Carbon dioxide and methane fluxes from mounds of African fungus-growing termites

Matti Räsänen[1], Risto Vesala[2], Petri Rönnholm[3], Laura Arppe[2], Petra Manninen[1], Markus Jylhä[1], Jouko Rikkinen[2,4], Petri Pellikka[1,5], and Janne Rinne[6,7]

5 [1]Department of Geosciences and Geography, University of Helsinki, P.O. Box 64, 00014, Helsinki, Finland
[2]Finnish Museum of Natural History, University of Helsinki, P.O. Box 64, 00014, Helsinki, Finland
[3]Department of Built Environment, Aalto University, P.O. Box 14100, 00076, Aalto, Finland
[4]Organismal and Evolutionary Biology Research Programme, Faculty of Biological and Environmental Sciences, P.O. Box 64, 00014, Helsinki, Finland
10 [5]Wangari Maathai Institute for Environmental and Peace Studies, University of Nairobi, P.O. Box 29053, 00625, Kangemi, Kenya
[6]Natural Resources Institute Finland, P.O. Box 2, 00791 Helsinki, Finland
[7]Department of Physical Geography and Ecosystem Science, Lund University, Lund, Sweden

Correspondence to: Matti Räsänen (matti.rasanen@helsinki.fi)

Abstract. Termites play an essential role in decomposing dead plant material in tropical ecosystems and are thus major sources of gaseous C emissions in many environments. In African savannas, fungus-growing termites are among the ecologically most
20 influential termite species. We studied the gas exchange from mounds of two closely related fungus-growing species (*Macrotermes subhyalinus* and *M. michaelseni*, respectively) in two habitats representing different vegetation types (grassland, bushland) together with soil fluxes around the mounds. The fluxes from active termite mounds varied from 120 to 2100 mg CO_2-C m^{-2} h^{-1} for CO_2 and from 0.06 to 3.7 mg CH_4-C m^{-2} h^{-1} for CH_4 fluxes. Mound CO_2 fluxes varied seasonally with a 64 % decrease and 41 % increase in the fluxes from dry to wet season at the grassland and bushland sites, respectively. During
25 the wet season, the CO_2 fluxes were significantly correlated with termite mound volume. The diurnal measurements from two *M. michaelseni* mounds suggest that the gas fluxes peak during daytime, possibly reflecting changes in mound internal air circulation. Soil fluxes of both CO_2 and CH_4 were enhanced at up to 2 m distance from the mounds compared to the local soil respiration, indicating that, in addition to mound ventilation structures, a small proportion of the produced metabolic gases leave the nest also via surrounding soils.

30

1   Introduction

Termites are major degraders of dead organic plant matter in many tropical and subtropical ecosystems (Bignell and Eggleton 2000; Jouquet et al., 2011), also making them a significant source of atmospheric carbon dioxide (CO_2) and methane (CH_4) (Zimmerman et al., 1982; Khalil et a., 1990). Especially in African dry savannas, the fungus-growing species comprise the most common and ecologically important termite group that may recycle a quarter of total dead plant matter and even 90 % of the woody litter in some arid ecosystems (Collins 1981; Buxton 1981). Fungus-growing termites cultivate symbiotic termite fungi (*Termitomyces* spp., Basidiomycota) in fungus combs, which are specialized structures within underground nest chambers. The combs are built from feces of termite workers and consist of largely undigested plant matter, initially ingested by foraging termites, that the *Termitomyces* further degrades (Rouland-Lefèvre 2000; Vesala et al., 2022a). Eventually, termite hosts get their energy and nutrition from the degraded plant matter and/or the fungal mycelium (Sieber and Leuthold, 1981; Hyodo et al., 2003; Vesala et al., 2019a).

Fungus-cultivation within termites is always associated with a complex caste system including numerous workers, soldiers, and reproductive individuals, and the total number of termites within a colony typically ranges from hundreds of thousands to up to a few million individuals (Darlington, 1986, 1990). Such large insect populations are notable sources of CO_2 already in themselves but, within nests of fungus-growing termites, a major proportion of the nest CO_2 emission is produced by the extensive fungus gardens whose total biomass in mature termite colonies may exceed 20 kilograms (Darlington, 1986; Darlington et al., 1997; Noirot and Darlington, 2000). Due to their methanogenic gut symbionts, termites are also among the major sources of atmospheric CH_4 although estimates about their contribution to the global CH_4 budged vary highly (currently considered to represent 1–4 % of the natural sources) due to uncertainties in methane-related processes and global termite biomass (Sanderson, 1996; Kirschke et al., 2013; Saunois et al., 2020). Methane can also be oxidized by soil methanotrophic microbes occurring within and around termite nests (Chiri et al., 2020). It has been evaluated that methane oxidizing bacteria can mitigate even half of the produced methane in nests of some mound-building termite species (Sugimoto et al., 1998; Nauer et al., 2018).

Maintenance of large termite populations and the extensive fungal gardens necessitates effective gas-exchange and stable conditions within the nest interior. Termites of the genera *Macrotermes* and *Odontotermes* build aboveground soil mounds to stabilize temperature, maintain humidity and enhance gas exchange (Noirot and Darlington, 2000; Korb 2003, 2011). Mound structure can vary a lot depending on termite species and environmental conditions (Korb and Linsenmair 1998; Korb 2003, 2011). Even closely related species may rely on fundamentally different mechanisms of nest ventilation, as in case of Kenyan *Macrotermes michaelseni* and *Macrotermes subhyalinus* that build closed and open mounds, respectively (Darlington 1984, 1985). The open *M. subhyalinus* mounds have multiple large ventilation shafts at different elevations on the mound surface, that promote wind-induced Venturi effect, resulting in airflow through the shafts that ventilate the underground nest (Weir,

1973; Korb 2011). The closed mounds of *M. michaelseni* lack these openings and, instead, the air is circulated internally within the mound until the gas-exchange between the nest interior and ambient air takes place through the porous mound surface (Noirot and Darlington, 2000; Ocko et al., 2017). Direct measurements of air velocities and temperatures within closed mounds have shown that air moves in convective cells following a diurnally oscillating thermal schedule (King et al., 2015; Ocko et al., 2017).

Despite the well-recognized importance of termite mounds as significant sources of greenhouse gases, field studies quantifying gas fluxes from termite mounds are rare and often limited to species that build relatively small mounds. Previous CO_2 flux measurements from termite mounds have ranged from 40 to 2200 mg CO_2-C m^{-2} h^{-1} (van Asperen et al., 2021; Jamali et al., 2013; Brümmer et al., 2009). For wood-feeding termites in Australia, the seasonal variability in CO_2 and CH_4 was high with larger fluxes occurring during the wet season (Jamali et al., 2013). For soil and wood-feeding termites the relationship between mound CO_2 and CH_4 fluxes has been species-specific (Jamali et al., 2013). With the assistance of *Termitomyces* symbionts, fungus-growing termites can utilize widely different types of plant matter including grasses, leaf litter, and dead wood (Collins 1981; Lepage 1981a) and the proportion of utilized food sources may vary both geographically and seasonally (Boutton et al., 1983; Lepage et al., 1993; Vesala et al., 2022b). Alternative food sources may also differ in their nutritional value with potential consequences for the gas fluxes (Zhou et al. 2023). For example, a lower nitrogen content associated with grass-based compared to woody plant-based fungus combs found in Vesala et al., (2022b) could necessitate relatively higher CO_2 and CH_4 emissions, as more carbon needs to be eliminated to gain sufficiently protein from the N deficient diet (Higashi et al., 1992; Eggleton and Tayasu, 2001). Whether such factors could affect the mound gas fluxes is currently not known.

In this study, we used static chamber method to investigate CO_2 and CH_4 fluxes originating from mounds of two common species of fungus-growing termites, *M. michaelseni* and *M. subhyalinus*, in southern Kenya during a period in the dry and the wet season. As, in the area, both species inhabit a wide range of different environments, termite mounds were measured in two contrasting habitats (open grassland and dense bushland). Distribution of the two species is not completely overlapping and, thus, in our sampling *M. michaelseni* was dominant at the grassland and *M. subhyalinus* at the bushland site. In Kenyan grasslands, *M. michaelseni* mounds are surrounded by dense networks of foraging tunnels with several openings to soil surface per each m^2 (Lepage 1981a; Darlington 1982) that could also increase soil CO_2 and CH_4 fluxes in mound proximity. Thus, in addition to direct gas fluxes from the mounds, we also measured soil CO_2 and CH_4 fluxes around the mounds. The study objectives were: (1) to quantify the gas fluxes from the fungus-growing termite mounds with variable mound volumes and from the soil around the mounds, (2) study the interactions between the fluxes and different environmental variables and to (3) observe the diurnal and seasonal variation in mound fluxes.

2   Materials and methods

2.1   Site description

The chamber measurements were conducted at the lowland areas surrounding Taita Hills, Kenya (Fig. 1). The mean annual rainfall is 433 mm based on measurements at the Maktau weather station (Räsänen et al., 2020). Termite mounds were

5   measured at bushland and grassland locations that are 15 km apart. The bushland is characterized by over 50 % of thorny shrubs and small *Acacia* spp. and *Commiphora* spp. trees (Wachiye et al., 2020). All termite mounds measured in bushland were located in shaded locations. The grassland site is located at a private game sanctuary for wildlife conservation. The vegetation is characterized by common savanna grasses such as *Chloris roxburghiana* and *Cenchrus ciliaris* and scattered trees (e.g. *Acacia tortilis*, *Albizia anthelmintica, Balanites aegyptica*). Majority of bushland mounds were open mounds build

10   by *M. subhyalinus*, whereas most of the grassland mounds were closed type build by *M. michaelseni* (Table 1, Fig. S1). The grassland ecosystem is assumed to be a result of decades long wildlife conservation, which causes high population of mega-herbivore, namely elephants, which forage with leaves of the trees and bushes, thus destroying the tree cover. The tree cover and above ground biomass is much higher in the bushland areas, which are not inhabited by elephants as shown in Figure 1B (Amara et al., 2020; Pellikka et al., 2018).
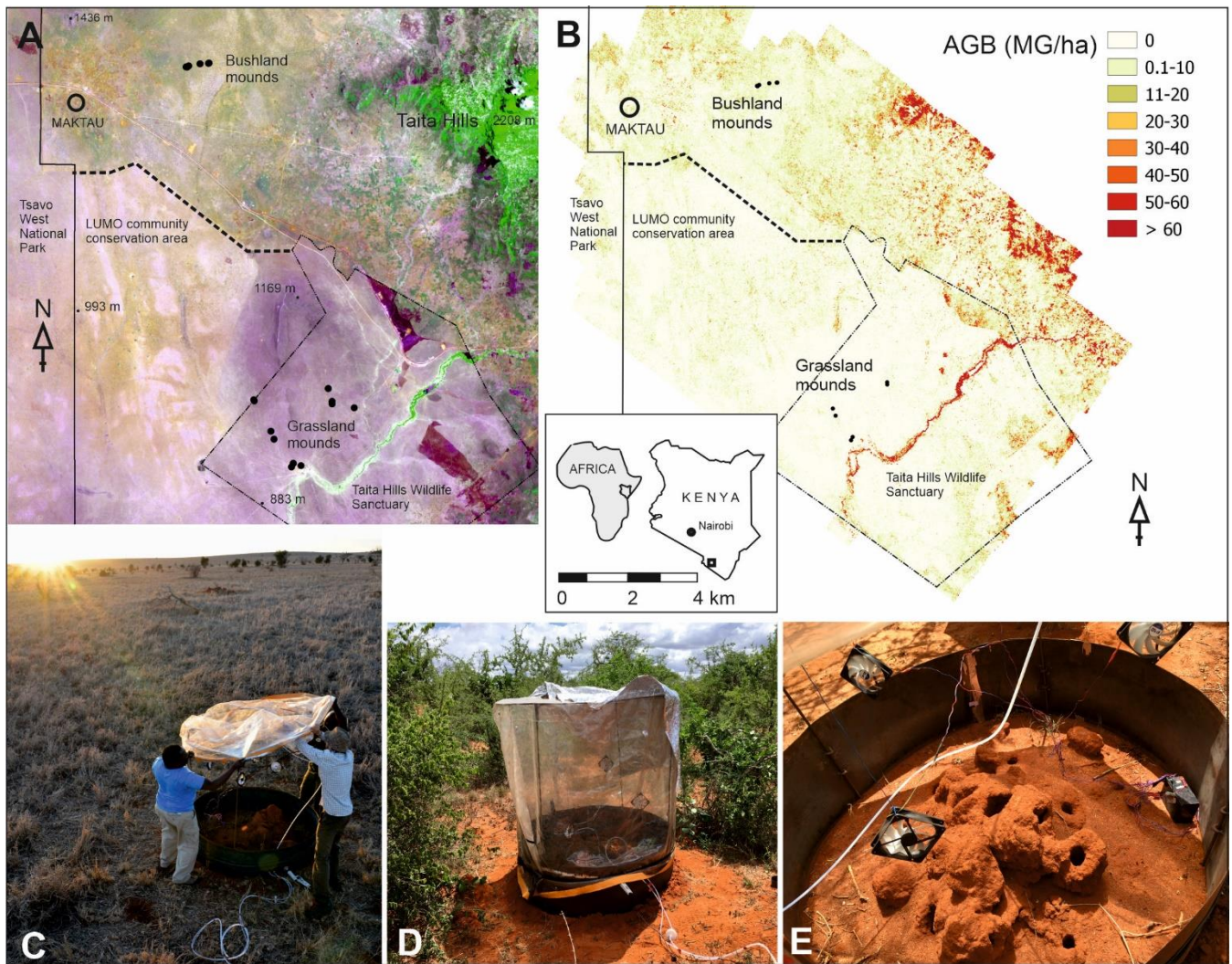
Figure 1. Locations of the measured termite mounds (dots) at two study sites and the Maktau weather station shown on (A) Sentinel-2A satellite image (acquired 20 December 2020, magenta color indicate grasslands, while brownish colors indicate bushlands) and (B) above ground biomass map (Amara et al., 2020; Pellikka et al., 2018). Chamber measurement at the grassland (C) and the bushland site (D). Metal collar and wireframe of the measurement chamber around an open *M. subhyalinus* mound (E). Sentinels Scientific Data HubCE4 (ESA, 2015). Photo credits: Petri Pellikka (C), and Markus Jylhä (D, E).

Table 1. Characteristics of the measured *Macrotermes* termite mounds. R is the average mound radius, H is height and V$_m$ is calculated above ground mound volume (see section 2.2). The status (active or dead) of the colonies was determined after the second measurement campaign by excavation.

Mound id	Termite species (mound type)	Site location	R (m)	H (m)	V_m (m³)	Status in April 2017
MR1	*M. michaelseni* (closed)	Bushland	0.75	0.50	0.256	active
MR2	*M. subhyalinus* (open)	Bushland	0.65	0.15	0.058	active
MR3	*M. subhyalinus* (open)	Bushland	0.28	0.33	0.023	dead
MR4	*M. subhyalinus* (open)	Bushland	0.75	0.45	0.231	active
MR5	*M. subhyalinus* (open)	Bushland	0.30	0.25	0.020	active
MR6	*M. subhyalinus* (open)	Bushland	0.40	0.30	0.044	active
S1	*M. michaelseni* (closed)	Grassland	0.75	0.70	0.259[a]	active
S2	*M. michaelseni* (closed)	Grassland	0.65	0.35	0.106[a]	active
S3	*M. michaelseni* (closed)	Grassland	0.55	0.30	0.217[a]	dead
S4	*M. michaelseni* (closed)	Grassland	0.35	0.40	0.074[a]	dead
S5[b]	*M. subhyalinus* (open)	Grassland	0.75	0.40	0.193[a]	active
S6	*M. subhyalinus* (open)	Grassland	0.72	0.15	0.072	dead
	[a] These values were estimated using photogrammetric technique. [b] The gas fluxes of this mound were not estimated due to nonlinear concentration time series (Fig. S2)					

2.2 Estimation of mound volume

Volumes of the grassland mounds S1–S5 (Table 1) were measured photogrammetrically by taking a large number of digital images from different positions around the mound (method described in Vesala et al., 2019b). To increase the number of observations, this data was supplemented with five additional comparable-sized mounds measured earlier in a close by area (Vesala et al., 2019b). Linear regression with zero intercept was fitted between equivalent cone volume and photogrammetric mound volume (Fig. 2). This relationship was used to estimate the volume at the bushland site where the photogrammetric method was not feasible due to the surrounding dense vegetation. The equivalent cone volume was calculated as

$$V_{cone} = \frac{1}{3}\pi R^2 \times H, \tag{1}$$

where R is the average of North-South and West-East measured radii and H is height. The above ground termite mound volume (V_m) was $0.87 \cdot V_{cone}$ for mounds that were not sampled using the photogrammetric method. The above ground termite mound volumes ranged from 0.3 to 10 % of the total chamber volume.
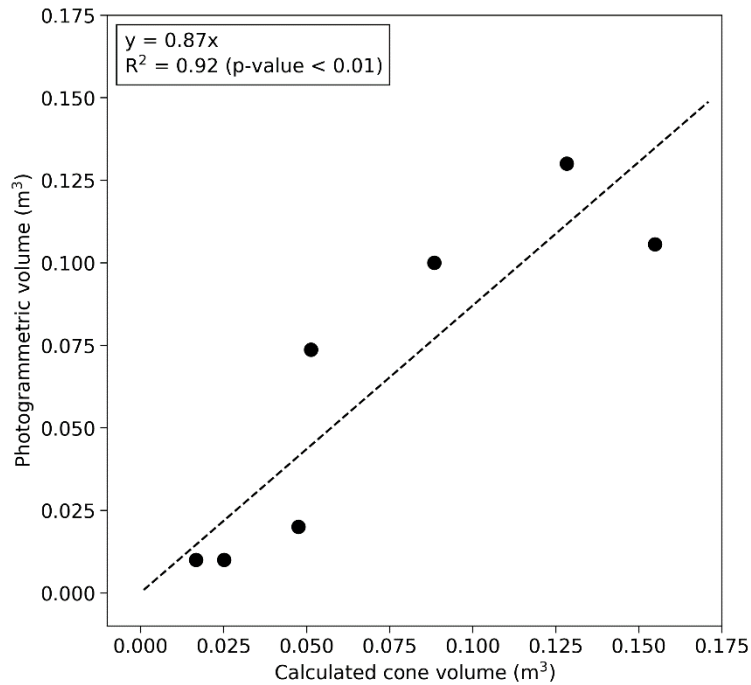
Figure 2. The relationship between the photogrammetrically measured mound volume and calculated cone volume (Eq. 1) according to equation 1. The data points include grassland mounds (S2 and S4) of this study and five additional mounds measured in Vesala et al., (2019b) (Table S1).

2.3   Gas flux measurements from termite mounds and soil

CO_2 and CH_4 fluxes were measured using a static chamber method in November 2016 (end of long dry season) and April 2017 (wet season) (Table S2). The chamber collar was installed before each measurement and surrounding sand was applied to insulate collar. The chamber closure time was 15 minutes, and each mound was measured three times with five-minute breaks

10   in between the repetitions. The mean and standard deviation of the flux was calculated from the three repeated measurements. Daytime flux measurements were made between 10 am and 4 pm. To study diurnal variation in gas fluxes, the mound S1 and S2 were measured during at least three different time periods from evening until next day with three repeated measurements each time. Mound S1 was measured on 15 November 2016 and mound S2 was measured on 7 November 2016.

15   The size of the measurement chamber was a compromise between practicality and typical size of termite mounds in the area. The radius of the chamber was 0.75 m and height was 1.5 m, still excluding the vast majority of *Macrotermes* mounds occurring in the area, which are larger on average. The metal collar height was 40 cm. Four upright positioned steel rods and an attaching circular steel frame were used to support the cylindrical shape of the custom made polyvinylchloride sheet. A rubber band was used to seal the polyvinylchloride sheet against the collar. Three people were needed to open and close the chamber. The gas

analyzer (LGR Ultra-Portable Greenhouse Gas Analyzer Model 915-0011) was connected to the collar using Swagelok fittings. Chamber air was sampled continuously into the gas analyzer and circulated back to the chamber. The air was sampled inside the chamber using a 2.5 m long teflon tube which had small holes along its length. The sampling line was attached in a spiral shape by supporting it from the middle points of the supporting steel rods and it was connected to the inlet of the gas analyzer

5   at the inside wall of the collar. The air inside the chamber was mixed using three 12 cm fans that were hanging in the middle point of the chamber. The gas analyzer recorded concentration every second. Temperature and relative humidity inside the chamber were measured using a Campbell CS215 T/RH sensor attached to the collar. A cellphone timing application (Time meter) was used to record the precise start and end times of each measurement because the gas analyzer produces one continuous measurement file per day. Also, the manual soil moisture and temperature measurements were noted in the timing

10   application. The notes were exported to CSV file which was parsed into numerical form. This procedure enabled to automate flux calculation from raw data and minimize note taking errors.

After termite mound measurement, the inlet lines were connected to a small opaque soil chamber (radius 7 cm, height 22 cm) to measure soil CO_2 and CH_4 fluxes around the termite mound. The soil gas flux measurements were made once for two

15   opposing directions from 2, 4 and 6 m distance from the perimeter of the mound. The soil chamber was placed on patches of bare soil to minimize the effect of vegetation. The sampling time was two minutes. One CH_4 flux measurement around S1 mound at 6 m distance during wet season was discarded because the flux was over thousand times higher than the mean of other measurements around the mound (most likely due to an underground termite nest).

Methane and carbon dioxide fluxes were calculated as

$$F = \frac{PV}{RTA}\frac{dC}{dt},$$
(2)

where $V = V_c - V_m$ for termite mound measurements and $V = 0.0034$ m^3 for the soil measurements, $V_c = 2.65$ m^3 is the termite chamber volume, P is pressure (Pa), A is the area of the chamber (m^2), R is gas constant (8.314 $Jmol^{-1}K^{-1}$) and T is air temperature in Kelvin. The slope of concentration increase $\frac{dC}{dt}$ (µmol mol^{-1} s^{-1}) was determined from a linear regression of

25   the 1 Hz concentration measurements.

2.4   Environmental measurements

The soil moisture and temperature were measured manually nearby the mound during each chamber measurement. A handheld soil moisture probe Campbell HydroSense II was used to measure surface soil moisture. Soil temperature was measured using a stainless-steel temperature probe. Termite nest temperature measurements were used from an earlier study (Vesala et al.,

30   2019b) where small temperature sensors (iButton Thermochron DS1922L) were placed next to the first fungus combs that were encountered by digging small hole to the mound. The nest temperature measurements made at the grassland location in 2015 from large open and closed mounds (IDs TS56 and TS19 in Vesala et al., 2019b) were used. These nest temperatures

were compared to continuous soil temperature measurements at the Maktau weather station. The weather station soil temperature (Campbell CS650) probe was measuring at 30 cm depth inside a fenced area.

The CO_2 and CH_4 fluxes measured for each mound were combined with above ground biomass (AGB) data, assessed using airborne laser scanning and field measurements (Amara et al., 2020; Pellikka et al., 2018). This combination aimed to investigate the working hypothesis that fluxes might be related to the C:N ratios of termite diets that correlate negatively with vegetation density in the area (Vesala et al., 2022b).

2.5 Statistical analysis

Simple linear regression was used to test the statistical relationship between the measured fluxes and explanatory variables. The relationship between fluxes and mound volume was tested separately during the dry season (n=11) and wet season (n=7). The relationship of the environmental variables to the fluxes and to the ratio of CH_4 to CO_2 flux was tested using all the measurements (n = 18). The mound fluxes and AGB relationship was tested with simple linear regression during the dry season (n=11). Statistical analyses were done using the Scipy Python package (Virtanen et al., 2020).

3 Results

3.1 Environmental conditions

Total precipitation before the first measurement campaign was 10 mm from September to early November (Fig. 3), meaning that the short rainy season had not yet started. The precipitation between the campaigns was 153 mm corresponding to a typical dry year amount. The annual mean precipitation during this period between the campaigns was 287 mm with 154 mm standard deviation calculated from six years of precipitation measurements at the weather station. The surface soil moisture was twice as high during the second campaign compared to first campaign (Fig. 3a). The wind speed had a consistent trend during the measurement campaign days showing a minimum around 6 am and a maximum during the early afternoon. Revisiting the data collected in Vesala et al. (2019b) shows that termite mounds in the area have a consistent diurnal temperature rhythm with the maximum nest temperature being always around 8 pm, whereas the soil temperature at 30 cm depth has a maximum around midnight.
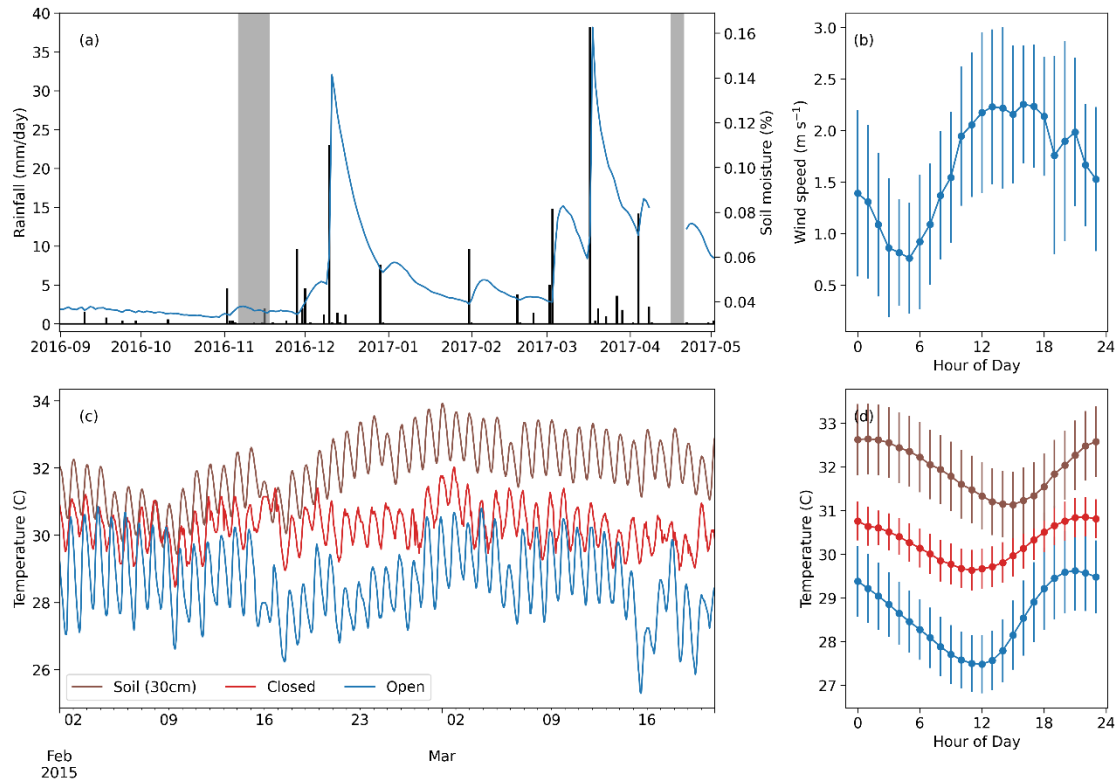
Figure 3. Meteorological data from the study area. (a) Time series of daily rainfall (black bars) and daily mean soil moisture at 10 cm depth (blue line). The gray blocks indicate the days of the two measurement campaigns. (b) Diurnal mean and standard deviation of the wind speed during the first measurement campaign. (c) Soil temperature at 30 cm depth compared with nest temperatures within an open (TS56) and a closed (TS19) termite mound at the grassland site (measured in 2015 during period of no rainfall, Vesala et al., 2019b). (d) Diurnal mean of the soil and nest temperatures during the time period presented in panel c. The error bars indicate one standard deviation.

3.2 Mound CO_2 and CH_4 fluxes

The mean CO_2 fluxes ranged from 35 to 2100 mg CO_2-C m^{-2} h^{-1} for closed *M. michaelseni* mounds and from 120 to 800 mg CO_2-C m^{-2} h^{-1} for open *M. subhyalinus* mounds (Fig. 4). The mean CO_2 flux was 1000 mg CO_2-C m^{-2} h^{-1} for the grassland site and 380 mg CO_2-C m^{-2} h^{-1} for the bushland site from the active mounds listed in Table 1. The largest CO_2 fluxes were measured during the dry season at the grassland site. The site level mean CO_2 flux decreased 64 % at the grassland and increased 41 % at the bushland from dry to wet season. The lowest CO_2 fluxes were registered from the grassland mounds S3 and S4, which turned out to be dead when excavated after the second measurement campaign (Table 1).

The mean CH_4 fluxes ranged from 0.02 to 3.7 mg CH_4-C m^{-2} h^{-1} for closed *M. michaelseni* mounds and 0.06 to 1.2 mg CH_4-C m^{-2} h^{-1} for open *M. subhyalinus* mounds. The ratio of mound CH_4 flux to mound CO_2 flux ranged from $0.4 \cdot 10^{-3}$ to $2.8 \cdot 10^{-3}$ with no clear difference between termite species or mound volume. The mean ratio was $1.6 \cdot 10^{-3}$ for grassland and $1.2 \cdot 10^{-3}$

for bushland sites. The ratio of CH_4 flux to CO_2 flux reduced 36 % at the grassland and 49 % at the bushland site from dry to wet season. The dry season mound CO_2 and CH_4 fluxes were not significantly correlated with the AGB (Fig. S3).
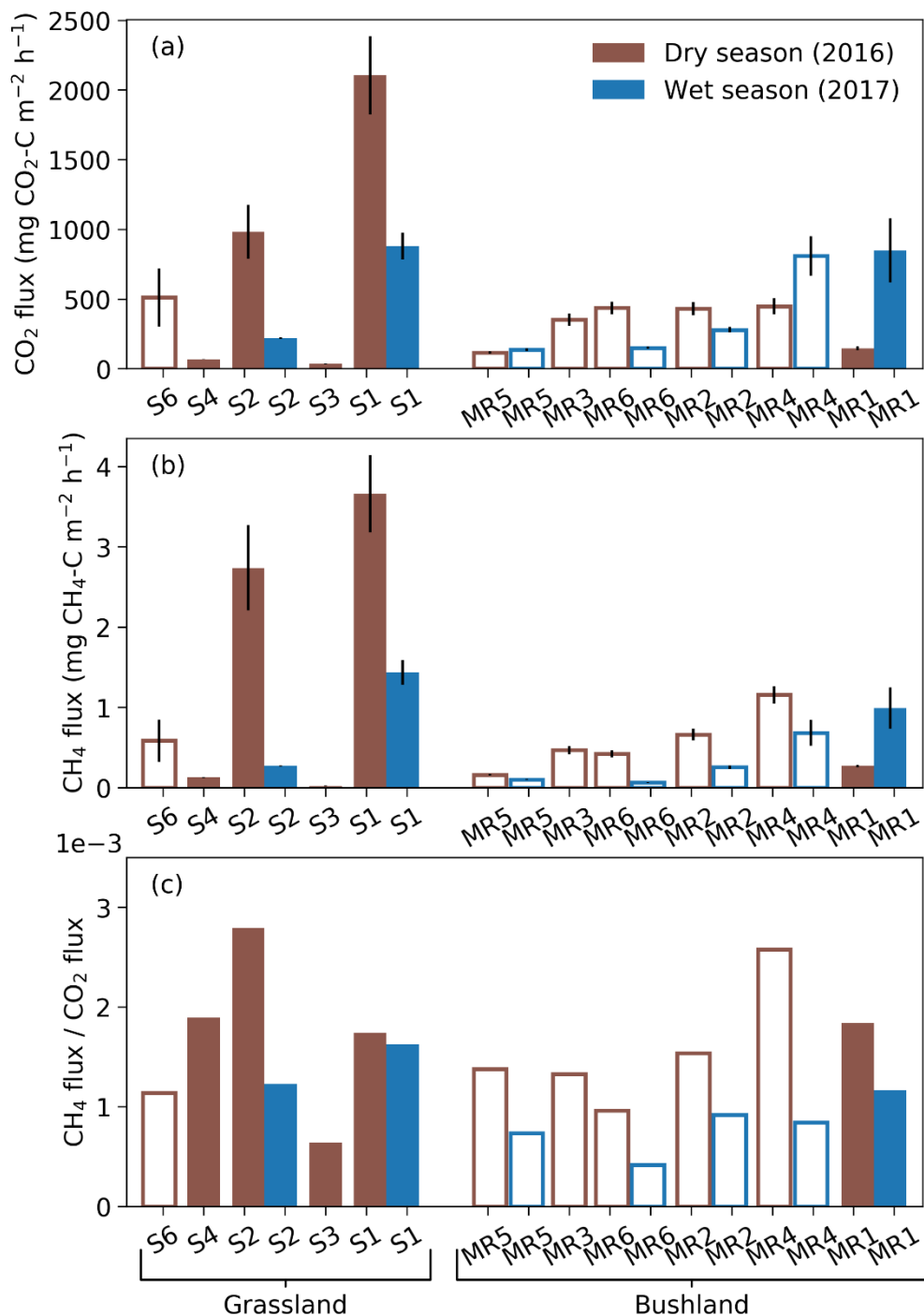
Figure 4. Mean termite mound CO_2 (a) and CH_4 (b) fluxes and their relationship, i.e., CH_4 to CO_2 flux ratios (c) measured from grassland and bushland sites during dry and wet seasons. Each mound was sampled once during each season by three repeated measurements. All measurements shown in this figure took place between 10 am and 4 pm. Error bars in panels a and b indicate standard errors. Hollow bars represent open and solid bars closed mounds. Termite colonies that were found to be dead in April

Based on diurnal measurements in two closed mounds, the largest CO_2 flux was measured around noon at the mound S1 (Fig. 5). However, the CO_2 flux increased also during the midnight for both S1 and S2 mounds. For both mounds, the difference between maximum nighttime CO_2 flux compared with daytime maximum was less than 2 standard errors. For S1 mound, the maximum flux value was 1.4 times the daily average for CO_2 and 1.5 times for CH_4. The nighttime peak in the CO_2 flux coincides with the maximum soil temperature at 30 cm depth at midnight (Fig. 3d). The diurnal cycle of the ratio of CH_4 to CO_2 flux showed one peak around the noon for S1 mound and at 6 pm for S2 which was not sampled during the noon. These peaks are due to the increase in CH_4 flux in proportion to CO_2 flux during the daytime.
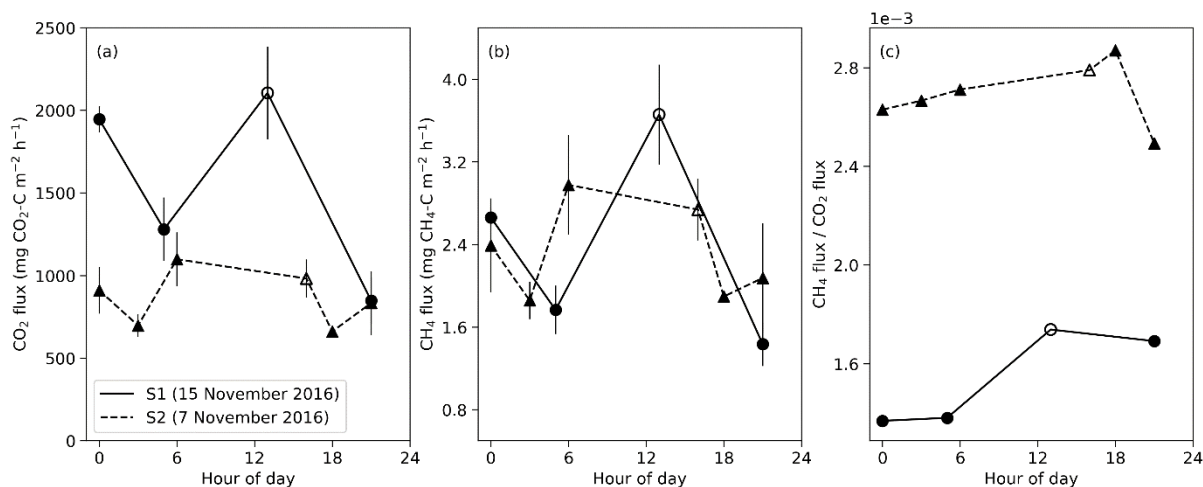
Figure 5. Diurnal variation of CO_2 and CH_4 fluxes during 2016 dry season for closed mounds S1 (measured 15th Nov) and S2 (measured 7th Nov). Error bars indicate standard error calculated from three repeated measurements. The hollow symbols indicate daytime measurements that were done nine days before nighttime measurements for S1 and one day before for S2.

3.3   Drivers of mound CO_2 and CH_4 fluxes

The mean mound CO_2 flux was significantly correlated with the termite mound volume during the wet season ($R^2 = 0.96$, p-value < 0.01; Fig. 6b), while the relation was not statistically significant during the dry season ($R^2 = 0.12$, p-value $= 0.30$; Fig. 6a). The CO_2 flux and CH_4 flux were not explained by surface soil moisture or soil temperature during the dry or wet season (Fig. S4). The soil moisture values were low for most mounds due to low precipitation amount during the wet season. The mean CO_2 and CH_4 flux were linearly related (Fig. 6c). The ratio of CH_4 and CO_2 fluxes had no significant correlation with environmental variables and only a weak correlation with the magnitude of CH_4 flux ($R^2 = 0.34$, p-value $= 0.01$). The CH_4 flux was significantly correlated with the mound volume during the wet season ($R^2 = 0.85$, p-value < 0.01; Fig. 6e). The standard deviation of CO_2 flux was increasing linearly with the mean flux magnitude (Fig. 6f).
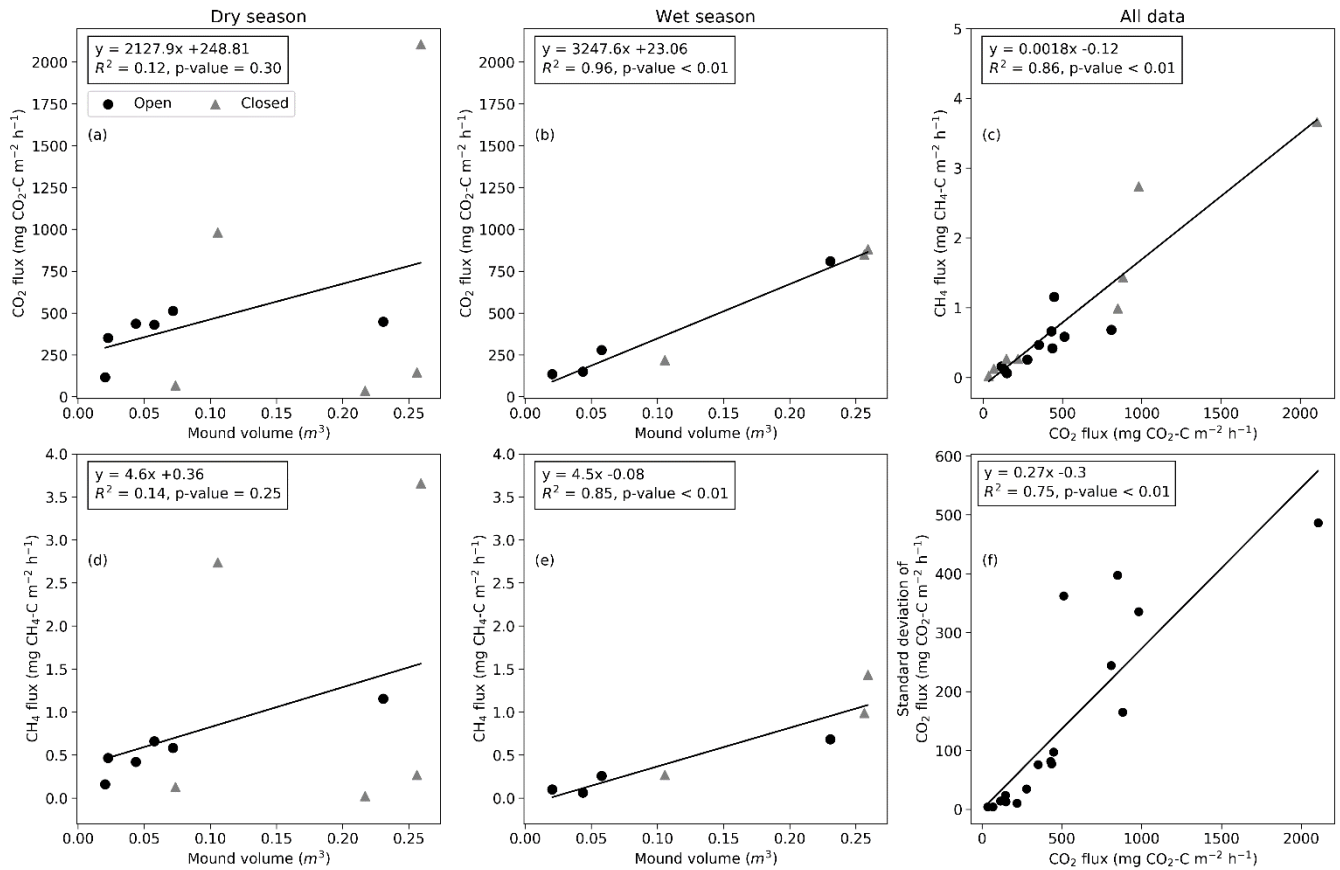
Figure 6. The relationship between mound volume and mean CO_2 and CH_4 fluxes during dry and wet seasons (a-b and d-e). (c) The relationship between CH_4 and CO_2 fluxes. Circles indicate open mounds and triangles indicate closed mounds. (f) The relationship between standard deviation and mean of the CO_2 flux calculated from three repeated measurements.

3.4   Soil CO_2 and CH_4 fluxes around termite mounds

The soil CO_2 and CH_4 fluxes around the mounds were sampled to determine the effect of termites on soil fluxes around the mound. The site mean soil CO_2 and CH_4 were always higher at a 2 m distance compared to a 4 and 6 m distance from the perimeter of the mound (Fig. 7 and Table 2). The mean soil CO_2 flux at the bushland was only 29 % of the mean soil flux at the grassland. The dry season means of all soil CO_2 flux measurements were 62 mg CO_2-C m^{-2} h^{-1} and 27 mg CO_2-C m^{-2} h^{-1} at 2 m and 4 to 6 m distance (Table 2). The difference between soil CO_2 flux at 2 m and 4 to 6 m distance from the mound was less pronounced during the wet season. The mean mound CO_2 fluxes were a factor of 25 and 6 higher at the dry and wet seasons in comparison to the 4 to 6 m distance soil CO_2 fluxes (Table 2). The dry season means of all soil CH_4 flux measurements were 0.07 mg CH_4-C m^{-2} h^{-1} and 0.02 mg CH_4-C m^{-2} h^{-1} at 2 m and 4 to 6 m distance (Table 2). The dry season

mean soil CH_4 flux was positive at the grassland and bushland site, whereas the mean wet season flux was nearly zero with most fluxes being negative (Fig. 7, S5 and S6). The soil CH_4 fluxes at a 2 m distance from the mound are much higher in proportion to fluxes at a 4 m distance at the grassland compared to the bushland (Fig. 7).

Table 2. Mean CO_2 and CH_4 fluxes of termite mounds and surrounding soils during dry and wet season. Data includes all active mounds measured at the grassland and the bushland sites. The range of measured values for each group is given in parenthesis.

	CO_2 flux (mg CO_2-C m^{-2} h^{-1})	CH_4 flux (mg CH_4-C m^{-2} h^{-1})
	Dry season	
Termite mound	666 (116–2105)	1.294 (0.159–3.659)
Soil at 2 m distance	62 (10–122)	0.065 (0.001–0.186)
Soil at 4–6 m distance	27 (6–123)	0.020 (–0.003–0.108)
	Wet season	
Termite mound	475 (136–881)	0.542 (0.062–1.433)
Soil at 2 m	90 (29–243)	0.006 (–0.034–0.104)
Soil at 4–6 m	83 (15–251)	–0.004 (–0.032–0.065)
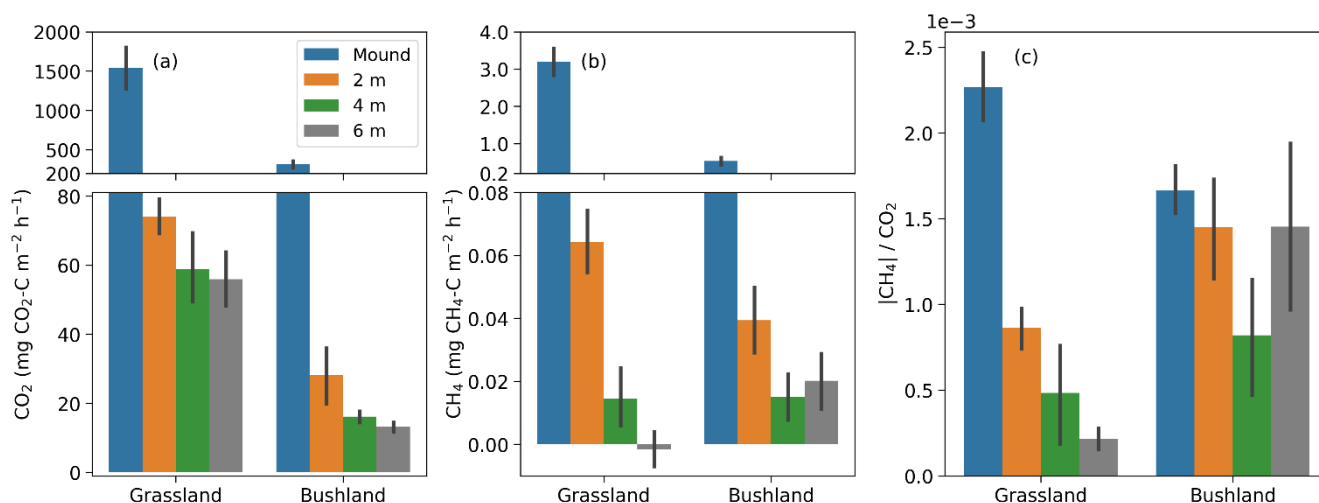
Figure 7. (a-b) Mean CO_2 and CH_4 fluxes from termite mounds and surrounding soils during the dry season. Soil fluxes were always measured on two opposite sides of the mounds at distances 2, 4, and 6 m from the mound perimeter (three repeated measurements at each specific location). Mean values and standard errors are calculated from all (dry season) measurements at the site. (c) The ratio of absolute value of CH_4 and CO_2 flux.

4   Discussion

4.1   Mound CO_2 and CH_4 fluxes

The measured CO_2 fluxes (from 35 to 2100 mg CO_2-C m^{-2} h^{-1}) were in similar range as reported in two earlier comparable studies where chamber measurements have been used to study greenhouse gas emissions from termite mounds in Australia (up to 1600 mg CO_2-C m^{-2} h^{-1}, Jamali et al., 2013) and Amazonia (190–2200 mg CO_2-C m^{-2} h^{-1}, van Asperen et al., 2021). Methane fluxes ranged from 0.02 to 3.7 mg CH_4-C m^{-2} h^{-1} and were 2–20 times lower than those reported in earlier studies (0.4–6 mg CH_4-C m^{-2} h^{-1}, van Asperen et al., 2021; Jamali et al., 2013). In most fungus-growing species studied so far, workers have exhibited relatively high CH_4 production rates (Rouland et al., 1993; Zhou et al., 2023). Thus, the lower CH_4 emissions, in relation to CO_2, observed in this study compared to mounds of previously studied termite species (which all have been other than fungus-growing termites) could be attributed to the fact that a large proportion of the total CO_2 in our measurements was originating from the aerobic fungus gardens which do not produce CH_4 (Darlington et al., 1997). Our biased sampling design, with one termite species dominating the bushland and the other the grassland site, does not allow us to reliably compare the two termite species. However, the relatively similar gas fluxes of the two species, or mound types, (Figures 4 and 6) imply that they do not exhibit major differences in terms of CO_2 or CH_4 emissions. This result is also highly expected as the two termite species are closely related (Bagine et al., 1994; Vesala et al., 2017), have very similar population sizes and compositions (Darlington, 1984), and also share their dietary niches (Vesala et al., 2022b). The highest fluxes of both gases were registered from two closed mounds of *M. michaelseni* in the grassland. It is important to notice that we did not obtain any information about the population sizes and, thus, these two *M. michaelseni* mounds may simply have housed larger termite populations with correspondingly larger fungus gardens than the studied *M. subhyalinus* mounds.

As found by previous studies, the mound outer dimensions of both *Macrotermes* species correlate positively with the size of the termite population and the total biomass of fungus combs (Darlington and Dransfield 1987; Darlington 1990). Thus, the fluxes of metabolic gases should logically also show correlation with the mound volume. However, considering the high variation associated with the fluxes, it seems obvious that if the sizes of the studied mounds are too close to each other, the relationships between mound volume and gas fluxes are difficult to detect. In this study, the mound volumes ranged from 0.023 to 0.259 m^3 (Table 1) including notably more size variance than the earlier comparable studies (0.02 to 0.077 m^3) (Jamali et al., 2013; van Asperen et al., 2021). We found that the measured CO_2 fluxes were linearly correlated with the termite mound volume during the wet season (Fig. 6b) but the relationship was more indistinct during the dry season (Fig 6a). Determining the relationship between mound volume and gas fluxes more reliably would require measurements from still much larger mounds, which however is problematic due to technical limitations. In East Africa, average volumes of *Macrotermes* mounds range from 2 to 3 m^3 depending on the geographical area, and the maximum volumes can exceed 12 m^3 (Pomeroy, 1977). Also in our study area, *M. subhyalinus* mounds with volumes of up to 6 m^3 have been recorded (Vesala et al., 2019b), which is more than 20 times the volume of the largest mound measured here. Thus, the reported average flux values in this study are

representative for the smallest *Macrotermes* mounds but when scaling the results to the level of larger *Macrotermes* mounds (or calculating area-based estimates), the effect of mound volumes should be considered to avoid serious underestimations.

The mounds at the grassland and bushland sites had contrasting seasonality of CO_2 fluxes with 64 % decrease at the grassland and 41 % increase at the bushland site from dry to wet season (Fig. 4). This seasonal change is smaller than what has been measured for grass and wood-feeding termites in Australia, which had a 90 % decrease in CO_2 flux from wet to dry season (Jamali et al., 2013). For fungus-growing termites, intra-annual variation can be caused by the annually produced brood of alates that, in Kenyan *M. michaelseni,* reaches its maximum biomass just before swarming in October–November (Darlington 1986). Correspondingly, storages of fungus combs are typically at their largest soon after the long rains in May–June after which they start to decline (Lepage 1981b). Such seasonal changes in biomasses of different nest components could cause intra-annual variation in gas fluxes. Additionally, differences in food quality could potentially affect nest CO_2 emissions. Within our study area, fungus combs of grassland mounds had significantly lower nitrogen contents than those situated in more wooded habitats suggesting that, on average, grass-based diets have lower nutritional value than wood-based diets (Vesala et al., 2022b). Such differences in food nutritional quality may reflect to nest CO_2 fluxes as more carbohydrates needs to be eliminated to accumulate sufficiently proteins from low-nitrogen food sources compared to those with a higher nitrogen content (Higashi et al, 1992). Most likely, food nutritional quality also changes during the year, with the changes possibly being more dramatic in grasslands having fewer and more competed food sources available for termites than bushlands with more abundant and diverse food sources. Such local differences in food availability and quality could potentially lead to different seasonality in nest living biomass which might explain the contrasting seasonal changes observed in CO_2 fluxes between the two habitats and the higher intra-annual variance in gas fluxes observed in grassland than in bushland mounds. We note that our seasonal sampling was limited to one measurement period during dry and wet season which does not capture the seasonal variability throughout the whole year.

There was a clear decrease in CH_4 to CO_2 flux ratios from dry to wet season measurements at both study sites. This difference might be partially explained by the smaller biomass of fungus gardens (produce only CO_2) in relation to that of termites (produce both CO_2 and CH_4) during dry season than during wet season (Darlington, 1986). Another explanation could be linked to the activity of methanotrophic bacteria within mound structures and/or surrounding soils that have been reported to consume a notable proportion of CH_4 produced in nests of several mound-building termite species (Sugimoto et al., 1998; Nauer et al., 2018). Although the humidity within termite nests remain at a constantly high level throughout the year (Lüscher, 1961; Agarwal, 1980), water content in surrounding soils and mound soil structures can decrease notably during periods with low precipitation (Jamali et al., 2011; Chen et al., 2019) (Figure 3a). Dry soil conditions during periods with low precipitation most likely limit microbial activity (including the methane oxidizing bacteria) within termite mound walls and surrounding soils, whereas increases in soil water content after rains could oppositely lead to increased microbial activity and enhanced methanotrophy. This result is also in congruence with our measurements of nest internal gas concentrations within *M.*

michaelseni mounds, which tended to have higher CH_4 to CO_2 concentration ratios during the driest period compared to seasons with higher soil moisture (Vesala et al., submitted).

Four mounds that were measured during the first campaign were determined to be dead at the end of the second campaign (Table 1). The exceptionally low CO_2 fluxes measured from the mounds S3 and S4, however, strongly suggest that these two mounds were dead, or at least seriously weakened, already during the first measurement campaign. An average lifespan of a *Macrotermes bellicosus* colony is thought to be around four years, whereas the mounds that they build persist typically much longer (Pomeroy, 1976). However, a recent long-term monitoring study in Namibia found that 57% of initially active *M. michaelseni* mounds were still active after 12 years (Wildermuth et al., 2022), demonstrating that some colonies can live much longer. These authors also found that small mounds were more likely to be dead than large mounds after 12 years, showing that large well-established colonies are less vulnerable to disruptions. Hence, dead *Macrotermes* mounds are a common feature in many landscapes and for example, in many places within our study area, their number exceeds that of the active mounds (Vesala et al., 2017). Thus, determination of the proportion of active mounds in a landscape is a necessary precondition for ecosystem-level termite flux estimations for all such termite species that build persistent soil mounds.

4.2   Diurnal variation

Diurnal variation of CO_2 and CH_4 fluxes were measured in two closed *M. michaelseni* mounds over a period of one day. The afternoon peaks were on average 46 % and 57 % higher compared to the daily averages for CO_2 and CH_4 fluxes, respectively (Fig. 5). Our observations are in congruence with the nest internal CO_2 concentration measurements by Ocko et al. (2017) who found that CO_2 levels within *M. michaelseni* nests in Namibia peaked in early afternoon, whereas concentrations in night-time and especially soon after sunrise were somewhat lower. A corresponding trend has been documented also from outflow chimneys of Kenyan *Macrotermes jeanneli* that had the highest CO_2 concentrations at 3 pm and the lowest around 3–6 am (Darlington et al., 1997). The daily maximum CO_2 flux in early afternoon found in this study (Fig. 5) agrees well with these earlier data suggesting that the internal CO_2 concentrations within *M. michaelseni* mounds show similar diurnal patterns to the mound CO_2 fluxes. A positive relationship between the nest internal gases and mound fluxes has been demonstrated for a few of mound-building termites (Khalil et al., 1990; Jamali et al., 2013). In agreement with our CH_4 measurements, a similar peak in CH_4 fluxes soon after midday was documented by Jamali et al. (2011) from mounds of three Australian termite species.

The lower CO_2 and CH_4 fluxes during nighttime compared to daytime fluxes are probably mostly associated with the diurnal movements of termites: after sunset a proportion of termite workers and soldiers leave the nest due to foraging activities, thus decreasing the CO_2 and CH_4 production within the nest. During night, termites also open the numerous foraging passages that directly connects the nest interior space to the soil surface near the mound (Lepage 1981a; Darlington 1982). This might lead in enhanced nest ventilation and could additionally affect gas fluxes originating from the mound. In addition to the afternoon

flux peaks, we registered another peak in both CO_2 and CH_4 fluxes at midnight, which has not been documented in earlier studies (Fig. 5). However, more measurements would be needed to understand the drivers of diurnal variation because we measured only two mounds in one location during the dry season. It would be especially useful to continuously measure the mound internal gas concentrations together with the mound fluxes.

In addition to the daily cycles of CO_2 and CH_4 fluxes, the relationship between CO_2 and CH_4 showed a clear diurnal pattern. The mound CH_4 to CO_2 flux ratio was higher during the daytime than during the nighttime measurements (Fig 5c). This result also supports the hypothesis that termite population within the mound is smaller during nighttime than during daytime due to foraging activity. Metabolism of termites (together with gut microbiota) produces both CH_4 and CO_2, but a major proportion

10 of CO_2 originates from the fungal gardens, which are sessile and do not produce CH_4 (Darlington et al., 1997). Thus any changes in termite biomass within the nest should inevitably reflect to the mound CH_4 to CO_2 flux ratios.

After all, the diurnal changes in gas fluxes measured in this study were relatively small. This underlines the fact that plant biomass degradation within mounds of fungus-growing termites is a continuously ongoing process and show only minor

15 diurnal changes. Therefore, also a large proportion of termites stay constantly in the nest taking care of the fungus gardens and thus the diurnal biomass changes within the nest are relatively small. The stable diurnal flux variability is in line with the stable humidity and temperature conditions within mounds of fungus-growing termites. Constant temperature and high humidity are of key importance for the fungal *Termitomyces* symbionts which have relatively narrow range of optimal microclimatic conditions (Lüscher, 1961; Thomas 1981; Wood and Thomas, 1989).

20 **4.3 Soil CO_2 and CH_4 fluxes around the mounds**

The soil CO_2 and CH_4 fluxes were always higher close to the mound (at 2 m distance from the mound perimeter) compared to further distances (4 to 6 m from the mound perimeter) (Fig. 7). The mean soil CO_2 flux from 4 to 6 m distance was 27 mg CO_2-C m^{-2} h^{-1} during the dry season, which is comparable to the measured soil CO_2 flux seasonal minimum of 20 mg CO_2-C m^{-2} h^{-1} at the grassland site (Wachiye et al., 2020). Correspondingly, the mean soil CH_4 fluxes at 4 to 6 m distances from the

25 mounds were 0.020 and -0.004 mg CH_4-C m^{-2} h^{-1} at dry and wet seasons, respectively (Table 2), which is similar to the earlier field study where the soil CH_4 fluxes were slightly negative with no seasonality at the grassland site (Wachiye et al., 2020). Our results thus demonstrate that, although the majority of the gas-exchange between termite nests and ambient air takes place through the mound structures, a small proportion of gases leave the nest also via adjacent soils at up to 2 m distance. These results differ from the earlier measurements in soil feeding termites in Amazon which had enhanced soil fluxes around the

30 mound only up to 0.5 m from the perimeter of the mound (van Asperen et al., 2021). The difference can be largely explained by the much larger size of the measured mounds in our study but it most likely reflects also some fundamental differences between the mounds of soil-feeding and fungus-growing termites. While within soil-feeding species the mound itself acts as a nest for the colony, mounds built by especially *Macrotermes michaelseni* are more or less empty from the insects and the

actual nests are largely located underground below the mounds (Noirot and Darlington, 2000; Korb, 2011). Thus, the actual nests of fungus-growing termites may be much larger and extend to a somewhat wider area than their aboveground mounds. *Macrotermes* termites also have an extensive network of foraging tunnels surrounding their nest with the largest radial tunnels having width of 4–7 centimeters (Darlington, 1982). Such structures increase soil porosity around the mounds enhancing water

5   infiltration (Jouquet et al., 2011) and, obviously, also enable some gas-exchange to occur through the soil.

Soil CH4 fluxes around the mounds were systematically lower during wet than during dry season at all three distances (Table 2, Figures S5 and S6). As the CH_4 fluxes from the soils unaffected by termite mounds are shown to be slightly negative in grasslands of the same ecosystem (Wachiye et al., 2020) we are confident that termites were the main source of the soil CH_4

10   fluxes detected in the current study. Seasonal changes in soil fluxes could thus be caused either by changes in number of termites, their CH_4 production rates, or methane oxidation. During the rainy seasons, termite foraging activity is at the lowest (Lepage, 1981a), which could potentially decrease CH_4 fluxes in mound surroundings as the foragers move from foraging tunnels towards the nests. This should, however, concurrently increase the CH_4 fluxes from the mounds, which was not observed. Instead, we found also the mound CH_4 fluxes to be lower during the rainy than during the dry season. Thus, we

15   suspect that, similarly as discussed above in case of mound fluxes, the soil CH_4 fluxes near the mounds are largely regulated by CH_4 oxidation within the soils surrounding the mounds, which could be enhanced by the increased soil water content after rains (Figure 3a).

5   Conclusions

The CO_2 and CH_4 fluxes from fungus-growing termite mounds show diurnal and seasonal variation, albeit lower in magnitude than their wood, grass, and soil-feeding counterparts. The likely reason for this stability is the needed temperature and humidity control for the fungal symbiont. The CO_2 and CH_4 fluxes scale with mound volume over a large volume range during the wet season. The soil flux measurements around the mound also show that the soil CO_2 and CH_4 fluxes are significantly affected by the termites at a 2 m distance from the perimeter of the mound. The fungus-growing termite mounds have lower CH_4 fluxes per unit CO_2 than soil and grass-feeding termites, which is due to the plant matter decomposition by *Termitomyces* fungi that do not emit CH_4. For upscaling the greenhouse gas fluxes originating from mounds of fungus-growing termites, the work highlights the need to include the mound volume in the models, as well as to consider the potentially high proportion of inactive termite mounds in the landscape.

Data availability. The data used in this study are available online: https://doi.org/10.6084/m9.figshare.21739484.v1 (Räsänen et al., 2022).

Author contributions. MR, PM, MJ, PP, JR conducted the measurements; MR, RV, PR, LA, PP, JR designed the analysis; All authors contributed to the final version of the manuscript.

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

Acknowledgments. This work was supported by the Academy of Finland through the projects SMARTLAND (grant number 318645)— Environmental sensing of ecosystem services for developing climate smart landscape to improve food security in East Africa (PI P. Pellikka) and IsoTermes (grant number 333868). We thank Venla Pellikka, Mwadime Mjomba, Muhia Gicheru and Darius Kimuzi from Taita Research Station of the University of Helsinki and Remig Righa Mjomba, Wilson Mkala and Tobius Mwamburi from Taita Hills Wildlife Sanctuary for the support during the field work campaign. Research permit from the National Council for Science and Technology, Kenya, permit N° NCST/RCD/17/012/33 is appreciated.

References

Agarwal, V. B.: Temperature and relative humidity inside the mound of Odontotermes obesus (Rambur) (Isoptera: Termitidae). Proc. Indian Acad. Sci. (Anim. Sci.) 89, 91–99, https://doi.org/10.1007/BF03179148, 1980.

5   Amara, E., Adhikari, H., Heiskanen, J., Siljander, M., Munyao, M., Omondi, P., and Pellikka, P.: Aboveground Biomass Distribution in a Multi-Use Savannah Landscape in Southeastern Kenya: Impact of Land Use and Fences, Land, 9, 381, https://doi.org/10.3390/land9100381, 2020.

Bagine, R., Brandl, R., Kaib, M.: Species Delimitation in Macrotermes (Isoptera: Macrotermitidae): Evidence from
10   Epicuticular Hydrocarbons, Morphology, and Ecology, Annals of the Entomological Society of America, 87, 498-506, 1994.

Bignell, D. E. and Eggleton, P.: Termites in ecosystems, in Termites: Evolution, Sociality, Symbioses and Ecology, edited by T. Abe, D. E. Bignell, and M. Higashi, pp. 363–387, Springer, 2000.

15   Boutton, T. W., Arshad, M. A. and Tieszen, L. L.: Stable isotope analysis of termite food habits in East African grasslands, Oecologia, 59(1), 1–6, doi:10.1007/BF00388065, 1983.

Brümmer, C., Papen, H., Wassmann, R., and Brüggemann, N.: Fluxes of CH_4 and CO_2 from soil and termite mounds in south Sudanian savanna of Burkina Faso (West Africa), Global Biogeochemical Cycles, 23(1),
20   https://doi.org/10.1029/2008GB003237, 2009.

Buxton, R. D.: Termites and the turnover of dead wood in an arid tropical environment, Oecologia, 51(3), 379–384, doi:10.1007/BF00540909, 1981.

25   Chen, C., Wu, J., Zhu, X., Jiang, X., Liu, W., Zeng, H., and Meng, F.-R.: Hydrological characteristics and functions of termite mounds in areas with clear dry and rainy seasons, Agriculture, Ecosystems & Environment, 277, 25–35, https://doi.org/10.1016/j.agee.2019.03.001, 2019.

Chiri, E., Greening, C., Lappan, R., Waite, D. W., Jirapanjawat, T., Dong, X., Arndt, S. K. and Nauer, P. A.: Termite mounds
30   contain soil-derived methanotroph communities kinetically adapted to elevated methane concentrations, ISME J., 14(11), 2715–2731, doi:10.1038/s41396-020-0722-3, 2020.

Collins, N. M.: Populations, Age Structure and Survivorship of Colonies of Macrotermes bellicosus (Isoptera: Macrotermitinae), J. Anim. Ecol., 50(1), 293–311, doi:10.2307/4046, 1981.Collins, N. M.: The role of termites in the decomposition of wood and leaf litter in the Southern Guinea savanna of Nigeria, Oecologia, 51(3), 389–399, doi:10.1007/BF00540911, 1981.

Darlington, J. P. E. C.: Seasonality in mature nests of the termite Macrotermes michaelseni in Kenya, Insectes sociaux, 33(2), 168–189, 1986.

Darlington, J. P. E. C.: Populations in nests of the termite Macrotermes subhyalinus in Kenya, Insectes sociaux, 37(2), 158–168, doi:10.1007/BF02224028, 1990.

Darlington, J. P. E. C. and Dransfield, R. D.: Size relationships in nest populations and mound parameters in the termite Macrotermes michaelseni in Kenya, Insectes sociaux, 34(3), 165–180, 1987.

15 Darlington, J. P. E. C., Zimmerman, P. R., Greenberg, J., Westberg, C. and Bakwin, P.: Production of metabolic gases by nests of the termite Macrotermes jeanneli in Kenya, Journal of Tropical Ecology, 13(4), 491–510, doi:10.1017/S0266467400010671, 1997.

Darlington, J. P. E. C.: A method for sampling the populations of large termite nests, Annals of applied biology, 104, 427-436, 20 1984.

Darlington, J. P. E. C.: Structure of mature mounds of the termite Macrotermes michaelseni in Kenya, International Journal of Tropical Insect Science, 6(2), 149–156, doi:https://doi.org/10.1017/S1742758400006536, 1985.

25 Darlington, J. P. E. C.: The underground passages and storage pits used in foraging by a nest of the termite Macrotermes michaelseni in Kajiado, Kenya, Journal of zoology, 198(2), 237–247, doi:10.1111/j.1469-7998.1982.tb02073.x, 1982.

Eggleton, P. and Tayasu, I.: Feeding groups, lifetypes and the global ecology of termites, Ecological research, 16(5), 941–960, doi:10.1046/j.1440-1703.2001.00444.x, 2001.

30

Higashi, M., Abe, T. and Burns, T. P.: Carbon-nitrogen balance and termite ecology, Proceedings of the Royal Society of London. Series B: Biological Sciences, 249(1326), 303–308, doi:10.1098/rspb.1992.0119, 1992.

Hyodo, F., Tayasu, I., Inoue, T., Azuma, J. I., Kudo, T. and Abe, T.: Differential role of symbiotic fungi in lignin degradation and food provision for fungus-growing termites (Macrotermitinae: Isoptera), Functional Ecology, 17(2), 186–193, doi:10.1046/j.1365-2435.2003.00718.x, 2003.

5 Jamali, H., Livesley, S. J., Dawes, T. Z., Cook, G. D., Hutley, L. B., and Arndt, S. K.: Diurnal and seasonal variations in CH_4 flux from termite mounds in tropical savannas of the Northern Territory, Australia, Agricultural and Forest Meteorology, 151, 1471–1479, https://doi.org/10.1016/j.agrformet.2010.06.009, 2011.

Jamali, H., Livesley, S. J., Hutley, L. B., Fest, B. and Arndt, S. K.: The relationships between termite mound CH_4/CO_2
10 emissions and internal concentration ratios are species specific, Biogeosciences, 10(4), 2229–2240, doi:10.5194/bg-10-2229-2013, 2013.

Jouquet, P., Traoré, S., Choosai, C., Hartmann, C. and Bignell, D.: Influence of termites on ecosystem functioning. Ecosystem services provided by termites, European Journal of Soil Biology, 47(4), 215–222, doi:10.1016/j.ejsobi.2011.05.005, 2011.

Khalil, M. A. K., Rasmussen, R. A., French, J. R. J. and Holt, J. A.: The Influence of Termites on Atmospheric Trace Gases: CH_4, CO_2, $CHC1_3$, N_2O, CO, H_2, and Light Hydrocarbons, Journal of Geophysical Research: Atmospheres, 95, 3619–3634, 1990.

20 King, H., Ocko, S. and Mahadevan, L.: Termite mounds harness diurnal temperature oscillations for ventilation, Proc. Natl. Acad. Sci. - PNAS, 112(37), 11589–11593, doi:10.1073/pnas.1423242112, 2015.

Kirschke, S., Bousquet, P., Ciais, P., Saunois, M., Canadell, J. G. Dlugokencky, E. J. Bergamaschi, P. Bergmann, D., Blake, D. R., Bruhwiler, L., Cameron-Smith, P., Castaldi, S., Chevallier, F., Feng, L., Fraser, A., Heimann, M., Hodson, E. L.,
25 Houweling, S., Josse, B., Fraser, P. J., Krummel, P. B., Lamarque, J. F. Langenfelds, R. L., Le Quere, C., Naik, V., O'Doherty, S., Palmer, P. I., Pison, I., Plummer, D., Poulter, B., Prinn, R. G., Rigby, M., Ringeval, B., Santini, M., Schmidt, M., Shindell, D. T., Simpson, I. J., Spahni, R., Steele, L. P., Strode, S. A., Sudo, K., Szopa, S., Werf, van der, G. R., V., A., van W., M., Weiss, R. F., Williams, J. E. and Zeng, G.: Three decades of global methane sources and sinks, Nat. Geosci., 6, 813–823, doi:10.1038/ngeo1955, 2013.

30

Korb, J. and Linsenmair, K. E.: The effects of temperature on the architecture and distribution of Macrotermes bellicosus (Isoptera, Macrotermitinae) mounds in different habitats of a West African Guinea savanna, Insectes Soc., 45(1), 51–65, doi:10.1007/s000400050068, 1998.

Korb, J.: Thermoregulation and ventilation of termite mounds, Naturwissenschaften, 90(5), 212–219, doi:10.1007/s00114-002-0401-4, 2003.

5   Korb, J.: Termite Mound Architecture, from Function to Construction, in Biology of Termites: A Modern Synthesis, edited by D. E. Bignell, Y. Roisin, and N. Lo, pp. 349–373, Springer, Dordrecht, 2011.

Lepage, M. G.: L'impact des populations récoltantes deMacrotermes michaelseni (Sjöstedt) (Isoptera: Macrotermitinae) dans un écosystème semi-aride (Kajiado-Kenya), I - L'activité de récolte et son déterminisme, Insectes Soc., 28(3), 297–308, 1981a.
10
Lepage, M. G.: L'impact des populations récoltantes de Macrotermes michaelseni (Sjöstedt) (Isoptera: Macrotermitinae) dans un écosystème semi-aride (Kajiado-Kenya), II - La nourriture récoltée, comparaison avec les grands herbivores, Insectes Soc., 28(4), 309–319, 1981b.

15   Lepage, M., Abbadie, L. and Mariotti, A.: Food Habits of Sympatric Termite Species (Isoptera, Macrotermitinae) as Determined by Stable Carbon Isotope Analysis in a Guinean Savanna (Lamto, Cote d'Ivoire), J. Trop. Ecol., 3(3), 303–311, 1993.

Lüscher, M.: Air-Conditioned Termite Nests, Sci. Am., 205(1), 138–145, doi:10.1038/scientificamerican0761-138, 1961.
20
Nauer, P. A., Hutley, L. B. and Arndt, S. K.: Termite mounds mitigate half of termite methane emissions, Proc. Natl. Acad. Sci. - PNAS, 115(52), 13306–13311, doi:10.1073/pnas.1809790115, 2018.

Noirot, C. and Darlington, J. P. E. C.: Termite nests: Architecture, Regulation and Defence, in Termites: Evolution, Sociality,
25   Symbioses, Ecology, edited by T. Abe, D. E. Bignell, and M. Higashi, pp. 121–139, Springer., 2000.

Ocko, S. A., King, H., Andreen, D., Bardunias, P., Turner, J. S., Soar, R. and Mahadevan, L.: Solar-powered ventilation of African termite mounds, J. Exp. Biol., 220(18), 3260–3269, doi:10.1242/jeb.160895, 2017.

30   Pellikka, P. K. E., Heikinheimo, V., Hietanen, J., Schäfer, E., Siljander, M., and Heiskanen, J.: Impact of land cover change on aboveground carbon stocks in Afromontane landscape in Kenya, Applied Geography, 94, 178–189, https://doi.org/10.1016/j.apgeog.2018.03.017, 2018.

Pomeroy, D. E.: Studies on a population of large termite mounds in Uganda, Ecol. Entomol., 1(1), 49–61, doi:10.1111/j.1365-2311.1976.tb01204.x, 1976.

Pomeroy, D. E.: The Distribution and Abundance of Large Termite Mounds in Uganda, J. Appl. Ecol., 14(2), 465–475,
5   doi:10.2307/2402559, 1977.

Rouland-Lefèvre, C.: Symbiosis with fungi, in Termites: Evolution, Sociality, Symbioses and Ecology, pp. 289–306., 2000.

Räsänen, M., Merbold, L., Vakkari, V., Aurela, M., Laakso, L., Beukes, J. P., Zyl, P. G. V., Josipovic, M., Feig, G., Pellikka,
10 P., Rinne, J. and Katul, G. G.: Root-zone soil moisture variability across African savannas: From pulsed rainfall to land-cover switches, Ecohydrology, 13(5), e2213, doi:10.1002/eco.2213, 2020.

Räsänen, M., Vesala, R., Rönnholm, P., Arppe, L., Manninen, P., Jylhä, M., Rikkinen, J., Pellikka, P., and Rinne, J.: Dataset for "Influence of termite mound structure and habitat on the mound CO2 and CH4 fluxes for fungus-growing termites", figshare
15 [data set], https://doi.org/10.6084/m9.figshare.21739484.v1, 2022.

Sanderson, M. S.: Biomass of termites and their emissions of methane and carbon dioxide: A global database, Global Biogeochem. Cycles, 10(4), 543–557, doi:10.1029/96GB01893, 1996.

20 Saunois, M., Stavert, A. R., Poulter, B., Bousquet, P., Canadell, J. G., Jackson, R. B., Raymond, P. A., Dlugokencky, E. J., Houweling, S., Patra, P. K., Ciais, P., Arora, V. K., Bastviken, D., Bergamaschi, P., Blake, D. R., Brailsford, G., Bruhwiler, L., Carlson, K. M., Carrol, M., Castaldi, S., Chandra, N., Crevoisier, C., Crill, P. M., Covey, K., Curry, C. L., Etiope, G., Frankenberg, C., Gedney, N., Hegglin, M. I., Höglund-Isaksson, L., Hugelius, G., Ishizawa, M., Ito, A., Janssens-Maenhout, G., Jensen, K. M., Joos, F., Kleinen, T., Krummel, P. B., Langenfelds, R. L., Laruelle, G. G., Liu, L., Machida, T., Maksyutov,
25 S., McDonald, K. C., McNorton, J., Miller, P. A., Melton, J. R., Morino, I., Müller, J., Murguia-Flores, F., Naik, V., Niwa, Y., Noce, S., O'Doherty, S., Parker, R. J., Peng, C., Peng, S., Peters, G. P., Prigent, C., Prinn, R., Ramonet, M., Regnier, P., Riley, W. J., Rosentreter, J. A., Segers, A., Simpson, I. J., Shi, H., Smith, S. J., Steele, L. P., Thornton, B. F., Tian, H., Tohjima, Y., Tubiello, F. N., Tsuruta, A., Viovy, N., Voulgarakis, A., Weber, T. S., van Weele, M., van der Werf, G. R., Weiss, R. F., Worthy, D., Wunch, D., Yin, Y., Yoshida, Y., Zhang, W., Zhang, Z., Zhao, Y., Zheng, B., Zhu, Q., Zhu, Q. and Zhuang, Q.:
30 The Global Methane Budget 2000-2017, Earth Syst. Sci. Data, 12(3), 1561–1623, doi:10.5194/essd-12-1561-2020, 2020.

Sieber, R. and Leuthold, R. H.: Behavioural elements and their meaning in incipient laboratory colonies of the fungus-growing Termite Macrotermes michaelseni (Isoptera: Macrotermitinae), Insectes Soc., 28(4), 371–382, doi:10.1007/BF02224194, 1981.

Sugimoto, A., Inoue, T., Kirtibutr, N. and Abe, T.: Methane oxidation by termite mounds estimated by the carbon isotopic composition of methane, Global Biogeochem. Cycles, 12(4), 595–605, doi:10.1029/98GB02266, 1998.

5   Thomas, R. J.: Ecological studies on the symbiosis of Termitomyces Heim with Nigerian Macrotermitinae, University of London., 1981.

Wachiye, S., Merbold, L., Vesala, T., Rinne, J., Räsänen, M., Leitner, S. and Pellikka, P.: Soil greenhouse gas emissions under different land-use types in savanna ecosystems of Kenya, Biogeosciences, 17(8), 2149–2167, doi:10.5194/bg-17-2149-2020, 10   2020.

van Asperen, H., Alves-Oliveira, J. R., Warneke, T., Forsberg, B., de Araújo, A. C. and Notholt, J.: The role of termite CH_4 emissions on the ecosystem scale: A case study in the Amazon rainforest, Biogeosciences, 18(8), 2609–2625, doi:10.5194/bg-18-2609-2021, 2021.

Vesala, R., Niskanen, T., Liimatainen, K., Boga, H., Pellikka, P. and Rikkinen, J.: Diversity of fungus-growing termites (Macrotermes) and their fungal symbionts (Termitomyces) in the semiarid Tsavo Ecosystem, Kenya, Biotropica, 49(3), 402–412, doi:10.1111/btp.12422, 2017.

20   Vesala, R., Arppe, L. and Rikkinen, J.: Caste-specific nutritional differences define carbon and nitrogen fluxes within symbiotic food webs in African termite mounds, Sci. Rep., 9(1), 16611–16698, doi:10.1038/s41598-019-53153-x, 2019a.

Vesala, R., Harjuntausta, A., Hakkarainen, A., Rönnholm, P., Pellikka, P. and Rikkinen, J.: Termite mound architecture regulates nest temperature and correlates with species identities of symbiotic fungi, PeerJ, 6, e6237, doi:10.7717/peerj.6237, 25   2019b.

Vesala, R., Arppe, L. and Rikkinen, J.: Termitomyces fungus combs - formation, structure and functional aspects, in Microbial Symbionts: Functions and Molecular Interactions on Host, edited by D. Dhanasekaran, Academic Press., 2022a.

30   Vesala, R., Rikkinen, A., Pellikka, P., Rikkinen, J. and Arppe, L.: You eat what you find – local patterns in vegetation structure control diets of African fungus-growing termites, Ecol. Evol., 12, e8566, 2022b.

Virtanen, P., Gommers, R., Oliphant, T. E., Haberland, M., Reddy, T., Cournapeau, D., Burovski, E., Peterson, P., Weckesser, W., Bright, J., van der Walt, S. J., Brett, M., Wilson, J., Millman, K. J., Mayorov, N., Nelson, A. R. J., Jones, E., Kern, R.,

Larson, E., Carey, C. J., Polat, İ., Feng, Y., Moore, E. W., VanderPlas, J., Laxalde, D., Perktold, J., Cimrman, R., Henriksen, I., Quintero, E. A., Harris, C. R., Archibald, A. M., Ribeiro, A. H., Pedregosa, F., van Mulbregt, P., and SciPy 1.0 Contributors: SciPy 1.0: fundamental algorithms for scientific computing in Python, Nat. Methods, 17, 261–272, https://doi.org/10.1038/s41592-019-0686-2, 2020.

Weir, J. S.: Air Flow, Evaporation and Mineral Accumulation in Mounds of Macrotermes subhyalinus (Rambur), J. Anim. Ecol., 42(3), 509–520, doi:10.2307/3120, 1973.

Wildermuth, B., Oldeland, J., Arning, C., Gunter, F., Strohbach, B. and Juergens, N.: Spatial patterns and life histories of
10 Macrotermes michaelseni termite mounds reflect intraspecific competition: Insights of a temporal comparison spanning 12 years, Ecography, 9, e06306, doi:10.1111/ecog.06306, 2022.

Wood, T. G. and Thomas, R. J.: The mutualistic association between Macrotermitinae and Termitomyces, in Insect-fungus interactions, edited by N. Wilding, N. M. Collins, P. M. Hammond, and J. F. Webber, pp. 69–92, Academic Press., 1989.

Zhou, Y., Staver, A. C., and Davies, A. B.: Species-level termite methane production rates, Ecology, 104, e3905, https://doi.org/10.1002/ecy.3905, 2023.

Zimmerman, P. R., Greenberg, J. P., Wandiga, S. O. and Crutzen, P. J.: Termites: A Potentially Large Source of Atmospheric Methane, Carbon Dioxide, and Molecular Hydrogen, Science, 218, 563–565, 1982.