R. bra for Rotunditermes bracantinus, and E. neo for Enbiratermes neotenicus. The five mounds indicated in bold (mound nr. 13, nr. 14, nr. 15, nr.16 and nr. 19) were the mounds selected for flux measurements.

Nr	Location	Height	Perimeter	Estimated mound volume <u>Estimated mound volume</u>	Estimated mound surface <u>Estimated mound surface</u>	Species
1	valley	50 cm	128 cm			Neocapritermes brasiliensis, Heterotermes tenuis <u>N. bra, H. ten</u>
2	slope	45 cm	145 cm			Neocapritermes brasiliensis <u>N. bra</u>
3	plateau	35 cm	128 cm			Neocapritermes brasiliensis <u>N. bra</u>
4	plateau	55 cm	138 cm			Neocapritermes brasiliensis <u>N. bra</u>
5	plateau	45 cm	148 cm			Rotunditermes bracantinus <u>R. bra</u>
6	plateau	47 cm	99 cm	33.8 L	4653 cm²	Enbiratermes neotenicus <u>E. neo</u>
7	plateau	50 cm	160 cm			Enbiratermes neotenicus <u>E. neo</u>
8	slope	35 cm	160 cm			Enbiratermes neotenicus <u>E. neo</u>
9	valley	37 cm	105 cm			Neocapritermes brasiliensis <u>N. bra</u>
10	valley	50 cm	94 cm			Neocapritermes brasiliensis <u>N. bra</u>
11	valley	45 cm	111 cm			Neocapritermes brasiliensis <u>N. bra</u>

Table 2. Overview of literature values for CH₄ and CO₂ emission of termites per weight (upper part table), emission per termite mound (middle part table), and emission per area (lower part table). Values from this study for the soil-feeding species *N. brasiliensis* are indicated in bold. If reported, the average and sd are given, otherwise a range is indicated. If multiple values were found in literature, measurements from higher soil-feeding termite species were chosen to report selected. For each study, the graph or table where the data was found, is indicated given. The CH₄/CO₂ is given in the first column molar ratio (10⁻³). a) Sawadogo et al. (2011) reported emissions per dry weight mass. To convert to fresh weight, a formula as reported by Pequeno et al. (2017) was used: $\log_{10}(\text{fresh weight}) = 0.51 + 1.04 \log_{10}(\text{with an assumed dry weight})$. Assuming a dry weight of ~0.5 mg, gives a fresh weight of 1.57 mg, and a conversion factor of 3.14, is deducted. b) Mound emissions are divided by collar area of 0.25 m²; c) *Neocapritermes brasiliensis* Calculated based on average values in this table; d) *Neocapritermes brasiliensis*; e) *Crenetermes albotarsalis*, *Cubitermes fungifaber*, *Cubitermes speciosus*, *Noditermes* sp., *Procupitermes* sp., *Thoracotermes macrothorax*; f) *Dicuspiditermes santschii*, *Dicuspiditermes nemorosus*, *Pericapritermes semarangi*, *Procapritermes* nr. *Sandakanensis*, *Homalotermes eleanorae*, *Proaciculitermes* sp. A, *Pericapritermes nitobei*; g) *Coptotermes lacteus*; h) *Ancistrotermes cavithorax*, *Odontotermes n. pauperans*; i) *Nasutitermes macrocephalus*, *Nasutitermes corniger*, *Nasutitermes surinamensis*, *Nasutitermes* sp., *Nasutitermes ephratae*, *Nasutitermes araujoi*; j) *Noditermes* sp., *Crenetermes albotarsalis*, *Cubitermes speciosus*, *Thoracotermes macrothorax*, *Astratotermes* sp.; k) *Macrotermes bellicosus*; l) *Microcerotermes* sp., *Globitermes sulphureus*, *Termes* sp., *Dicuspiditermes* sp.; m) *Sugimoto et al. (1998b)*, see Appendix 1; n) *Drepanotermes perniger*, *Nasutitermes magnus*, *Nasutitermes triodiae*, *Tumulitermes pastinator*, *Amitermes laurenensis*, *Coptotermes lacteus*; o) *Bulbitermes* sp. C, *Dicuspiditermes nemorosus*, *Dicuspiditermes santschii*; p) *Macrotermes* and *Odontotermes* (Macrotermitinae), *Trinervitermes* (Nasutitermitinae), *Amitermes* and *Cubitermes* (Termitinae), *Hodotermes* (lower termite); q) *Cubitermes fungifaber*; r) *Microcerotermes nervosus*, *Turnulitermes pastinator*, *Turnulitermes hastilis*, *Amitermes meridionalis*.

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Study	Study area	Studies reporting emission per gram termite					
		Reported values	CH ₄ emission (μmol g _{tm} ⁻¹ h ⁻¹)	Reported unit	CO ₂ emission (μmol g _{tm} ⁻¹ h ⁻¹)	Converted values CH ₄ /CO ₂	Converted unit Species
This study, Fig. 54	Amazon	0.0002985 0.35 (0.2)	nmol termite⁻¹ s⁻¹ (0.0002985 nmol tm ⁻¹ s ⁻¹)	0.3286.8 (10.0)	μmol g_{termite}⁻¹ h⁻¹ (0.074 nmol tm ⁻¹ s ⁻¹)	~4 ^c	Soil feeders ^{(c)(d)}
Brauman et al. (1992), Table Tab. 1	Congo	0.39-1.09	μmol g_{termite}⁻¹ h⁻¹ (0.39-1.09 μmol g _{tm} ⁻¹ h ⁻¹)	0.39-1.09	μmol g_{termite}⁻¹ h⁻¹	Soil feeders ^(d)	Soil feeders ^(e)
Eggleton et al. (1999), Table- Eggleton et al. (1999), Tab. 4	Australia	0.17-0.27	μmol g_{termite}⁻¹ h⁻¹ (0.17- 0.27 μmol g _{tm} ⁻¹ h ⁻¹)	0.17-0.27 1.4-9.0	μmol g_{termite}⁻¹ h⁻¹ (1.4- 36.4 μmol g _{tm} ⁻¹ h ⁻¹)	Soil feeders ^(e) 10-154	Soil feeders ^(f)
Fraser et al. (1986), Table- Fraser et al. (1986), Fig. 2	Australia	0.67-0.04 (0.01)	mg kg_{termite}⁻¹ h⁻¹ (0.67 (0.2) mg kg _{tm} ⁻¹ h ⁻¹)	0.04-107 (4.5)	μmol g_{termite}⁻¹ h⁻¹ (4.7 (0.2) g kg _{tm} ⁻¹ h ⁻¹)	Wood feeders ^(f) ~0.38 ^c	Wood feeders ^(g)
Martius et al. (1993), Table- Konaté et al. (2003), Tab. 1	Ivory Coast			31.4-133.5	(31.4-133.5 nmol mg _{tm} ⁻¹ h ⁻¹)		Fungi feeders ^(h)
Martius et al. (1993), Tab. 1	Amazon	0.4-4.9-0.19 (0.08)	μg g_{termite}⁻¹ h⁻¹ (3.0 (1.3) μg g _{tm} ⁻¹ h ⁻¹)	0.03-0.31	μmol g_{termite}⁻¹ h⁻¹	Wood feeders ^(g)	Wood feeders ⁽ⁱ⁾
Rouland et al. (1993), Table Tab. 1	Congo	0.53-1.09	μmol g_{termite}⁻¹ h⁻¹ (0.53-1.09 μmol g _{tm} ⁻¹ h ⁻¹)	0.53-1.09	μmol g_{termite}⁻¹ h⁻¹	Wood feeders ^(h)	Soil feeders ^(j)
Sawadogo et al. (2011), Table Tab. 1	Burkina Faso	0.30-0.39 μmol g_{termite}⁻¹ h⁻¹	μmol g_{termite}⁻¹ h⁻¹ (0.30-0.39 μmol g _{tm} ⁻¹ h ⁻¹) ^a	Wood feeders ⁽ⁱ⁾ 19-25	(59.4-78.4 μmol g _{tm} ⁻¹ h ⁻¹) ^a	~5 ^c	Wood feeders ^(k)

Elaboration of Table 2 on studies which reported as well as termite emission values. Upper part: emission of termites per weight; middle part: emission per termite mound; lowest part: termite emission per area. Values from this study for the soil-feeding species *N. brasiliensis* are indicated in bold. If multiple values were found in literature, measurements from higher soil-feeding termite species were chosen to report. For each study, the graph or table where the data was found, is indicated in the first column. a) Calculated based on values in study; b) Converted from /to /and given values are for higher soil-feeding termites; c) Sawadogo et al. (2011) reported emissions per dry weight mass. To convert to fresh weight, a formula as reported by Pequeno et al. (2017) was used: $\log_{10}(\text{fresh weight}) = 0.51 + 1.04 \log_{10}(\text{dry weight})$. Assuming a dry weight of ~0.5 mg, gives a fresh weight of 1.57 mg, and a conversion factor of 3.14.; d) Mound emissions are divided by collar area of 0.25 m².

	Study	Reported values	Reported unit	Converted values	Converted unit	Ratio $(\times 10^{-3})$
	This study, Fig. 5	0.000076	$\mu\text{mol termite}^{-1} \text{s}^{-1}$	82.2	$\mu\text{mol g}_{\text{termite}}^{-1} \text{h}^{-1}$	3.9
	Fraser et al. (1986), Fig. 2	4.7	$\text{g kg}_{\text{termite}}^{-1} \text{h}^{-1}$	294	$\mu\text{mol g}_{\text{termite}}^{-1} \text{h}^{-1}$	0.1 (a)
	Sugimoto et al. (1998b), Appendix 1	15	$\text{g g}_{\text{termite}}^{-1} \text{h}^{-1}$	91	$\mu\text{mol g}_{\text{termite}}^{-1} \text{h}^{-1}$	(b)
775	Eggleton et al. (1999), Table 4	1.4	$\mu\text{mol g}_{\text{termite}}^{-1} \text{h}^{-1}$	1.4	$\mu\text{mol g}_{\text{termite}}^{-1} \text{h}^{-1}$	10-154
	Sawadogo et al. (2011), Table 1	59.4	$\mu\text{mol g}_{\text{termite}}^{-1} \text{h}^{-1}$	78.4	$\mu\text{mol g}_{\text{termite}}^{-1} \text{h}^{-1}$	5.0-5.3 (a)
	This study, Fig. 1	1.6	$\mu\text{mol mound}^{-1} \text{s}^{-1}$	6	$\text{mmol mound}^{-1} \text{h}^{-1}$	2.4-5.9
	Khalil et al. (1990), Fig. 4, Table 3	0.05	$\text{mg mound}^{-1} \text{s}^{-1}$	11	$\text{mmol mound}^{-1} \text{h}^{-1}$	0.12-11
	Seiler et al. (1984), Table 1	0.03	$\text{g nest}^{-1} \text{h}^{-1}$	2	$\text{mmol nest}^{-1} \text{h}^{-1}$	0.1-8.7
780	This study, Fig. 1	1.6	$\mu\text{mol mound}^{-1} \text{s}^{-1}$	23	$\text{mmol m}^{-2} \text{h}^{-1}$	(d), 2.4-5.9
	Jamali et al. (2013), Fig. 3	0	$\text{mg C m}^{-2} \text{h}^{-1}$	129	$\text{mmol m}^{-2} \text{h}^{-1}$	2.7-11.0
	Brümmer et al. (2009a), Fig. 5	100	$\text{mg C m}^{-2} \text{h}^{-1}$	8	$\text{mmol m}^{-2} \text{h}^{-1}$	

Table 3. Colony size estimates (CSE) based on different methods: values given per thousand ($\times 10^3$). 'Mound volume' is estimated mound volume as given in Table 1, and 'Mound emission' is highest measured emission per individual mound. a) population estimate CSE based on highest measured mound CH₄ emission, and combined with the observed emission factor of 0.0002985 nmol CH₄ termite⁻¹ s⁻¹ (se=1.77 $\times 10^{-5}$); b) population estimate CSE based on mound volume (given in Table 1), by use of mound termite density values (0.2-5.6 termite cm⁻³ (Lepage and Darlington, 2000)); c) population estimate CSE based on mound surface area (given in Table 1), by use of mound termite surface values (5.6-16.7 termite cm⁻² (Lepage and Darlington, 2000)); d) Population estimate CSE based on mound volume (given in Table 1), by species-specific volume-population equation of $y=47.94*x^{0.47}$ (x is mound volume (L), y is colony biomass (g)), as given by Pequeno et al. (2013). To convert from population mass to population numbers, a for termite mass of 3.33 weight 3.07 mg termite⁻¹ (sd=0.18) was taken used. Mound Since mound nr. 6 contained was of a different species, wherefore this formula was it is not applied included in this table.

6-Nr	Estimated Mound volume	Highest measured Mound emission	Estimated colony size CSE by emission	Estimated colony size CSE by mound volume	Estimated colony size CSE by surface area	Estimated colony size CSE by volume Pequeno et al. (2013) species-specific volume
6-Nr	Estimated Mound volume	Highest measured Mound emission	Estimated colony size CSE by emission	Estimated colony size CSE by mound volume	Estimated colony size CSE by surface area	Estimated colony size CSE by volume Pequeno et al. (2013) species-specific volume
6-Nr	33.8 L	16.3 nmol mound⁻¹ s⁻¹ emission	54.6 emission^a	6.5 - 182.3 volume^b	26.1-77.7 surface area^c	species-specific volume^d
13	77.6 L	28.3 nmol mound ⁻¹ s ⁻¹	94.8-89.6 - 100.9	15.5 - 434.6	54.6-162.8	111.3-114.0 - 128.2
14	48.0 L	34.8 nmol mound ⁻¹ s ⁻¹	116.6-110.1 - 124.0	9.6 - 268.8	35.7-106.4	88.8-91.0 - 102.3
15	50.5 L	29.5 nmol mound ⁻¹ s ⁻¹	98.8-93.4 - 105.1	10.1 - 282.8	39.3-117.2	90.9-93.2 - 104.8
16	49.7 L	18.2 nmol mound ⁻¹ s ⁻¹	61.0-57.6 - 64.9	9.9 - 278.3	39.0-116.2	90.3-92.5 - 104.0
19	38.0 L	20.4 nmol mound ⁻¹ s ⁻¹	68.3-64.6 - 72.7	7.6 - 212.8	26.5-78.9	79.6-81.5 - 91.7

~~Overview of termite-derived emissions, based on two different approaches. For comparison, the lowest row shows total (not termite-specific) ecosystem and flux values, measured at the same field site by previous studies. a) Querino et al. (2011) performed Eddy Covariance (EC) above-canopy flux measurements, and reported an averaged EC flux of $\sim 2 \text{ nmol m}^{-2} \text{ s}^{-1}$; b) Chambers et al. (2004) quantified different respiratory sources in this ecosystem, and estimated the total ecosystem respiration to be $7.8 \mu\text{mol m}^{-2} \text{ s}^{-1}$.~~

Table 4. Overview of termite-induced CH_4 and CO_2 emissions, based on two different approaches. For comparison, the lowest row shows total (not termite-specific) ecosystem CH_4 and CO_2 flux values, measured at the same field site by previous studies. a) Querino et al. (2011) performed above-canopy Eddy Covariance CH_4 flux measurements, and reported an averaged CH_4 flux of $\sim 2 \text{ nmol m}^{-2} \text{ s}^{-1}$; b) Chambers et al. (2004) quantified different respiratory CO_2 sources in this ecosystem, and estimated the total ecosystem respiration to be $7.8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.

<u>Estimation approach</u>	Approach CH_4 (nmol $\text{m}^{-2} \text{ s}^{-1}$)	CO_2 ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)
Method 1 Mound per hectare (nr) <u>Mounds per hectare</u> * emission per mound ($\text{mol mound}^{-1} \text{ s}^{-1}$)	0.15-0.71	0.05- 0.24 <u>0.23</u>
Method 2 <u>Termite density</u> * <u>Termite biomass estimate</u> (g m^{-2}) * termite emission factor ($\text{mol g}_{\text{termite}}^{-1} \text{ s}^{-1}$)	0.5- 1.0 <u>1.1</u>	0.25 <u>0.27</u>
Literature <u>Total (not termite-specific) ecosystem fluxes</u>	Ecosystem flux values from local studies $\sim 2^a$	7.8^b