**Title**

The challenge of estimating global termite methane emissions

**Journal**

Global Change Biology, 30(6)

**ISSN**

1354-1013

**Authors**

Law, Stephanie J
Allison, Steven D
Davies, Andrew B
et al.

**Publication Date**

2024-06-01

**DOI**

10.1111/gcb.17390

# The challenge of estimating global termite methane emissions.

Stephanie J. Law[1*], Steven D. Allison[2,3], Andrew B. Davies[4], Habacuc Flores-Moreno[5], Baptiste J. Wijas[6], Abbey R. Yatsko[6], Yong Zhou[7,8], Amy E. Zanne[6], Paul Eggleton[1].

[1] Life Sciences Department, The Natural History Museum, London, UK; [2]Department of Ecology and Evolutionary Biology, University of California, Irvine, California, USA; [3]Department of Earth System Science, University of California, Irvine, California, USA; [4]Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts, USA; [5]CSIRO Health and Biosecurity, GPO Box 2583, Brisbane, Queensland, 4001 Australia; [6]Department of Biology, University of Miami, Miami, Florida, USA; [7]Department of Wildland Resources, Utah State University, Logan, Utah, USA; [8]Ecology Center, Utah State University, Logan, Utah, USA.

* Correspondence: Stephanie Jane Law (stephaniejanelaw@gmail.com).

ORCID:

Stephanie Jane Law 0000-0002-8362-4702

Steven D. Allison 0000-0003-4629-7842

Andrew B. Davies 0000-0002-0003-1435

Habacuc Flores-Moreno 0000-0002-7083-0005

Baptiste J. Wijas 0000-0001-7895-083X

Abbey R. Yatsko 0000-0001-8515-7629

Yong Zhou 0000-0003-2546-8462

Amy E. Zanne 0000-0001-6379-9452

Paul Eggleton 0000-0002-1420-7518

Running title: Global termite methane emissions

## Abstract

Methane is a powerful greenhouse gas, more potent than carbon dioxide, and emitted from a variety of natural sources including wetlands, permafrost, mammalian guts, and termites. As increases in global temperatures continue to break records, quantifying the magnitudes of key methane sources has never been more pertinent. Over the last 40 years, the contribution of termites to the global methane budget has been subject to much debate. The most recent estimates of termite emissions range between 9 and 15 Tg $CH_4$ $y^{-1}$, approximately 4% of emissions from natural sources (excluding wetlands). However, we argue that the current approach for estimating termite contributions to the global methane budget is flawed. Key parameters, namely termite methane emissions from soil, deadwood, living tree stems, epigeal mounds and arboreal nests, are largely ignored in global estimates. This omission occurs because data are lacking and research objectives, crucially, neglect variation in termite ecology. Furthermore, inconsistencies in data collection methods prohibit the pooling of data required to compute global estimates. Here, we summarise the advances made over the last 40 years and illustrate how different aspects of termite ecology can influence the termite contribution to global methane emissions. Additionally, we highlight technological advances that may help researchers investigate termite methane emissions on a larger scale. Finally, we consider dynamic feedback mechanisms of climate warming and land-use change on termite methane emissions. We conclude that ultimately the global contribution of termites to atmospheric methane remains unknown and thus present an alternative framework for estimating their emissions. To significantly improve estimates, we outline outstanding questions to guide future research efforts.

Keywords: deadwood, methane budget, methane emissions, methane oxidation, methanotrophs, termites, termite mesocosm, tree stems

## 1. Introduction

The latest IPCC report highlights the role of methane in the historic rise in global temperatures, accounting for 0.5°C of warming since pre-industrial times (IPCC, 2021). The global methane budget has therefore received mounting scrutiny (Kirschke et al., 2013; Saunois et al., 2020). Uncertainty remains, however, due to an incomplete understanding of heterogeneous natural sources, unknown biogeochemical feedback mechanisms and the difficulties unravelling the complex atmospheric chemistry influencing the breakdown of methane (Nisbet et al., 2019; Skeie et al., 2023).

Natural sources of methane account for between 38% and 50% of global methane emissions (Saunois et al., 2020). The least understood is vegetation decomposition (Carmichael et al., 2014; Saunois et al., 2020), to which termites make a considerable contribution in the tropics (Griffiths et al., 2019; Walker et al., 2022). Termites are therefore recognised as one of the four largest natural sources of methane, comprising around 4% of non-wetland emissions, and are usually included in global methane budgets (Kirschke et al., 2013; Saunois et al., 2020; Stavert et al., 2022). The decadal negative shift in the isotopic signature of atmospheric methane implies marked changes in the relative proportion of emissions from methane sources and possible increases in microbial sources (Chandra et al., 2024; Nisbet et al., 2019). Comparable to enteric fermentation of ruminant animals, methane is a by-product from microbial digestion of lignocellulose in the hindgut of termites (Brune, 2014). However, as the carbon isotopic signature of methane emitted from termites is indistinguishable from other methanogenic bacteria (i.e., from ruminants or wetlands) (Sherwood et al., 2017), a bottom-up approach is needed to better understand biogenic methane sources and help explain the shift in the isotopic signature of atmospheric methane. The global biomass of termites, estimated at approximately 0.8 Gt and equivalent to that of livestock (Bar-On et al., 2018; Rosenberg et al., 2023), is concentrated in tropical latitudes where emissions from methanogenic bacteria are highest (Chandra et al., 2024), so termites are potentially contributing to this significant biogenic source of methane to the global methane budget.

The inaugural paper by Zimmerman et al., (1982) on global termite methane emissions stimulated active debate and a new research field. Initial global estimates relied on laboratory experiments with limited termite species and upscaled measurements based on population size or estimates of plant biomass consumed by termites (Rasmussen & Khalil, 1983; Seiler et al., 1984; Zimmerman et al., 1982). Later studies attempted to improve estimates by using more termite species, differentiating emissions among feeding groups, taking field measurements from mounds, accounting for oxidation rates, and using estimates of termite biomass in a wider range of ecological regions to upscale (Table S1). With more data, the estimated contribution of termites to the methane budget dropped from ~30% to ≤2% of the annual global total (Ito, 2023; Saunois et al., 2020; Zimmerman et al., 1982). Over the last 40 years, empirical measurements have largely focused on two main areas: methane production rates from individual termites at the species level, and emissions from termite mounds. However, emissions directly quantified from individual termites remain decoupled from upscaled ecosystem estimates where substantial questions remain regarding accuracy.

Most upscaled estimates quantify global termite methane emissions as the product of an emission factor ($\mu g\ CH_4\ g^{-1}_{(termite)}h^{-1}$) and biomass density ($g_{(termite)}m^{-2}$), summed across ecosystems (Ito, 2023; Saunois et al., 2020). This method is problematic because existing emission factors only account for <5% of termite species (105/2951 named species from individuals) (Constantino, 2018). Families, feeding groups and biogeographical areas are also unevenly represented (six subfamilies comprise 76% of emission factors and 68% are from wood or soil-feeders, Tables S4.1 and S4.2, Fig. 2), and factors can vary by two orders of magnitude (Zhou et al., 2023) amplifying uncertainties when using a single emission factor to represent all termite diversity. In addition, quantification of how individual emission factors scale with colony emissions is scarce, and methane oxidation by methanotrophs occurring within and near the termite colony (i.e., in mound material, soil or wood) is unaccounted for in incubation experiments, so emission factors do not accurately reflect net methane emissions from the colony to the atmosphere. A lack of termite biomass data (Rosenberg et al., 2023) means that current estimates of global termite methane emissions (Kirschke et al., 2013; Saunois et al., 2020) either rely heavily on data which is almost thirty years old (Sanderson, 1996), or estimate termite biomass within an ecosystem from regression analyses with ecosystem GPP based on a limited number of measurements (Kirschke et al., 2013). Furthermore, emission factors omit important aspects of termite ecology. Termites are included in the methane budget as a homogenous group using a single estimate of biomass density for each ecosystem, yet termite distributions across the landscape differ widely among functional groups. While mound building termites can form predictable patterns in some ecosystems (Castillo Vardaro et al., 2021; Tarnita, 2018), quantifying subterranean nests is inherently more challenging (Davies et al., 2021). Additionally, climate can influence community structure, such as feeding groups (e.g., wood, soil, or fungus feeder) and nesting strategy (above or belowground) (Lind et al., 2022; Wijas et al., 2022) which in turn has implications for methane emissions. For example, as methane emission rates differ between feeding groups (Zhou et al., 2023) and nesting substrate (Sugimoto et al., 1998), differences in the distribution of termite biomass among functional groups can substantially alter upscaled estimates.

Net methane emissions by termites are achieved only where termite biomass is sufficiently concentrated to overcome methane oxidation. Therefore, key questions remain about how termite biomass is distributed and how methane oxidation differs in areas where termites are found. Termites occur in multiple locations that could potentially produce net methane emissions, including in deadwood, living tree stems, termite mounds, arboreal nests or in the ground. Yet the relative importance of each source for global termite methane emissions remains unclear. For example, while biomass of subterranean termites is high (Rosenberg et al., 2023), termite biomass may seldom reach the density required to overcome high levels of methane oxidation in unsaturated, oxic soil (MacDonald et al., 1998, 1999; Saunois et al., 2020). A lower termite biomass in deadwood or arboreal nests, however, could make a greater contribution to global termite methane emissions if abundance of methanotrophs is substantially lower than in soil.

Here, we present an alternative framework for estimating global termite-methane emissions considering the distribution of termites across the landscape and the factors that ultimately influence net methane emissions from termites. First, we outline progress made and existing understanding in methane emissions from different termite sources, including wood, mounds, and soils, highlighting current limitations and uncertainties. Second, we discuss future directions for advancing estimates of global termite methane emissions, specifically we consider new remote sensing technology (e.g., gas mapping LiDAR), the potential role of termite mesocosms and the implications of anthropogenic global change on termite methane production. Third, we propose research objectives needed to address the current paucity in data and better estimate the contribution of termites to the global methane budget. We present the parameters required in our alternative framework for estimating the global contribution of termite-related methane emissions and the dynamic factors influencing net methane emissions in Fig. 1 and Table 1 which we refer to throughout.

## 2. Progress and challenges

### *2.1 Emissions from deadwood and tree stems*

The importance of termites in breaking down wood across different habitats has been highlighted in several recent studies (Flores-Moreno et al., 2023; Law et al., 2023; Seibold et al., 2021; Wijas et al., 2024; Yatsko et al., 2024; Zanne et al., 2022) yet there have been no studies measuring termite-related methane emissions from decomposing wood. While microbial methanogenesis in the heartwood of tree stems has received increasing attention (Barba et al., 2019; Covey & Megonigal, 2019), methane emissions have not been linked to termite presence despite termites, e.g. *Coptotermes*, causing high levels of tree stem decay (Werner & Prior, 2007; Yatsko et al., 2024). Emissions from wood-feeding termites may have been overlooked because incubation experiments indicate that emission factors for wood-feeding termites are generally smaller than for soil-feeders (Fig. S4.1). Preliminary experimental data (see supplementary materials, S2, for details, Table 1) shows for the first time that methane emissions from deadwood can be as much as 30 times greater when termites are present compared with their absence, and that termite-related methane emissions from deadwood can vary between ecosystems suggesting greater termite-related methane emissions from deadwood in savanna landscapes compared with rainforest (Fig. S2.1). Using these preliminary data, back-of-the-envelope calculations indicate that methane emissions from deadwood are likely to be negligible when compared with termite mound emissions (Table S2.5). However, these upscaled estimates are made from few data points and without local data on termite biomass in deadwood.

Net methane emissions from wood-feeding termites may be substantial if the biomass density of termites in deadwood is large and if methane oxidation is low. The available data suggest that in some tropical forests between 15% (rainforest) and 21% (dry-forest) of termite biomass is present in deadwood, equivalent to that found in epigeal mounds (Vasconcellos, 2010; Yamada et al., 2003) (Fig. 1b). Furthermore, encounter rates in Australian savanna have also indicated a similar distribution between deadwood (standing and fallen deadwood) and epigeal mounds (Dawes-Gromadzki, 2008), although there can be large differences in termite distribution between ecosystems (Clement et al., 2021). Methanotrophs have also been detected in bark but with lower oxidative capacity than soil-based epigeal mounds, reducing methane emissions from tree stems by 36% (Jeffrey et al., 2021) compared with a mean 50% reduction from mounds (range across three termite species was 20 to 80%) (Nauer, Hutley, et al., 2018). If termite biomass in deadwood is comparable with epigeal mounds we could expect equivalent methane emissions, particularly if less methane is oxidised. Furthermore, emissions from foraging and nesting termites in deadwood are likely to depend on termite biomass and how long they spend in deadwood. More extensive studies are needed to determine the contribution of deadwood-feeding termites to global termite emissions (Fig. 1a).

### *2.2 Emissions from mounds*

Epigeal termite mounds (visible mound aboveground) have received attention primarily because they are where termite biomass is obviously concentrated and can overcome methane oxidation in soils or mound material resulting in a point source of methane (Chiri et al., 2020, 2021; Nauer, Hutley, et al., 2018). However, existing research on termite mounds is largely focused on northern Australia and Central Africa (Fig. 2) and covers only 1% of named termite species (30/2951, Table S4.3) (Constantino, 2018). Most of the mound emission estimates (64%) were based on just 3 subfamilies, and 68% were from wood or soil feeders (Flores-Moreno et al., 2024, Table S4.1, Table S4.2). While it is not feasible to collect data on all species, a broader representation is needed.

Drawing comparisons among existing studies on termite mounds is challenging due to insufficient data and inconsistencies in methods and reporting (Table 1). Limited data indicates that patterns at the individual level may not hold true at the colony level. For example, differences in emissions across feeding groups are smaller at the mound level (Fig. S4.1) (Zhou et al., 2023). Colony biomass, mound structure and degree of methane oxidation, rather than individual capacity to produce methane, are likely to be more important for determining net emissions at the mound level (Fig. 1a) and need to be considered when scaling up mound-based methane emissions.

Little is known regarding differences in oxidative capacity of methanotrophs among termite mounds. All current studies are based on epigeal, soil-based, mounds (Table S4.3), for which recorded estimated rates of oxidation vary between 20% and 83% across nine species (Khalil et al., 1990; MacDonald et al., 1998; Nauer, Hutley, et al., 2018; Sugimoto et al., 1998). In epigeal mounds the methanotroph community of three termite species was found to have adapted to elevated levels of methane, yet mound methanotrophs remained rare and were derived from the microbial community in surrounding soil (Chiri et al., 2020). However, to date, the presence of methanotrophs in termite nests within deadwood (section 2.1) or in arboreal, carton-based nests remains undocumented. Accordingly, as they have no connection with surrounding soil, we predict that few methanotrophs occur in arboreal termite nests. This potential absence of methanotrophs, along with differences in mound structure, may explain greater than expected methane emissions in arboreal nests than epigeal mounds (Fig. S4.1).

Interspecific variation in methane emissions from epigeal mounds is influenced by several factors including: (1) methanotroph location; oxidation can occur in the mound wall or in soil beneath the mound (Nauer, Hutley, et al., 2018); (2) concentration of termite biomass within the mound and proximity to methanotrophs; e.g. nests of *Macrotermes michaelseni* (Sjöstedt, 1914) are largely located below the ground leaving the mound essentially empty of termites, and instead termites are in direct contact with soil methanotrophs such that methane emissions can be detected from both the mound and surrounding soils (Korb, 2011; Räsänen et al., 2023); (3) the permeability of mound material; less dense, porous material can increase methanotroph abundance in mound material (Chiri et al., 2020) but also aid gas emissions to the atmosphere (Singh et al., 2019); and (4) mound structures can control permeating gases in a trade-off between gas-exchange and thermoregulation (Korb, 2003); mound chimneys, or better connectivity between cavities, improve ventilation and limit time for methane oxidation resulting in greater emissions (Darlington et al., 1997; Sugimoto et al., 1998), while mounds with fewer conduits and limited ventilation may have lower emissions.

Intraspecific variation in mound emissions is not well documented, yet within species, mound structure can vary greatly between habitats (Fagundes et al., 2021; Korb, 2003, 2011). Gas emissions from mounds vary both diurnally and seasonally (Jamali, Livesley, Dawes, Cook, et al., 2011; Jamali, Livesley, Dawes, Hutley, et al., 2011; Räsänen et al., 2023). Greater methane emissions are linked to enhanced methanogenesis in the termite gut at higher temperatures (Jamali, Livesley, Dawes, Cook, et al., 2011) and increased mound termite biomass during wet seasons (Jamali, Livesley, Dawes, Hutley, et al., 2011). Yet few data exist regarding the proportion of termite biomass present in the mound at any time and, while some methane produced within a mound will be oxidised by methanotrophs, methane produced by termites foraging above ground will not be removed. However, in the absence of more rigorous data, rough calculations indicate that it is unlikely that foraging termites can produce methane in amounts comparable with a mound. For example, using estimates of methane emissions, the biomass density of the harvester termite *Tumulitermes pastinator* (Hill, 1912) would need to reach 0.7 $g_{(termite)}m^{-2}$ with termites foraging continuously above ground to produce the same emissions as a mound (see S4 for details). Still, questions remain regarding how within mound population dynamics and termite behaviour affect methane emissions.

Because quantifying termite biomass from termite mounds is laborious and difficult, many biomass estimates arise from regression analyses using abundance and mound volume (Josens & Soki, 2010) and, as with regressions based on GPP at the ecosystem level (Kirschke et al., 2013; Saunois et al., 2020), they are based on few data points. Following the paucity of biomass data, mound emissions can be upscaled using mound density or mound basal area. Yet this approach presents additional problems. Like individual emission factors, using mound emissions from one or two species fails to account for species-specific variations. Furthermore, extrapolating mound density across ecosystems is problematic. For example, mound density in northeast Australian savanna was approximately threefold that in the Northern Territory Australian savanna (Clement et al., 2021; Jamali, Livesley, Grover, et al., 2011). Using a single estimate of mound density can vastly under or overestimate emissions across the landscape. Additionally, estimating termite methane contribution by solely upscaling mound estimates overlooks other potential sources such as arboreal nests and deadwood (see Fig. 1a).

### *2.3 Termite-related soil emissions (excluding termite mounds)*

In some ecosystems, most termites are subterranean (Vasconcellos, 2010; Wijas et al., 2022; Yamada et al., 2003) and soils represent a potentially large source of termite-related methane. However, soils are frequently characterised as methane sinks due to the high presence of methanotrophs and are only considered as potential methane sources when inundated with water as anoxic conditions favour methanogenic bacteria (IPCC, 2021; Le Mer & Roger, 2001; Saunois et al., 2020). For subterranean termites to be a significant source of soil methane emissions, their biomass and thus methane production would have to outweigh methane oxidation by soil methanotrophs (Fig. 1a). Although subterranean termites are present in waterlogged soils and anoxic peatlands (Kouakou et al., 2022; Muhammad et al., 2012; Saputra et al., 2018), it is unlikely that subterranean termite biomass contributes significantly to the high methane emissions measured from wetlands (IPCC, 2021; Saunois et al., 2020). Conversely, methane produced from non-inundated, aerobic soils is likely to be due to the presence of subterranean termites, yet they are rarely considered.

Few studies quantify biomass density of soil inhabiting termites. Most studies instead ask whether methane emissions from termite mounds offset the soil's sink capacity (Jamali et al., 2013; Jamali, Livesley, Grover, et al., 2011; van Asperen et al., 2021). When quantified, subterranean termite biomass varies based on species and season, and only turns soils to a methane source at densities between 3.8 $g_{(termite)}m^{-2}$ and 18 $g_{(termite)}m^{-2}$, a range that was rarely observed; however, methane production was not determined from the colony centre (MacDonald et al., 1998, 1999). Moreover, data quantifying methane emissions from soil above subterranean nests report negligible fluxes (Seiler et al., 1984) suggesting that the importance of subterranean nests for the methane budget is probably minor. Furthermore, emissions from non-inundated, upland soils are often minimal when compared with emissions from adjacent termite mounds. For example, emission factors (e.g. $\mu g\ CH_4\ m^{-2}\ h^{-1}$) from termite mounds were between 100 and 600 times greater than emission factors from soil in the same savanna and rainforest sites respectively (Brümmer et al., 2009; van Asperen et al., 2021). However, as mounds are only a fraction of the landscape, soil emissions can be substantially higher when scaled up. For instance, Brümmer et al., (2009) reported a methane flux of 3.45 $kg\ CH_4\ ha^{-1}\ y^{-1}$ from soils compared with 0.27 $kg\ CH_4\ ha^{-1}\ y^{-1}$ from mounds, although the causes of soil emissions were not directly established. The spatial variability in soil emissions due to the patchy distribution of termite biomass has not been well quantified and presents problems in upscaling estimates of methane emissions (Fig. 1a).

To truly exclude soils as a significant source of termite-related methane, more data are needed on (1) emissions above subterranean nests along with soil termite biomass, and (2) variation in the distribution of soil methanotrophs and correspondingly the sink capacity of soil, according to biogeography, ecosystem, and level of disturbance.

## 3. Future directions

### *3.1 Technological advances*

The development of remote sensing techniques such as LiDAR and optical satellite imagery provides new methods to improve estimates of mound density, revealing predictable patterns in spatial distribution of mounds across the landscape (Davies et al., 2014, 2016; D'hont et al., 2021; Martin et al., 2018), and mound dimensions (D'hont et al., 2021). However, the ability of these techniques to detect mounds below dense forest canopies needs to be improved before these technologies can be expanded beyond open (e.g., grasslands) and partially open (e.g., savannas) canopy ecosystems.

Methane detection techniques have also utilised these technologies, e.g. gas mapping LiDAR and unmanned aerial vehicles (UAVs, e.g. drones) with absorption spectroscopy and hyperspectral imaging capabilities, enabling aerial detection and quantification of methane sources, including from some natural sources (Bell et al., 2022; Erland et al., 2022; Hollenbeck et al., 2021; Kumar et al., 2020; Shaw et al., 2020). However, the sensitivity required to detect emissions from termite sources, including concentrated points like mounds, is below current detection limits for most remote sensing techniques (Bell et al., 2022; Shaw et al., 2020; Thompson et al., 2015). It is feasible that such technology will become available in the future and could be used to detect methane hotspots attributable to termites. For now, data on mound distributions collected via remote sensing should be coupled with information on mound occupation and termite biomass data to accurately scale up emissions from mound observations or experiments. Recent application of ground imaging techniques (including CT and X-ray scanning, photogrammetry, and cross-sectional imagery) to termite mounds is not only improving estimates of mound volume but providing a mechanistic understanding of how mound structure influences gas diffusion and emissions through the porosity of mound material and connectivity of chambers (Nauer, Chiri, et al., 2018; Singh et al., 2019). Moreover, ground penetrating radar, a non-destructive tool able to locate subterranean termite nests and tunnels (Xu et al., 2010; Yang et al., 2009), could be used to identify areas where subterranean termite biomass is concentrated.

### *3.2 Termite mesocosms*

Mesocosms present an alternative method to study mound emissions, by allowing for experimental manipulation of termite mounds under controlled conditions. Field mesocosms have addressed questions regarding gas exchange and thermoregulation (Korb & Linsenmair, 1998; Schmidt et al., 2014), still the ability to manipulate field conditions is limited. Laboratory mesocosms have been established for a few termite species (Fraser et al., 1986; Harit et al., 2017; Lee & Lee C. Y., 2015), yet these studies lack sufficient replication. Moreover, most studies investigate termite ecology at the microcosm level (i.e. using incipient colonies or subterranean termites) or maintain colonies for weeks or months rather than years (Donovan et al., 2001; Hartke & Rosengaus, 2013; Neupane et al., 2015). The difficulties of successful translocation and maintenance of large termite mounds may have prevented the widespread use of termite mesocosms. However, once termite mesocosms are established, questions regarding factors that influence methane production from mounds can be addressed. This method may be particularly useful for collecting data to predict methane production under future scenarios, be it land-use change and subsequent different feeding substrates (e.g., wood species) or a response to changes in temperature (see supplementary materials S3 for details of a preliminary mesocosm study on *Microcerotermes*, an epigeal mound-building termites).

### *3.3 Implications of anthropogenic change on termite methane production*

Ito (2023) estimates that global termite methane emissions have increased by ca. 0.7 Tg $CH_4$ $y^{-1}$ (from 1901-2021) and will continue to increase by 0.5 to 5.9 Tg $CH_4$ $y^{-1}$ through 2100, attributed chiefly to projected global increases in termite biomass driven by greater GPP. While such recent assessments of available data highlight the importance of termites to the methane budget, broad statements can be misleading as estimates do not account for differing responses among feeding groups or nesting substrates. Although the range of wood-feeding termites is predicted to expand under climate change scenarios, enhancing decomposition processes and potentially resulting in greater methane emissions (Zanne et al., 2022), impacts of climate change on soil-feeding termites are largely unknown. Any impact of climate change on termite distribution and biomass is likely to be compounded by land conversion and agricultural development. Several studies indicate that wood-feeding termites persist and sometimes thrive following logging or conversion to plantations, yet soil-feeding termites do not (Eggleton et al., 1996; Jones et al., 2003; Luke et al., 2014). Thus, while soil-feeding termites are generally thought to have greater methane emission rates, the contribution of wood-feeding termites to global termite methane emissions may become more important in the future.

Greater methane production from termite mounds may not solely be attributed to greater termite biomass but also to a greater production rate of methane as temperatures rise. The thermal response of methane production can be quantified by estimating the effective Q10 value (i.e., the rate of change in methane production for a 10$^{o}$C increase in temperature). Existing effective Q10 values for methane production from epigeal-mound building termites are estimated by comparing production rates at two discrete temperatures (Jamali, Livesley, Dawes, Cook, et al., 2011; Jamali, Livesley, Dawes, Hutley, et al., 2011). An alternative approach is to fit thermal performance curve models to methane production rates across a range of temperatures (see supplementary material S3 for details). We carried out a pilot study on the thermal response of an epigeal-mound building termite of the genus *Microcerotermes* by fitting thermal response curves and found that, while the estimated effective Q10 for methane production rate of 2.09 was in line with previous estimates from *Microcerotermes* (Jamali, Livesley, Dawes, Cook, et al., 2011; Jamali, Livesley, Dawes, Hutley, et al., 2011)*,* methane production rate fell at temperatures over 35$^o$C (Fig. S3.6) Thus, while methane production rate is likely to increase with rising temperatures, responses may attenuate in extremely hot areas, and further studies on methane production may be needed where termites exist at their extreme thermal limits.

An important parameter, overlooked in predictions of termite methane emissions, is the impact of climate change and disturbance on the oxidative capacity of methanotrophs in mounds and soils. Complex, dynamic interactions regulate methane oxidation, including among temperature, soil water-content, ammonium toxicity and methane diffusivity (King, 1997). However, it is likely that water stress and anthropogenic disturbance will cause a decrease in methane oxidative capacity (King, 1997; MacDonald et al., 1999). We speculate that any increase in atmospheric methane resulting from a decline in soil oxidation will be compounded by the persistence of termites in dry environments. Notably, mound building termites are better suited to resist environmental change via the homeostatic properties of mounds (Korb, 2011) and have a greater impact on ecosystem processes in dry environments (Veldhuis et al., 2017). Thus, we predict the relative contribution of termite mounds to methane emissions will increase in drier climates, particularly if oxidative capacity falls. Ultimately, there remains a dearth of knowledge on the dynamic interactions between termite-related methane-emissions under different climatic scenarios and in disturbed environments. Future research must address this shortcoming to predict current and future roles of termites in the methane budget.

## 4. Research Objectives

To significantly improve global estimates of termite methane emissions, we suggest a focus on addressing the following seven areas: (1) expand estimates of mound emissions to include a wider range of species (subfamilies and feeding groups) and biogeographical areas, particularly in South America where data are lacking (Fig. 2); (2) examine how variation in diel and seasonal methane emissions depend on abiotic conditions and colony dynamics; (3) determine the significance of termite methane emissions from deadwood and tree stems; (4) define methane oxidation capacity for a variety of termite-associated substrates, including arboreal carton-nests, epigeal soil-based mounds, deadwood and soil; (5) quantify termite biomass distribution for each substrate (wood, mound, soil) across different ecosystems, and understand the breakdown of species and feeding guild within each of these groups; (6) improve estimates of landscape level distribution of epigeal termite mounds, arboreal nests and subterranean nests; and (7) evaluate impacts of temperature, precipitation and land-use change on termite-related methane emissions.

Constructing a database or open repository with these areas in mind would facilitate the development of data-driven models incorporating uncertainties and variation in methane emissions from a variety of sources at local to global scales. In Table 1, we outline key parameters needed to produce a more accurate global estimate of termite methane emissions. Where possible, we include approximate figures from existing literature, illustrating the large range in values. The level of uncertainty for most parameters is high due to a paucity of data. We argue that future research efforts should homogenise methods and units of data collected to facilitate data comparison and integration. By constraining the parameters outlined in Table 1 we can arrive at a more accurate estimate of global termite-related methane emissions and potentially help resolve some of the discrepancy between top-down and bottom-up methane estimates. By determining the true significance of termites on the global methane budget we can improve predictions of future methane emissions.

## 5. Conclusion

Despite more than 40 years of research on termite-related methane emissions, there remains inadequate data to accurately account for termite ecology and contributions to the methane budget. We argue that the distribution of termite biomass must be accounted for in estimates of global termite methane flux. Specifically, studies must address where and when termite biomass is sufficiently concentrated to overcome methane oxidation, turning the substrate from a methane sink to a source. Termite mounds are likely locations, yet further research is needed to exclude deadwood, living tree stems and subterranean nests as potential sources. Without additional studies to reduce uncertainty in emission sources, we conclude that the global contribution of termites to atmospheric methane remains unknown. Prior estimates are poorly informed by relevant data, making them irrelevant at best and misleading at worst, especially if they are used in projections of future atmospheric greenhouse gas levels. On the bright side, a growing focus on termite methane emissions in studies around the world combined with advances in remote sensing and modelling offer promise that estimates of termite contribution to global methane budgets can be constrained to a useful range.

## Acknowledgements

This research was funded by grants from the Natural Environment Research Council (NERC) to PE (NE/K01613X/1) to PE and the National Science Foundation to AEZ (DEB-1655759 and DEB-2149151) and to SDA (DEB-1655340). Thanks to Lucas Cernusak, Alex Cheesman, Eleanor Speare, Emma Carmichael and James Cook University, Australia, for resources, logistical and field support in data collection. Images used to depict landscapes in Figure 1 are adapted from images freely available and designed by Freepik at www.freepik.com.

## Conflict of Interest Statement

The authors have no conflict of interest to declare.

## Data Availability Statement

The data and code that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.11089744

Author Contributions

The manuscript was conceived and designed by PE and SJL. All authors discussed the concept, provided intellectual input, reviewed, and edited the manuscript which was written by SJL. Data for pilot studies described in supplementary materials were collected by ARY and HFM. Data were curated and analysed by SJL and HFM. Concept and method for the mesocosm pilot study was designed and conducted by HFM.

References

Abensperg-Traun, M., & de Boer, E. S. (1990). Species abundance and habitat difference in biomass of subterranean termites (Isoptera) in the wheatbelt of Western Australia. *Australian Journal of Ecology*, *15*(2), 219–226.

Barba, J., Bradford, M. A., Brewer Paul E., Bruhn, D., Covey, K., van Haren, J., Megonigal, J. P., Mikkelsen, T. N., Pangala, S. R., Pihlatie, M., Poulter, B., Rivas-Ubach, A., Schadt, C. W., Terazawa, K., Warner, D. L., Zhang, Z., & Vargas, R. (2019). Methane emissions from tree stems: a new frontier in the global carbon cycle. *New Phytologist*, *222*, 18–28. https://doi.org/10.1111/nph.15582

Bar-On, Y. M., Phillips, R., & Milo, R. (2018). The biomass distribution on Earth. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(25), 6506–6511. https://doi.org/10.1073/pnas.1711842115

Bell, C., Rutherford, J., Brandt, A., Sherwin, E., Vaughn, T., & Zimmerle, D. (2022). Single-blind determination of methane detection limits and quantification accuracy using aircraft-based LiDAR. *Elementa*, *10*(1), 186–188. https://doi.org/10.1525/elementa.2022.00080

Brümmer, C., Papen, H., Wassmann, R., & Brüggemann, N. (2009). 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), GB1001. https://doi.org/10.1029/2008GB003237

Brune, A. (2014). Symbiotic digestion of lignocellulose in termite guts. *Nature Reviews Microbiology*, *12*(3), 168–180. https://doi.org/10.1038/nrmicro3182

Carmichael, M. J., Bernhardt, E. S., Bräuer, S. L., & Smith, W. K. (2014). The role of vegetation in methane flux to the atmosphere: Should vegetation be included as a distinct category in the global methane budget? *Biogeochemistry*, *119*(1–3), 1–24. https://doi.org/10.1007/s10533-014-9974-1

Chandra, N., Patra, P. K., Fujita, R., Hoglund-Isaksson, L., Umezawa, T., Goto, D., Morimoto, S., Vaughn, B. H., & Rockmann, T. (2024). Methane emissions decreased in fossil fuel exploitation and sustainably increased in microbial source sectors during 1990-2020. *Communications Earth & Environment*, *5*, 147. https://doi.org/10.1038/s43247-024-01286-x

Cheesman, A. W., Cernusak, L. A., & Zanne, A. E. (2018). Relative roles of termites and saprotrophic microbes as drivers of wood decay: A wood block test. *Austral Ecology*, *43*(3), 257–267. https://doi.org/10.1111/aec.12561

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

Chiri, E., Nauer, P. A., Lappan, R., Jirapanjawat, T., Waite, D. W., Handley, K. M., Hugenholtz, P., Cook, P. L. M., Arndt, S. K., & Greening, C. (2021). Termite gas emissions select for hydrogenotrophic microbial communities in termite mounds. *Proceedings of the National Academy of Sciences of the United States of America*, *118*, e2102625118. https://doi.org/10.1073/pnas.2102625118/-/DCSupplemental

Clement, R. A., Flores-Moreno, H., Cernusak, L. A., Cheesman, A. W., Yatsko, A. R., Allison, S. D., Eggleton, P., & Zanne, A. E. (2021). Assessing the Australian termite diversity anomaly: How habitat and rainfall affect termite assemblages. *Frontiers in Ecology and Evolution*, *9*, 657444. https://doi.org/10.3389/fevo.2021.657444

Constantino, R. (2018). Estimating global termite species richness using extrapolation. *Sociobiology*, *65*(1), 10–14. https://doi.org/10.13102/sociobiology.v65i1.1845

Covey, K. R., & Megonigal, J. P. (2019). Methane production and emissions in trees and forests. *New Phytologist*, *222*(1), 35–51. https://doi.org/10.1111/nph.15624

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

Davies, A. B., Baldeck, C. A., & Asner, G. P. (2016). Termite mounds alter the spatial distribution of African savanna tree species. *Source: Journal of Biogeography*, *43*(2), 301–313. https://doi.org/10.1111/jbl.12633

Davies, A. B., Levick, S. R., Asner, G. P., Robertson, M. P., Van Rensburg, B. J., & Parr, C. L. (2014). Spatial variability and abiotic determinants of termite mounds throughout a savanna catchment. *Ecography*, *37*(9), 852–862. https://doi.org/10.2307/ecography.37.9.852

Davies, A. B., Parr, C. L., & Eggleton, P. (2021). A global review of termite sampling methods. *Insectes Sociaux*, *68*(1), 3–14. https://doi.org/10.1007/s00040-020-00797-y

Dawes-Gromadzki, T. Z. (2008). Abundance and diversity of termites in a savanna woodland reserve in tropical Australia. *Australian Journal of Entomology*, *47*(4), 307–314. https://doi.org/10.1111/j.1440-6055.2008.00662.x

D'hont, B., Calders, K., Bartholomeus, H., Whiteside, T., Bartolo, R., Levick, S., Moorthy, S. M. K., Terryn, L., & Verbeeck, H. (2021). Characterising termite mounds in a tropical savanna with UAV laser scanning. *Remote Sensing*, *13*(3), 1–19. https://doi.org/10.3390/rs13030476

Donovan, S. E., Eggleton, P., Dubbin, W. E., Batchelder, M., & Dibog, L. (2001). The effect of a soil-feeding termite , *Cubitermes fungifaber* (lsoptera: Termitidae) on soil properties: termites may be an important source of soil microhabitat heterogeneity in tropical forests. *Pedobiologia*, *45*, 1–11. http://www.urbanfischer.de/journals/pedoPedobi0l0gia

Eggleton, P., Bignell, D. E., Sands, W. A., Mawdsley, N. A., Lawton, J. H., Wood, T. G., & Bignell, N. C. (1996). The diversity, abundance and biomass of termites under differing levels of disturbance in the Mbalmayo Forest Reserve, southern Cameroon. *Philosophical Transactions of The Royal Society Biological Sciences*, *351*, 51–68. https://doi.org/10.1098/rstb.1996.0004

Erland, B. M., Thorpe, A. K., & Gamon, J. A. (2022). Recent advances toward transparent methane emissions monitoring: A review. *Environmental Science and Technology*, *56*(23), 16567–16581. https://doi.org/10.1021/acs.est.2c02136

Fagundes, T. M., Ordonez, J. C., & Yaghoobian, N. (2021). The role of mound functions and local environment in the diversity of termite mound structures. *Journal of Theoretical Biology*, *527*. https://doi.org/10.1016/j.jtbi.2021.110823

Flores-Moreno, H., Law, S. J., Yatsko, A. R., Cheesman, A. W., Allison, S. D., Cernusak, L. A., Clement, R. A., Eggleton, P., Rosenfield, M., & Zanne, A. E. (2024). Wood Termite and Fungi (WTF): Termite and CWD emissions data (v0.0.0). In *[Data set]. Zenodo.* https://doi.org/10.5281/zenodo.11089744

Flores-Moreno, H., Yatsko, A. R., Cheesman, A. W., Allison, S. D., Cernusak, L. A., Cheney, R., Clement, R. A., Cooper, W., Eggleton, P., Jensen, R., Rosenfield, M., & Zanne, A. E. (2023). Shifts in internal stem damage along a tropical precipitation gradient and implications for forest biomass estimation. *New Phytologist*. https://doi.org/10.1111/nph.19417

Fraser, P. J., Rasmussen, R. A., Creffield, J. W., French, J. R., & Khalil, M. A. K. (1986). Termites and global methane-another assessment. *Journal of Atmospheric Chemistry*, *4*, 295–310.

Griffiths, H. M., Ashton, L. A., Evans, T. A., Parr, C. L., & Eggleton, P. (2019). Termites can decompose more than half of deadwood in tropical rainforest. *Current Biology*, *29*(4), R118–R119. https://doi.org/10.1016/j.cub.2019.01.012

Harit, A., Moger, H., Duprey, J. L., Gajalakshmi, S., Abbasi, S. A., Subramanian, S., & Jouquet, P. (2017). Termites can have greater influence on soil properties through the construction of soil sheetings than the production of above-ground mounds. *Insectes Sociaux*, *64*(2), 247–253. https://doi.org/10.1007/s00040-017-0541-3

Hartke, T. R., & Rosengaus, R. B. (2013). Costs of pleometrosis in a polygamous termite. *Proceedings of the Royal Society Biology*, *280*, 20122563. https://doi.org/10.1098/rspb.2012.2563

Hollenbeck, D., Zulevic, D., & Chen, Y. (2021). Advanced leak detection and quantification of methane emissions using sUAS. *Drones*, *5*(4). https://doi.org/10.3390/drones5040117

Inoue, T., Takematsu, Y., Hyodo, F., Sugimoto, A., Yamada, A., Klangkaew, C., Kirtibutr, N., & Abe, T. (2001). The abundance and biomass of subterranean termites (Isoptera) in a dry evergreen forest of northeast Thailand. *Sociobiology*, *37*(1), 41–52.

IPCC. (2021). *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (V. P. Masson-Delmotte, A. Zhai, S. L. Pirani, C. Connors, S. Pean, N. Berger, Y. Caud, L. Chen, M. I. Goldfarb, M. Gomis, R. Yelekci, O. Waterfield, T. Maycock, T. K. Matthews, J. B. R. Lonnoy, K. Huang, E. Leitzell, R. Yu, & B. Zhou, Eds.). Cambridge University Press. https://doi.org/10.1017/9781009157896

Ito, A. (2023). Global termite methane emissions have been affected by climate and land-use changes. *Scientific Reports*, *13*(1). https://doi.org/10.1038/s41598-023-44529-1

Jamali, H., Livesley, S. J., Dawes, T. Z., Cook, G. D., Hutley, L. B., & Arndt, S. K. (2011). Diurnal and seasonal variations in $CH_4$ flux from termite mounds in tropical savannas of the Northern Territory, Australia. *Agricultural and Forest Meteorology*, *151*(11), 1471–1479. https://doi.org/10.1016/j.agrformet.2010.06.009

Jamali, H., Livesley, S. J., Dawes, T. Z., Hutley, L. B., & Arndt, S. K. (2011). Termite mound emissions of $CH_4$ and $CO_2$ are primarily determined by seasonal changes in termite biomass and behaviour. *Oecologia*, *167*(2), 525–534. https://doi.org/10.1007/s00442-011-1991-3

Jamali, H., Livesley, S. J., Grover, S. P., Dawes, T. Z., Hutley, L. B., Cook, G. D., & Arndt, S. K. (2011). The importance of termites to the $CH_4$ balance of a tropical savanna woodland of northern Australia. *Ecosystems*, *14*(5), 698–709. https://doi.org/10.1007/S10021-01

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

Jeffrey, L. C., Maher, D. T., Chiri, E., Leung, P. M., Nauer, P. A., Arndt, S. K., Tait, D. R., Greening, C., & Johnston, S. G. (2021). Bark-dwelling methanotrophic bacteria decrease methane emissions from trees. *Nature Communications*, *12*(1). https://doi.org/10.1038/s41467-021-22333-7

Jones, D. T., Susilo, F. X., Bignell, D. E., Hardiwinoto, S., Gillison, A. N., & Eggleton, P. (2003). Termite assemblage collapse along a land-use intensification gradient in lowland central Sumatra, Indonesia. *Journal of Applied Ecology*, *40*(2), 380–391. https://doi.org/10.1046/j.1365-2664.2003.00794.x

Josens, G., & Soki, K. (2010). Relation between termite numbers and the size of their mounds. *Insectes Sociaux*, *57*, 303–316. https://doi.org/10.1007/s00040-010-0085-2

Khalil, M. A. K., Rasmussen, R. A., French, J. R. J., & Holt, J. A. (1990). The Influence of termites on atmospheric trace gases: CH4, CO2, CHC13, N20, CO, H2, and light hydrocarbons. *Journal of Geophysical Research*, *95*(D4), 3619–3634. https://doi.org/10.1029/JD095iD04p03619

King, G. M. (1997). Responses of atmospheric methane consumption by soils to global climate change. *Global Change Biology*, *3*(4), 351–362. https://doi.org/10.1046/j.1365-2486.1997.00090.x

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., Houweling, S., Josse, B., … Zeng, G. (2013). Three decades of global methane sources and sinks. *Nature Geoscience*, *6*(10), 813–823. https://doi.org/10.1038/ngeo1955

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

Korb, J. (2011). Termite mound architecture, from function to construction. In D. E. Bignell, Y. Roisin, & N. Lo (Eds.), *Biology of termites: A modern synthesis* (pp. 349–374). Springer.

Korb, J., & Linsenmair, K. E. (1998). Experimental heating of *Macrotermes bellicosus* (Isoptera, Macrotermitinae) mounds: what role does microclimate play in influencing mound architecture? *Insectes Sociaux*, *45*, 335–342. https://doi.org/10.1007/s000400050092

Kouakou, A. E., Dosso, K., Roisin, Y., Konate, S., & Kouassi, K. P. (2022). Soil-feeding termite diversity and abundance in a natural tropical humid forest (Tai National Park, Côte d'Ivoire). *Journal of Entomology and Zoology Studies*, *10*(1), 246–252. https://doi.org/10.22271/j.ento.2022.v10.i1c.8942

Kumar, S., Torres, C., Ulutan, O., Ayasse, A., Roberts, D., & Majunath, B. S. (2020). Deep remote sensing methods for methane detection in overhead hyperspectral imagery. *IEEE Winter*

*Conference on Applications of Computer Vision (WACV)*, 1765–1774. https://doi.org/10.1109/WACV45572.2020.9093600

Law, S., Flores-Moreno, H., Cheesman, A. W., Clement, R., Rosenfield, M., Yatsko, A., Cernusak, L. A., Dalling, J. W., Canam, T., Iqsaysa, I. A., Duan, E. S., Allison, S. D., Eggleton, P., & Zanne, A. E. (2023). Wood traits explain microbial but not termite-driven decay in Australian tropical rainforest and savanna. *Journal of Ecology*, *111*(5), 982–993. https://doi.org/10.1111/1365-2745.14090

Le Mer, J., & Roger, P. (2001). Production, oxidation, emission and consumption of methane by soils: A review. *European Journal of Soil Biology*, *37*, 25–50. https://doi.org/10.1016/S1164-5563(01)01067-6

Lee, C. C., & Lee C. Y. (2015). A Laboratory maintenance regime for a fungus-growing termite *Macrotermes gilvus* (Blattodea: Termitidae). *Journal of Economic Entomology*, *108*(3), 1243–1250. https://doi.org/10.1093/jee/tov112

Luke, S. H., Fayle, T. M., Eggleton, P., Turner, E. C., & Davies, R. G. (2014). Functional structure of ant and termite assemblages in old growth forest, logged forest and oil palm plantation in Malaysian Borneo. *Biodiversity and Conservation*, *23*(11), 2817–2832. https://doi.org/10.1007/s10531-014-0750-2

MacDonald, J. A., Eggleton, P., Bignell, D. E., Forzi, F., & Fowler, D. (1998). Methane emission by termites and oxidation by soils, across a forest disturbance gradient in the Mbalmayo Forest Reserve, Cameroon. *Global Change Biology*, *4*(4), 409–418. https://doi.org/10.1046/j.1365-2486.1998.00163.x

MacDonald, J. A., Jeeva, D., Eggleton, P., Davies, R., Bignell. D. E., Fowler, D., Lawton, J., & Maryati, M. (1999). The effect of termite biomass and anthropogenic disturbance on the $CH_4$ budgets of tropical forests in Cameroon and Borneo. *Global Change Biology*, *5*, 869–879. https://doi.org/10.1046/j.1365-2486.1999.00279.x

Martin, S. J., Funch, R. R., Hanson, P. R., & Yoo, E. H. (2018). A vast 4,000-year-old spatial pattern of termite mounds. *Current Biology*, *28*(22), R1292–R1293. https://doi.org/10.1016/j.cub.2018.09.061

Martius, C., Wassmann, R., Thein, U., Bandeira, A., Rennenberg, H., Junk, W., & Seiler, W. (1993). Methane emission from wood-feeding termites in Amazonia. *Chemosphere*, *26*(4), 623–632. https://doi.org/10.1016/0045-6535(93)90448-E

Meyer, V. W., Crewe, R. M., Braack, L. E. O., Groeneveld, H. T., & Van Der Linde, M. J. (2001). Biomass of *Macrotermes natalensis* in the northern Kruger National Park, South Africa-the Effects of land characteristics. *Sociobiology*, *38*, 431–448.

Muhammad, A., Ayu, F., Saputra, A., Yus, Y., Purnasari, T., & Salbiah, D. (2012). Subterranean termite fauna on a peatland: A preliminary assessment of the species diversity and biomass under different land use types. *Proceeding Seminar Bersama UR-UKM Ke-7, (Pekanbaru, Indonesia)*, 70–72.

Nauer, P. A., Chiri, E., De Souza, D., Hutley, L. B., & Arndt, S. K. (2018). Technical note: Rapid image-based field methods improve the quantification of termite mound structures and greenhouse-gas fluxes. *Biogeosciences*, *15*(12), 3731–3742. https://doi.org/10.5194/bg-15-3731-2018

Nauer, P. A., Hutley, L. B., & Arndt, S. K. (2018). Termite mounds mitigate half of termite methane emissions. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(52), 13306–13311. https://doi.org/10.1073/pnas.1809790115

Nauer, P. A., & Schroth, M. H. (2010). In situ quantification of atmospheric methane oxidation in near-surface soils. *Vadose Zone Journal*, *9*(4), 1052–1062. https://doi.org/10.2136/vzj2009.0192

Neupane, A., Maynard, D. S., & Bradford, M. A. (2015). Consistent effects of eastern subterranean termites (*Reticulitermes flavipes*) on properties of a temperate forest soil. *Soil Biology and Biochemistry*, *91*, 84–91. https://doi.org/10.1016/j.soilbio.2015.08.025

Nisbet, E. G., Manning, M. R., Dlugokencky, E. J., Fisher, R. E., Lowry, D., Michel, S. E., Myhre, C. L., Platt, S. M., Allen, G., Bousquet, P., Brownlow, R., Cain, M., France, J. L., Hermansen, O., Hossaini, R., Jones, A. E., Levin, I., Manning, A. C., Myhre, G., … White, J. W. C. (2019). Very strong atmospheric methane growth in the 4 Years 2014–2017: Implications for the Paris agreement. *Global Biogeochemical Cycles*, *33*(3), 318–342. https://doi.org/10.1029/2018GB006009

Räsänen, M., Vesala, R., Rönnholm, P., Arppe, L., Manninen, P., Jylhä, M., Rikkinen, J., Pellikka, P., & Rinne, J. (2023). Carbon dioxide and methane fluxes from mounds of African fungus-growing termites. *Biogeosciences*, *20*(19), 4029–4042. https://doi.org/10.5194/bg-20-4029-2023

Rasmussen, R. A., & Khalil, M. A. K. (1983). Global production of methane by termites. *Nature*, *301*, 700–702. https://doi.org/10.1038/301700a0

Rosenberg, Y., Bar-On, Y. M., Fromm, A., Ostikar, M., Shoshany, A., Giz, O., & Milo, R. (2023). The global biomass and number of terrestrial arthropods. *Science Advances*, *9*, eabq4049. https://doi.org/10.1126/sciadv.abq4049

Saputra, A., Muhammad Nasir, D., Jalaludin, N. A., Halim, M., Bakri, A., Mohammad Esa, M. F., Riza Hazmi, I., & Rahim, F. (2018). Composition of termites in three different soil types across oil palm agroecosystem regions in Riau (Indonesia) and Johor (Peninsular Malaysia). *Journal of Oil Palm Research*, *30*, 559–569. https://doi.org/10.21894/jopr.2018.0054

Saunois, M., R. Stavert, A., Poulter, B., Bousquet, P., G. Canadell, J., B. Jackson, R., A. Raymond, P., J. Dlugokencky, E., Houweling, S., K. Patra, P., Ciais, P., K. Arora, V., Bastviken, D., Bergamaschi, P., R. Blake, D., Brailsford, G., Bruhwiler, L., M. Carlson, K., Carrol, M., … Zhuang, Q. (2020). The global methane budget 2000-2017. *Earth System Science Data*, *12*(3), 1561–1623. https://doi.org/10.5194/essd-12-1561-2020

Schmidt, A. M., Jacklyn, P., & Korb, J. (2014). “Magnetic” termite mounds: Is their unique shape an adaptation to facilitate gas exchange and improve food storage? *Insectes Sociaux*, *61*(1), 41–49. https://doi.org/10.1007/s00040-013-0322-6

Seibold, S., Rammer, W., Hothorn, T., Seidl, R., Ulyshen, M. D., Lorz, J., Cadotte, M. W., Lindenmayer, D. B., Adhikari, Y. P., Aragón, R., Bae, S., Baldrian, P., Barimani Varandi, H., Barlow, J., Bässler, C., Beauchêne, J., Berenguer, E., Bergamin, R. S., Birkemoe, T., … Müller, J. (2021). The contribution of insects to global forest deadwood decomposition. *Nature*, *597*(7874), 77–81. https://doi.org/10.1038/s41586-021-03740-8

Seiler, W., Conrad, R., & Scharffe, D. (1984). Field studies of methane emission from termite nests into the atmosphere and measurements of methane uptake by tropical soils. *Journal of Atmospheric Chemistry*, *1*, 171–186. https://doi.org/10.1007/BF00053839

Shaw, J. T., Shah, A., Yong, H., & Allen, G. (2020). Methods for quantifying methane emissions using unmanned aerial vehicles: a review. *Philosophical Transactions of the Royal Society A*, *379*, 20200450. https://doi.org/10.1098/sta.2020.0450

Singh, K., Muljadi, B. P., Raeini, A. Q., Jost, C., Vandeginste, V., Blunt, M. J., Theraulaz, G., & Degond, P. (2019). The architectural design of smart ventilation and drainage systems in termite nests. *Science Advances*, *5*, eaat8520. https://doi.org/10.1126/sciadv.aat8520

Skeie, R. B., Hodnebrog, Ø., & Myhre, G. (2023). Trends in atmospheric methane concentrations since 1990 were driven and modified by anthropogenic emissions. *Communications Earth and Environment*, *4*(1). https://doi.org/10.1038/s43247-023-00969-1

Stavert, A. R., Saunois, M., Canadell, J. G., Poulter, B., Jackson, R. B., Regnier, P., Lauerwald, R., Raymond, P. A., Allen, G. H., Patra, P. K., Bergamaschi, P., Bousquet, P., Chandra, N., Ciais, P., Gustafson, A., Ishizawa, M., Ito, A., Kleinen, T., Maksyutov, S., … Zhuang, Q. (2022). Regional trends and drivers of the global methane budget. *Global Change Biology*, *28*(1), 182–200. https://doi.org/10.1111/gcb.15901

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

Thompson, D. R., Leifer, I., Bovensmann, H., Eastwood, M., Fladeland, M., Frankenberg, C., Gerilowski, K., Green, R. O., Kratwurst, S., Krings, T., Luna, B., & Thorpe, A. K. (2015). Real-time remote detection and measurement for airborne imaging spectroscopy: A case study with methane. *Atmospheric Measurement Techniques*, *8*(10), 4383–4397. https://doi.org/10.5194/amt-8-4383-2015

Urmann, K., Gonzalez-Gil, G., Schroth, M. H., & Zeyer, J. (2007). Quantification of Microbial Methane Oxidation in an Alpine Peat Bog. *Vadose Zone Journal*, *6*(4), 705–712. https://doi.org/10.2136/vzj2006.0185

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

Vasconcellos, A. (2010). Biomass and abundance of termites in three remnant areas of Atlantic Forest in northeastern Brazil. *Revista Brasileira de Entomologia*, *53*(3), 455–461. https://doi.org/10.1590/S0085-56262010000300017

Veldhuis, M. P., Laso, F. J., Olff, H., & Berg, M. P. (2017). Termites promote resistance of decomposition to spatiotemporal variability in rainfall. *Ecology*, *98*(2), 467–477. https://doi.org/10.1002/ecy.1658

Walker, A. E. L., Robertson, M. P., Eggleton, P., Bunney, K., Lamb, C., Fisher, A. M., & Parr, C. L. (2022). Indirect control of decomposition by an invertebrate predator. *Functional Ecology*, *36*(12), 2943–2954. https://doi.org/10.1111/1365-2435.14198

Werner, P. A., & Prior, L. D. (2007). Tree-piping termites and growth and survival of host trees in savanna woodland of north Australia. *Journal of Tropical Ecology*, *23*(6), 611–622. https://doi.org/10.1017/S0266467407004476

Wijas, B. J., Flores-Moreno, H., Allison, S. D., Chavez Rodriguez, L., Cheesman, A. W., Cernusak, L. A., Clement, R., Cornwell, W. K., Duan, E. S., Eggleton, P., Rosenfield, M. V., Yatsko, A. R., & Zanne, A. E. (2024). Drivers of wood decay in tropical ecosystems: Termites versus microbes along spatial, temporal and experimental precipitation gradients. *Functional Ecology*, *38*, 546–559. https://doi.org/doi: 10.1111/1365-2435.14494

Wijas, B. J., Lim, S., & Cornwell, W. K. (2022). Continental-scale shifts in termite diversity and nesting and feeding strategies. *Ecography*, *2022*(1). https://doi.org/10.1111/ecog.05902

Xu, X., Zeng, Q., Li, D., Wu, J., Wu, X., & Shen, J. (2010). GPR detection of several common subsurface voids inside dikes and dams. *Engineering Geology*, *111*(1–4), 31–42. https://doi.org/10.1016/j.enggeo.2009.12.001

Yamada, A., Inoue, T., Sugimoto, A., Takematsu, Y., Kumai, T., Hyodo, F., Fujita, A., Tayasu, I., Klangkaew, C., Kirtibutr, N., Kudo, T., & Abe, T. (2003). Abundance and biomass of termites (Insecta: Isoptera) in dead wood in a dry evergreen forest in Thailand. *Sociobiology*, *42*(3), 569–585.

Yang, X., Henderson, G., Mao, L., & Evans, A. (2009). Application of ground penetrating radar in detecting the hazards and risks of termites and ants in soil levees. *Environmental Entomology*, *38*(4), 1241–1249. https://doi.org/10.1603/022.038.0435

Yatsko, A. R., Wijas, B., Calvert, J., Cheesman, A. W., Cook, K., Eggleton, P., Gambold, I., Jones, C., Russell-Smith, P., & Zanne, A. E. (2024). Why are trees hollow? Termites, microbes, and tree internal stem damage in a tropical savanna. *PREPRINT (Version 1) Available at EcoEvoRxiv*. https://doi.org/doi.org/10.32942/X2WG75

Zanne, A. E., Flores-Moreno, H., Powell, J. R., Cornwell, W. K., Dalling, J. W., Austin, A. T., Classen, A. T., Eggleton, P., Okada, K., Parr, C. L., Carol Adair, E., Adu-Bredu, S., Azharul Alam, M., Alvarez-Garzón, C., Apgaua, D., Aragón, R., Ardon, M., Arndt, S. K., Ashton, L. A., … Zalamea, P.-C. (2022). Termite sensitivity to temperature affects global wood decay rates. *Science*, *377*, 1440–1444. https://doi.org/10.1126/science.abo3856

Zhou, Y., Staver, A. C., & Davies, A. B. (2023). Species-level termite methane production rates. *Ecology*, *104*(2). https://doi.org/10.1002/ecy.3905

Zimmerman, P. R., Greenberg, J. P., Wandiga, S. O., & Crutzen, P. J. (1982). Termites: A potentially large source of atmospheric methane, carbon dioxide, and molecular hydrogen. *Science*, *218*(4572), 563–565. https://doi.org/10.1126/science.218.4572.563

Figure Legends

Figure 1: Schematics illustrating termite contribution to the methane budget. Panel (a) depicts aspects of termite ecology to consider when estimating termite methane flux at the ecosystem scale. Box borders signify the certainty of each parameter: dotted border indicates no certainty (i.e., no available data), dot-dash border indicates low certainty (i.e., data available from < 5 studies), and dashed border indicates fair certainty (i.e., estimates ≥ 2 ecosystems and ≥ 5 studies). Parameter ID (corresponding to those in Table 1) are given in italics. Four main pathways of termite-related methane emissions are colour coded (mounds in blue, fallen deadwood in brown, living stems in green and soil in red). Panel (b) indicates probable differences in the distribution of termite biomass and net methane flux between ecosystems and among key termite sources (EM: Epigeal mounds; SN: Subterranean nests; F: Foragers; DW: Dead wood; LS: Living stems; and AN: Arboreal nests). Data are absent for most sources. For tropical forests, termite biomass data were taken from Vasconcellos, (2010) (Atlantic-forest, Brazil) and Yamada et al., (2003) (dry evergreen forest, Thailand) and for savanna, occurrence data by nesting substrate were taken from Dawes-Gromadzki, (2008) (savanna, Australia) to represent distribution of termite biomass. Ecosystems are likely to vary within and between regions. Mean net methane flux for mounds and soils for tropical forest were taken from MacDonald et al., (1998, 1999) (premontane tropical forest, Cameroon and tropical rainforest, Malaysia); and van Asperen et al., (2021) (tropical rainforest, Brazil), and for savanna from Jamali et al., (2013) and Jamali, Livesley, Grover, et al., (2011) (savanna, Australian); see Table S4.4. $^{*}$ Includes damp-wood and dry-wood termites.

Figure 2. Geographic distribution of termite methane studies. Dots represent location given in termite methane studies (either origin of termite sampled or of termite mound), scaled in size by the number of studies at each location. Some studies measured methane emissions across more than one location. Panel (a) shows 25 locations identified across 20 studies measuring termite methane emissions at the individual level (5 additional studies did not provide location information) (Flores-Moreno et al., 2024; Zhou et al., 2023). Panel (b) indicates 11 locations identified across 15 studies on termite mound emissions (including 1 unpublished, Yatsko, A., personal communication) (Flores-Moreno et al., 2024). Existing data are most limited for South America where estimated termite contribution to the methane budget is highest, alongside Africa (Ito, 2023; Kirschke et al., 2013), largely because upscaled estimates use termite biomass densities derived from ecosystem GPP, which is greatest in these regions.

Table 1: Parameters needed from different ecosystems to estimate global termite emissions. Parameter ID (P.ID) and description is included with example values from existing literature where possible. If no data are available for given units, data for alternative units are shown in italics. Biomass of termites is in fresh weight. A qualitative assessment of certainty is given using the following arbitrary classification system: (e.g. Very low: estimates from a single ecosystem or study; Low: estimates from ≥ 2 ecosystems and < 5 studies; Fair: estimates ≥ 2 ecosystems and ≥ 5 studies). For each P.ID the paucity in data can be addressed by focusing on specific research objectives (1 -7) described in section 4.

| **P.ID** | **Description** | **Range** | **Units *(alternative)*** | **Certainty** | **Ref.** | **Research objective** |
|---|---|---|---|---|---|---|
| $F_{md}$ | Emissions from termites in mounds** | 0.1 – 3.02 | kg $CH_4$ $ha^{-1}$ $y^{-1}$ | Fair | c | 1, 2, 7 |
| $F_{dw}$ | Emissions from termites in fallen deadwood | 0.01 – 0.13 | kg $CH_4$ $ha^{-1}$ $y^{-1}$ | Very low | Table S2.5 | 2, 3, 7 |
| $F_{ls}$ | Emissions from termites in living stems | NA | kg $CH_4$ $ha^{-1}$ $y^{1}$ | None | NA | 2, 3, 7 |
| $F_{sn}$ | Emissions from termites in soils (subterranean nests)* | NA<br>*0 - 123* | kg $CH_4$ $ha^{-1}$ $y^{-1}$<br>*$\mu g\ CH_4\ Nest^{-1} h^{-1}$* | NA<br>*Very low* | NA<br>a, b | 2, 7 |
| $G_{md}$ | Gross emissions from termites in mounds (before methane oxidation) | NA<br>*2.0 – 105* | kg $CH_4$ $ha^{-1}$ $y^{-1}$<br>*$\mu g\ CH_4\ kg^{-1}{}_{(mound)}\ y^{-1}$* | None<br>*Very low* | NA<br>*d* | 1, 2, 7 |
| $G_{dw}$ | Gross emissions from termites in fallen deadwood | NA | kg $CH_4$ $ha^{-1}$ $y^{-1}$ | None | NA | 2, 3, 7 |
| $G_{ls}$ | Gross emissions from termites in living stems | NA | kg $CH_4$ $ha^{-1}$ $y^{-1}$ | None | NA | 2, 3, 7 |
| $G_{sn}$ | Gross emissions from termites in soils | NA | kg $CH_4$ $ha^{-1}$ $y^{-1}$ | None | NA | 2, 7 |
| $O_{md}$ | Oxidation by methanotrophs in mounds | NA<br>*1.1 – 62* | kg $CH_4$ $ha^{-1}$ $y^{-1}$<br>*$\mu g\ CH_4\ kg^{-1}{}_{(mound)}\ y^{-1}$* | None<br>*Very low* | NA<br>*d* | 4, 7 |
| $O_{dw}$ | Oxidation by methanotrophs in fallen deadwood | NA | kg $CH_4$ $ha^{-1}$ $y^{-1}$ | None | NA | 4, 7 |
| $O_{ls}$ | Oxidation by methanotrophs in living stems | NA | kg $CH_4$ $ha^{-1}$ $y^{-1}$ | None | NA | 4, 7 |
| $O_{sn}$ | Oxidation by methanotrophs in soil | NA<br>*4 - 299* | kg $CH_4$ $ha^{-1}$ $y^{-1}$<br>*$\mu g\ CH_4\ kg^{-1}{}_{(soil)}\ y^{-1}$* | None<br>*Low* | NA<br>e, f | 4, 7 |
| $BD_{md}$ | Biomass density of termites in mounds | 346 – 5841 | $g_{(termite)}m^{-2}$ | Low | n | 5, 7 |
| $BD_{dw}$ | Biomass density of termites in fallen deadwood | 1.3 – 3.53 | $g_{(termite)}m^{-2}$ | Low | g, i | 5, 7 |
| $BD_{ls}$ | Biomass density of termites in living stems | NA | $g_{(termite)}m^{-2}$ | None | NA | 5, 7 |
| $BD_{sn}$ | Biomass density of termites in soils | 0.97 – 9.35 | $g_{(termite)}m^{-2}$ | Low | g, h, i, j | 5, 7 |

| | | | | | | |
|---|---|---|---|---|---|---|
| $C_{tb}$ | Methane emissions per termite biomass | 0 – 25.26 | $\mu g\ CH_4\ g^{-1}_{(termite)}h^{-1}$ | Fair | k | 1 |
| $D_{md}$ | Termite mound areal density | 4 - 215 | mound $ha^{-1}$ | Fair | l, m, n, o, p, | 6 |
| $B_{md}$ | Termite biomass per mound | 8 - 4160 | $g_{(termite)}mound^{-1}$ | Low | o, q, r | 5, 6 |
| $D_{dw}$ | Fallen deadwood areal density | 1.05 – 100.4 | $Mg_{(wood)}ha^{-1}$ | Low | s, t | 6 |
| $B_{dw}$ | Termite biomass per mass fallen deadwood | NA | $g_{(termite)}Mg^{-1}_{(deadwood)}$ | None | NA | 6 |
| $D_{ls}$ | Living stem areal density | 40 - 320 | $Mg_{(wood)}ha^{-1}$ | Very low | u | 6 |
| $B_{ls}$ | Termite biomass per mass living stems | NA | $g_{(termite)}Mg^{-1}_{(living\ wood)}$ | None | NA | 6 |
| $D_{sn}$ | Subterranean nests areal density | NA | nests $ha^{-1}$ | None | NA | 6 |
| $A_i$ | Geographic range of termite species $i^{***}$ | NA | $km^2$ | None | NA | 5 |

*Number of subterranean nests per hectare is unreported. **More common estimates from mounds are given in $\mu g\ CH_4\ mound^{-1}_{(mound)}\ h^{-1}$ or $\mu g\ CH_4\ m^{-2}_{(mound)}\ h^{-1}$ (see S3). ***Upscaled estimates use geographic range of an ecosystem rather than of termites. a: Seiler et al., 1984; b: Sugimoto et al., 1998; c: Jamali et al., 2013; d: Nauer, Hutley, et al., 2018; e: Nauer & Schroth, 2010; f: Urmann et al., 2007; g: Yamada et al., 2003; h: Inoue et al., 2001; i: Vasconcellos, 2010; j: Abensperg-Traun & de Boer, 1990; k: Zhou et al., 2023; l: Jamali, Livesley, Grover, Dawes, et al., 2011; m: Brümmer et al., 2009; n: MacDonald et al., 1998; o: MacDonald et al., 1999; p: van Asperen et al., 2021; q: Martius et al., 1993; r: Meyer et al., 2001; s: Cheesman et al., 2018; t: Clement et al., 2021; u: Flores-Moreno et al., 2023.

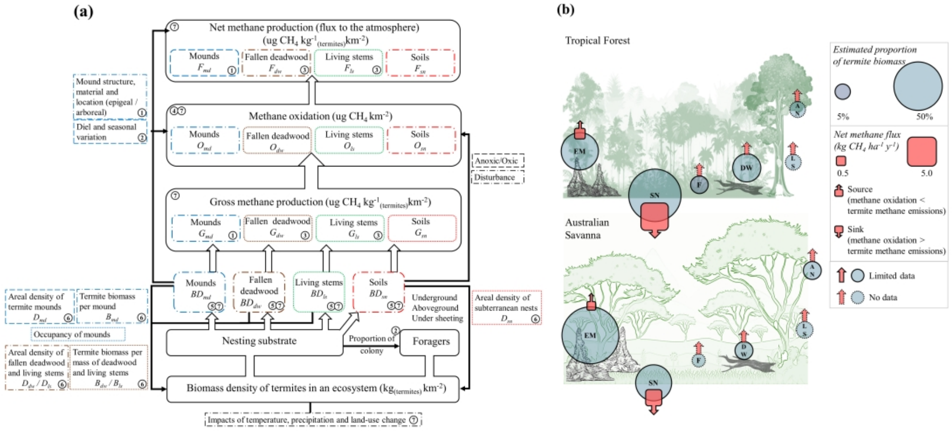
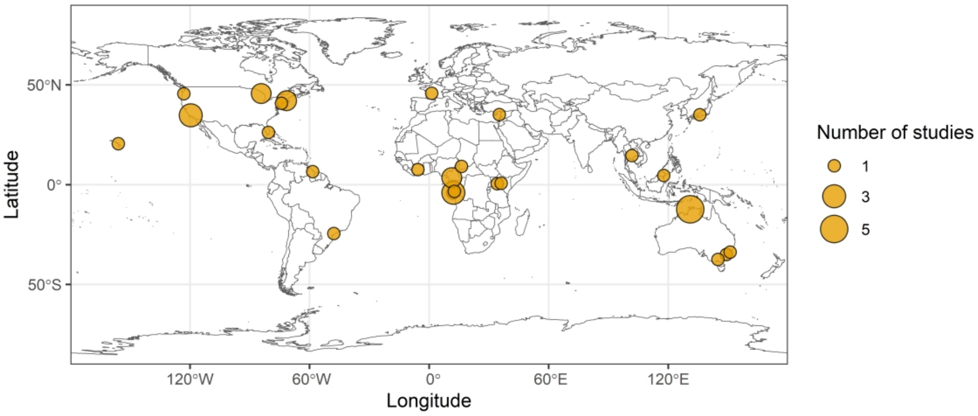


Figure 1: Schematics illustrating termite contribution to the methane budget. Panel (a) depicts aspects of termite ecology to consider when estimating termite methane flux at the ecosystem scale. Box borders signify the certainty of each parameter: dotted border indicates no certainty (i.e., no available data), dot-dash border indicates low certainty (i.e., data available from < 5 studies), and dashed border indicates fair certainty (i.e., estimates ≥ 2 ecosystems and ≥ 5 studies). Parameter ID (corresponding to those in Table 1) are given in italics. Four main pathways of termite-related methane emissions are colour coded (mounds in blue, fallen deadwood in brown, living stems in green and soil in red). Panel (b) indicates probable differences in the distribution of termite biomass and net methane flux between ecosystems and among key termite sources (EM: Epigeal mounds; SN: Subterranean nests; F: Foragers; DW: Dead wood; LS: Living stems; and AN: Arboreal nests). Data are absent for most sources. For tropical forests, termite biomass data were taken from Vasconcellos, (2010) (Atlantic-forest, Brazil) and Yamada et al., (2003) (dry evergreen forest, Thailand) and for savanna, occurrence data by nesting substrate were taken from Dawes-Gromadzki, (2008) (savanna, Australia) to represent distribution of termite biomass. Ecosystems are likely to vary within and between regions. Mean net methane flux for mounds and soils for tropical forest were taken from MacDonald et al., (1998, 1999) (premontane tropical forest, Cameroon and tropical rainforest, Malaysia); and van Asperen et al., (2021) (tropical rainforest, Brazil), and for savanna from Jamali et al., (2013) and Jamali, Livesley, Grover, et al., (2011) (savanna, Australian); see Table S4.4. * Includes damp-wood and dry-wood termites.

1740x801mm (130 x 130 DPI)

**(a)** Emissions from individual termites



**(b)** Emissions from termite mounds

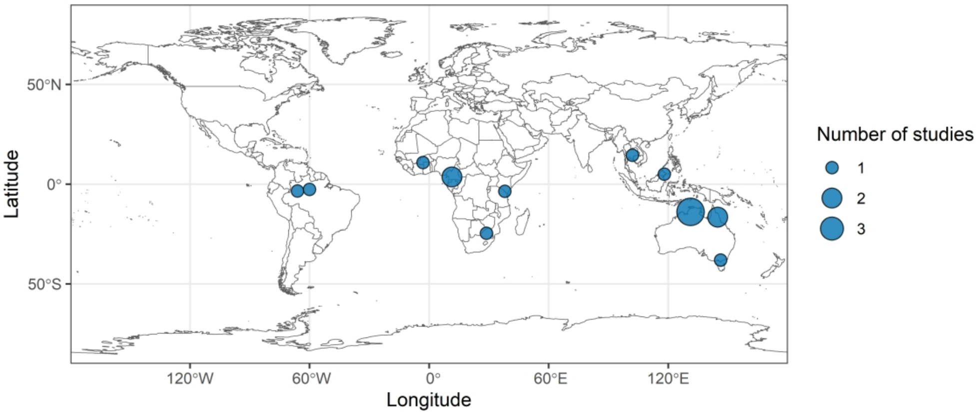


Figure 2. Geographic distribution of termite methane studies. Dots represent location given in termite methane studies (either origin of termite sampled or of termite mound), scaled in size by the number of studies at each location. Some studies measured methane emissions across more than one location. Panel (a) shows 25 locations identified across 20 studies measuring termite methane emissions at the individual level (5 additional studies did not provide location information) (Flores-Moreno et al., 2024; Zhou et al., 2023). Panel (b) indicates 11 locations identified across 15 studies on termite mound emissions (including 1 unpublished, Yatsko, A., personal communication) (Flores-Moreno et al., 2024). Existing data are most limited for South America where estimated termite contribution to the methane budget is highest, alongside Africa (Ito, 2023; Kirschke et al., 2013), largely because upscaled estimates use termite biomass densities derived from ecosystem GPP, which is greatest in these regions.

507x507mm (300 x 300 DPI)