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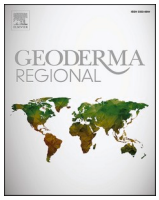

# The temperature dependence of greenhouse gas production from Central African savannah soils

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ABSTRACT

Savannahs cover 20 % of the global land surface, but there have been few studies of greenhouse gas (GHG) dynamics from savannah soils. Here, we assess potential turnover of carbon dioxide ($CO_2$), methane ($CH_4$) and nitrous oxide ($N_2O$) from surface (0–10 cm) and subsurface (20–30 cm) soils from two contrasting tropical savannah sites in the Republic of Congo, Central Africa, under dry (40 % water-filled-pore-space, WFPS) and wet (70 % WFPS) conditions. Under baseline conditions (25 °C), we found soils were sources of $CO_2$ and $N_2O$, but a sink for $CH_4$. Assessment of the temperature response of GHG fluxes between 20 and 35 °C revealed variable temperature dependences. That is, $CO_2$ fluxes showed a strong temperature response, whereas the temperature response of $N_2O$ fluxes was only significant under dry conditions, and no significant temperature response of $CH_4$ fluxes was observed. The temperature quotient ($Q_{10}$) of soil respiration increased from 1.58 ± 0.004 to 1.92 ± 0.006 at sites with lower soil organic carbon contents. The relative increase in $N_2O$ with $CO_2$ fluxes across temperatures was significantly influenced by moisture conditions at both sites. No temperature or soil moisture response was observed for $CH_4$ fluxes, collectively implying divergent GHG responses to changing climatic conditions. Using Rock-Eval pyrolysis we assessed the organic chemistry of all soil types, which indicated contrasting degrees of stability of carbon sources between sites and with depth which, alongside significant differences in a range of other soil parameters (including organic matter content, total carbon, total nitrogen, electrical conductivity, and pH), may account for site-specific differences in baseline GHG emissions. Taken together, our results are amongst the first measures of GHG temperature sensitivity of tropical savannah soils, and demonstrate that soil $CO_2$ emissions are more sensitive to warming and changes in moisture than the emissions of other GHGs, although relatively low compared to responses reported for soils from other tropical ecosystems. This implies that GHG fluxes form savannah soils in the region may be at least partially resilient to climate-induced soil warming compared to other ecosystems.

## 1. Introduction

Savannah ecosystems cover approximately 20 % of the global land surface (Pennington et al., 2018), with tropical savannahs alone covering 27.6 million km$^2$ (Hutley and Setterfield, 2008). Savannahs are generally dominated by grass and small shrub species, have distinct wet and dry seasons (Pennington et al., 2018), and have frequent fire disturbance (Govender et al., 2006). In addition to removing living and

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dead aboveground biomass, fires can significantly affect soil properties (Amoako and Gambiza, 2019), which may in turn affect the rates of greenhouse gas (GHG) production.

Savannahs will undergo significant changes by 2100 due to a combination of warming, altered precipitation patterns, fire regimes, land use change, and agricultural intensification. Current estimates of air temperature changes across the tropics are of 3–4 °C warming by 2100 but potentially up to 6 °C for Central Africa, alongside alterations in precipitation (IPCC, 2021). These changes are likely to drive significant alterations in the rates of GHG production and net emissions, with the potential for significant feedback loops from land-atmosphere exchange.

Governing the response of soil respiration and decomposition rates are thermodynamic and kinetic relationships, as described by the Arrhenius and Michaelis-Menten equations, respectively. The Arrhenius equation (Eq. (1)), broadly predicts a substrate of low-quality will require higher amounts of energy to be degraded, and therefore its rate of decomposition is slower (Fierer et al., 2005; Lloyd and Taylor, 1994). As the net activation energy ($E_a$) required for decomposition ($R_T$) increases, the temperature dependence of decomposition should also increase as a result, leading to an inverse relationship between organic matter quality and temperature sensitivity (Gershenson et al., 2009).

$$ln(R_T) = Be^{-E_a/kT} \quad (1)$$

Where $R_T$ is the reaction rate at a specified temperature (T, in Kelvins), $B$ is a normalization constant independent of temperature and the Boltzmann- Arrhenius factor, $e^{-Ea/kT}$, describes the temperature-dependence of reaction rate, where $E_a$ is the activation energy (eV) and $k$ is Boltzmann's constant ($8.62 \times 10^{-5}$ eV $K^{-1}$) (Davidson and Janssens, 2006). While many previous studies support this, other studies have reported equivalent values for both thermally stable ("refractory") and labile pools or a lower temperature dependence for recalcitrant organic carbon (Fang et al., 2005; Fierer et al., 2005; Giardina and Ryan, 2000; Leifeld and Fuhrer, 2005). Underpinning the relationship between substrate availability and the temperature dependence of decomposition pathways is the Michaelis-Menten equation (Davidson and Janssens, 2006; Michaelis et al., 1913):

$$R = \frac{(V_{max}[C])}{(K_m + [C])} \quad (2)$$

Where R is the rate of soil respiration, $V_{max}$ is the maximum rate of enzyme activity, [C] is the concentration of available carbon, and $K_m$ is the dissociation constant. Both $V_{max}$ and $K_m$ are temperature dependent. When systems are not kinetically limited i.e. there is no substrate limitation, the temperature dependence of soil respiration reduces to that of $V_{max}$ but under substrate limiting conditions, the temperature dependence of $K_m$ becomes increasingly important, and the overall sensitivity of respiration decreases (Gershenson et al., 2009). Based solely on the carbon quality hypothesis, temperature dependence should increase with increasingly recalcitrant substrates, and decrease with depth due to reduced labile carbon availability.

Previous studies of the temperature dependency of GHG emissions from tropical soils are limited. Prevailing expectations are that the temperature dependency of GHG production is lower in the tropics than in cooler higher latitudes (Bekku et al., 2003). However, recent findings suggest the potential for substantial feedback in GHG emissions following warming in the tropics. Recent in situ warming of a Central American forest soil showed 4 °C of soil warming increased $CO_2$ emissions by 55 % (Nottingham et al., 2020).

A range of $Q_{10}$ values (which describes the relative change in soil respiration due to an increase in temperature of 10 °C and is used as a proxy to quantify the feedback intensity of soil respiration to increasing temperatures) have been reported for tropical soils. For example, studies in tropical peats, which feature a large labile carbon pool report $Q_{10}$ values of approximately 1.4–2 for $CO_2$ production, 1.4–6.8 for methanogenesis, and 2.7 for methanotrophy (Girkin et al., 2020a, 2020b; Sjögersten et al., 2018). $Q_{10}$ values for $CO_2$ emissions in tropical mineral soils range from 2.1 to 2.7 (Bekku et al., 2003), while equivalent $Q_{10}$ values for $CO_2$ production in savannah soils specifically, include 1.9 for a North Australian savannah soil (Chen et al., 2002), 2.1 in Senegalese savannahs, (Elberling et al., 2003), 4.9 from a woody Brazilian savannah (da Rocha et al., 2002), and up to 5.0 for a burnt Brazilian savannah soil (Poth et al., 1995). $Q_{10}$ values for $N_2O$ fluxes are much less frequently assessed, but include $Q_{10}$ values of 2.8–3.6 for a temperate forest (Bagherzadeh et al., 2008), and 0.8–1.2 for mountain forest and meadow ecosystems in subtropical China (Zhang et al., 2016).

In this study, we assess the temperature dependency of GHG emissions from two tropical savannah soils from the Central African basin under wet and dry moisture states. We subsequently assess the extent to which soil properties predict the temperature dependency of GHG dynamics. We hypothesised that i) Baseline soil GHG emissions would differ between savannah soil types with greater rates in soils with greater labile carbon stocks; and that ii) temperature dependency would differ between sites and surface and subsurface soils, with greater temperature dependency in soils with more recalcitrant carbon.

## 2. Methods

### 2.1. Study sites

This study was conducted using soils collected from two savannah sites in Likouala province, Republic of Congo. The soils were collected during a field campaign between January – March 2019. Soils were collected near the villages of Ekolongouma (1.204 N, 17.909E) and Itanga (1.2025 N 17.4345E) (Fig. 1).

The Ekolongouma village site is a seasonally flooded savannah adjacent to the Ubangi River, dominated by *Poaceae* sp. The site was adjacent to seasonally flooded forest where vegetation was predominantly confined to higher ground*Trichilia welwitschi*, *Cola* sp., *Strombo-slopsis tetrandra*, *Guibourtia demeusei* and *Dialium pachyphilum* (Dargie, 2015).

The Itanga village site bordered the Likouala-aux-Herbes River. Close to the river, the site comprised seasonally flooded savannah and was dominated by *Poaceae* sp. and featured a largely flat micro-topography. After approximately 250 m, the site transitioned to a dominance of *Hyparenia diplondra*. After approximately 750 m, the site transitions to a seasonally flooded forest with an increasing abundance of *Raphia hookeri* canopy palms (Dargie, 2015).

At each site, four paired replicate surface (0–10 cm) and sub-surface (20–30 cm) soil samples were collected, with sub-surface samples collected directly under surface samples. Due to logistical limitations arising from the remote nature of the sites and the need to carry all collected material, soils from 10 to 20 cm were excluded. All collected samples were transported to the University of Nottingham, UK for analysis, where they were stored at 4 °C. Samples were collected by hand, with surface litter removed first, before soils were placed in zip-lock bags. Samples were located up to 100 m apart and collected from the approximate centre of both savannah sites to reduce edge effects from contrasting vegetation inputs and local village activities.

### 2.2. Soil properties

Gravimetric water content was determined from the mass of water lost from 10 g wet weight soil oven dried at 105 °C for 24 h. Soil organic matter content was determined as the mass lost after ignition for 7 h at 550 °C. Total carbon and total nitrogen were measured using a LEICO total elemental analyser. Electrical conductivity and pH were measured in soils extracts at a 1:5 ratio with deionised water.

Soil sub-samples were analysed using a Rock-Eval 6 analyser. Freeze-dried powdered soil samples (60 mg) were heated at 300 °C for three minutes before an increase in temperature to 650 °C at a rate of 25 °C per minute in an inert $N_2$ atmosphere. Residual carbon was oxidized from

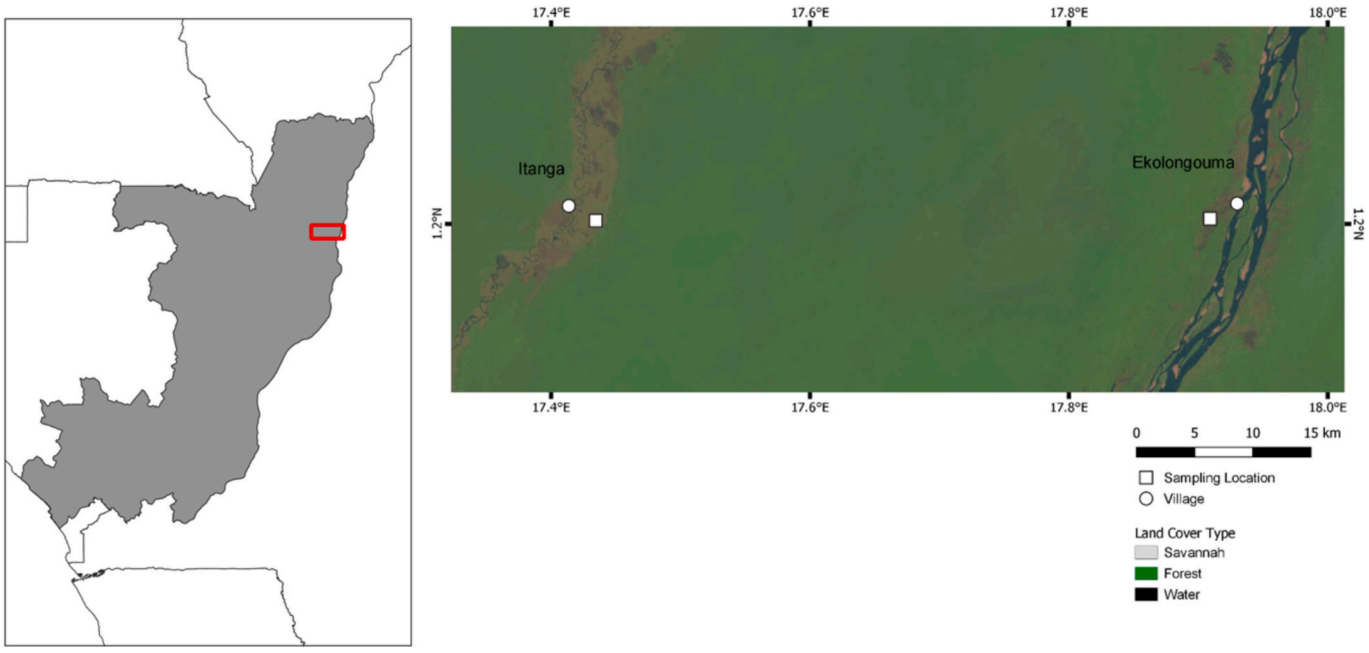


**Fig. 1.** Locations of Ekolongouma and Itanga savannah sites in the Republic of Congo.

300 °C to 850 °C at a rate of 20 °C per minute with the release of hydrocarbons during the two-stage pyrolysis process detected by a flame ionization detector, with an infrared cell detecting the release of CO and $CO_2$ during the thermal cracking of the organic matter.

Rock-Eval analysis produces a range of standard parameters including S1 (a measure of free hydrocarbons released on heating to 300 °C), S2 (hydrocarbons released on the thermal cracking of organic matter for temperatures up to 650 °C), S3CO and S3$CO_2$ (the CO and $CO_2$ yielded from the breakdown of kerogen), Tpk2 (the temperature associated with the highest yield of bound hydrocarbons) and total organic carbon ($TOC_{RE}$). The Hydrogen Index (HI, mg HC $g^{-1}$ $TOC_{RE6}$), a measure of hydrocarbons released relative to TOC was calculated as:

$$S2 \times 100/TOC_{RE} \quad (3)$$

The Oxygen Index (OI, mg $O_2$ $g^{-1}$ $TOC_{RE6}$), corresponding to the amount of oxygen released as $CO_2$ relative to $TOC_{RE}$ was calculated as:

$$S3 \times 100/TOC_{RE} \quad (4)$$

A set of indices, I (immature) and R (refractory), describing the preservation of thermally labile and highly thermostable organic matter respectively, were calculated using the approach proposed by Sebag et al. (2016) using the integrated areas under the S2 curve between given temperature nodes. Areas were calculated as 200–340 °C (A1, labile biopolymers), 340–400 °C (A2, resistant biopolymers), 400–460 °C (A3, immature geopolymers), and > 460 °C (A4, mature geopolymers). The I-index was calculated as log((A1 + A2)/A3) and the R-index was calculated as (A3 + A4)/100 and represents the contribution of mature organic matter to the S2 signal (Sebag et al., 2016). This set of indices has previously been applied to assessments of carbon thermostability in tropical forest peat soils (Cooper et al., 2019; Girkin et al., 2019; Girkin et al., 2020a, 2020b) but not tropical mineral savannah soils. Fresh and immature organic matter is characterised by a low R-index (i.e. low levels of refractory carbon), and a high I-index (increased labile carbon), with the inverse true for older more recalcitrant organic matter (Sebag et al., 2016).

### 2.3. Potential greenhouse gas emissions

Soil GHG emissions were measured across four temperatures (20, 25, 30 and 35 °C) and at two moisture states using an adapted approach previously described in Sjögersten et al. (2018), Girkin et al. (2020a, 2020b) and Dhandapani et al. (2020) developed for other tropical soils. In brief, soil samples (10 g dry weight equivalent of homogenised, sieved and repacked soil compacted to field bulk density (approximately 1.1 g $cm^{-3}$) were placed in 64 (2 sites × 2 depths × 4 replicates × 4 temperatures) glass serum bottles, each with a volume of 120 mL (Kinesis, St. Neots, UK). Soils were rewetted so all reached 20 % gravimetric moisture content, corresponding to approximately 40 % water-filled pore space (WFPS). These conditions represented the mean gravimetric moisture content of collected soil samples (Table 1). Soils were then maintained at this moisture content by regular weighing, with weights monitored daily during the sampling period. Gas sampling was carried out before rewetting of soil samples (Somers et al., 2019). Four replicates of each soil type were placed in 20–35 °C incubators for one month for acclimation prior to the first sampling event.

On each sampling day, bottles were removed from their incubators and placed on an orbital shaker for one hour to allow the exchange of headspace gases. Ten replicate air samples (20 mL) were collected from randomly selected unsealed bottles by syringe and injected at overpressure into pre-evacuated 12 mL glass silica gas vials (LABCO, UK). Bottles were then sealed with rubber butyl stoppers (13 × 19 × 12 mm; Rubber B.V., Hilversum, NL). Bottles were then returned to their incubators for 1 h after which a 20 mL gas sample was collected for analysis using a gas chromatograph (Shimadzu, 2014). $CO_2$, $CH_4$ and $N_2O$ concentrations of gas samples were measured using a single injection system with a 1 mL sample loop using $N_2$ as a carrier gas through a non-polar methyl silicone capillary column (CBP1-W12–100, 0.53 mm I. D., 12 m, 5 mm) and a porous polymer packed column (HayeSep Q 80/100). Thermal conductivity, flame ionization, and an electron capture detector were used to measure $CO_2$, $CH_4$ and $N_2O$, respectively (Girkin et al., 2020b).

After measuring fluxes at 20 % gravimetric moisture content on three occasions over four weeks, soils were further rewetted to 30 % gravimetric moisture, corresponding to approximately 70 % WFPS. Following rewetting, soils were left open to the atmosphere for one month (while being maintained at constant soil moisture content) before measurement of GHGs, to allow acclimation and to minimise any impact of the Birch effect (increased carbon and nitrogen mineralisation following

**Table 1**
Surface and subsurface soil biogeochemical properties for Ekolongouma and Itanga. Means ±1 SE ($n = 4$). * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

| | Ekolongouma | | Itanga | | Depth | Site | Depth*Site |
|---|---|---|---|---|---|---|---|
| | Surface | Subsurface | Surface | Subsurface | | | |
| Gravimetric moisture (%) | 28.7 ± 1.6 | 29.3 ± 0.7 | 79.9 ± 4.7 | 73.5 ± 1.9 | | *** | |
| Organic matter (%) | 16.3 ± 0.5 | 15.3 ± 0.5 | 52.8 ± 8.2 | 48.3 ± 9.8 | | *** | |
| pH | 4.1 ± 0.04 | 4.3 ± 0.1 | 3.1 ± 0.03 | 3.1 ± 0.02 | | *** | |
| Conductivity (μS) | 8.6 ± 0.6 | 7.8 ± 0.2 | 100.2 ± 17.5 | 75.4 ± 6.9 | | *** | |
| Total carbon (%) | 6.2 ± 0.5 | 5.2 ± 0.4 | 35.4 ± 1.0 | 33.5 ± 1.7 | | *** | |
| Total nitrogen (%) | 0.3 ± 0.02 | 0.3 ± 0.02 | 1.5 ± 0.1 | 1.3 ± 0.1 | * | *** | |
| TOC (%) | 5.3 ± 0.4 | 4.7 ± 0.4 | 23.2 ± 6.6 | 28.6 ± 2.3 | | *** | |
| HI (Hydrogen Index; mg HC $g^{-1}$ $TOC_{RE6}$) | 174 ± 10.2 | 155 ± 6.7 | 135.3 ± 20.2 | 125.5 ± 13.2 | | * | |
| OI (Oxygen Index; mg $O_2$ $g^{-1}$ $TOC_{RE6}$) | 232 ± 11.5 | 242.8 ± 12.1 | 152 ± 3.7 | 130.3 ± 3.6 | | *** | |
| I (Immature) Index | 0.3 ± 0.01 | 0.3 ± 0.03 | 0.2 ± 0.02 | 0.1 ± 0.03 | | * | *** |
| R (Refractory) Index | 0.6 ± 0.01 | 0.5 ± 0.02 | 0.6 ± 0.01 | 0.6 ± 0.02 | | | |

rewetting) on fluxes (Lopez-Sangil et al., 2018).

Fluxes were calculated using the concentration difference between the initial headspace concentrations compared to those measured after one-hour incubation, according to the ideal gas law (Girkin et al., 2018). These calculations also accounted for the volume of soil occupied by soil and water within the bottle. In total 375 greenhouse gas measurements were made during this study.

### 2.4. Data and statistical analysis

The temperature dependence of $CO_2$, $CH_4$ and $N_2O$ fluxes were first assessed by applying general linear models to flux measurements across the temperature range to solve the parameters in Eq. (1) (Johnston and Sibly, 2018). GHG fluxes were standardised prior to analyses in R v4.3.2 (R Core Team, 2023) to enable application of Eq. (1) to negative GHG flux measurements for $CH_4$ and $N_2O$, alongside $CO_2$ following: $\ln(R_T/\text{mean}(R_T))$. Arrhenius temperatures were similarly standardised followed: $1/kT_c - 1/kT$, where $T_c$ is the mean temperature (300.65 K: 27.5 °C).

First, all GHG flux measurements were analysed according to Eq. (1) to establish the temperature dependence and sensitivity across site, soil depth and moisture conditions. Relationships between GHG fluxes were also analysed, using one-way ANOVA and $p < 0.05$ to test their significance. For each GHG flux, we then explored whether temperature responses interacted significantly with additional predictors in the order: site, moisture, depth. For all models, a better goodness of fit to the GHG flux measurements depended on additional degrees of freedom (df) resulting in a difference in Akaike Information Criterion (ΔAIC) value >5 compared to the model with temperature as the only predictor. This condition ensures parsimony when additional predictor variables are selected (Johnston et al., 2021). Following regression analyses, we used $B$ and $E_a$ parameters for those sites and GHG fluxes that yielded significant Arrhenius temperature interactions ($p > 0.05$) to estimate $Q_{10}$ values. As $Q_{10}$ values are the proportional increase in non-logged GHG flux ($R$) with a 10 °C increase in temperature ($T + 10$), we calculated $R$ values between the observed temperature range of 20 and 35 °C ($T_{20–35}$) and estimated $Q_{10}$ as:

$$Q_{10} = R(T_{+10})/R(T_{20–35}) \quad (5)$$

We also tested relationships between non-standardised GHG fluxes and their interaction with predictor variables such as site, depth, moisture and temperature groupings. Differences between soil properties and GHG exchange between 0 and 35 °C were assessed using a mixed effects model fitted using Residual Maximum Likelihood (REML) to account for variable dependence. The model included sampling time point and soil replicates as random effects, and depth and site as fixed effects. Differences in baseline GHG fluxes (defined as the rate of emissions at ambient temperature (25 °C) under both moisture states were investigated using Tukey $t$-tests for pairwise comparisons between the two sites, depths and moisture conditions. Relationships between key environmental variables and mean GHG emissions were assessed using Principal Component Analysis (PCA), based on correlation matrices.

## 3. Results

### 3.1. Soil properties

A range of soil properties varied significantly between Ekolongouma and Itanga, but to a lesser extent between the surface and subsurface (Table 1). Soils from Ekolongouma had relatively low water content (approximately 29 %), with high organic matter content (15.2–16.3 %), acid pH (4.1–4.3), and low electrical conductivity (51.7–6.2 μS). Total carbon and nitrogen were in the range of 5.2–6.2 % and 0.3 %, respectively. In contrast, soils from Itanga had significantly greater gravimetric moisture (73.5–79.9 %), more acidic pH (3.1–3.1), higher electrical conductivity (75.4–100.2 μS), and total carbon and nitrogen (33.5–35.4 %, 1.3–1.5 % respectively). Ekolongouma soils had higher HI (hydrogen index) and OI (oxygen index) values, compared to soils from Itanga.

### 3.2. Baseline greenhouse gas emissions

Baseline $CO_2$ emissions ($CO_2$ emissions from dry and wet soils at 25 °C) ranged from 4 to 29 μg $CO_2$ $g^{-1}$ $h^{-1}$ across both sites and depths. $CO_2$ emissions were substantially higher from surface compared to subsurface soils from Itanga but was broadly comparable between Ekolongouma soils ($p = 0.046$, Fig. 2a).

Both sites were consistent sinks for $CH_4$ under both dry and wet conditions, indicating $CH_4$ oxidation (Fig. 2b), with uptake ranging from 0.7 to 4.1 ng $CH_4$ $g^{-1}$ $h^{-1}$. For Ekolongouma soils, oxidation was greater in surface than subsurface soils, but for Itanga, mean subsurface oxidation was greater ($p = 0.043$). Overall, $CH_4$ oxidation was higher in Itanga soils ($p = 0.002$).

Soils ranged from a source to a small sink for $N_2O$ (−0.2–2.5 ng $N_2O$ $g^{-1}$ $h^{-1}$). Emissions varied significantly by depth ($p = 0.049$) and between sites ($p < 0.001$, Fig. 2c). Emissions also varied significantly in the interaction between depth and location ($p = 0.04$). Ekolongouma soils were consistently a small sink under dry conditions and small source when wet, with somewhat greater emissions from surface soils, although soil moisture and interactions were not significant ($p = 0.557$). In contrast, soils from Itanga were consistently a source of $N_2O$, with substantial subsurface production, particularly following rewetting.

### 3.3. Temperature dependence of greenhouse gas exchange

Temperature responses of GHG fluxes were only significant for $CO_2$ emissions across the two sites, depths and moisture treatments (Fig. 3a), whereas there was no significant temperature response for $CH_4$ oxidation or $N_2O$ fluxes (Figs. 3b & d). While $CH_4$ oxidation showed no

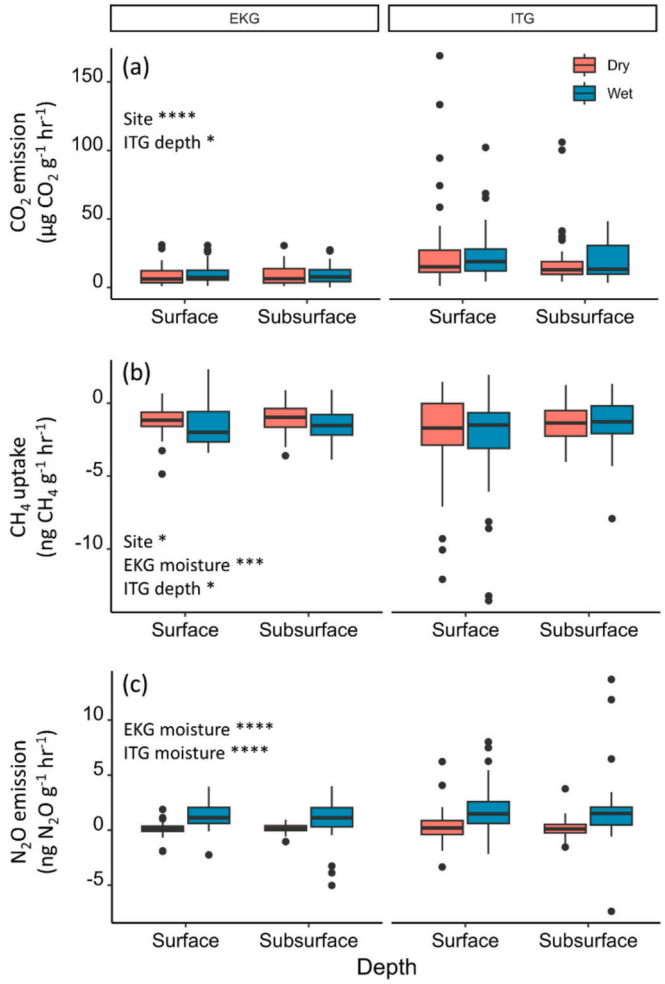


**Fig. 2.** Baseline (a) $CO_2$ emission, (b) $CH_4$ uptake, and (c) $N_2O$ fluxes at 25 °C at 30 % (dry) and 70 % (wet) gravimetric moisture content in surface and subsurface savannah soils at Ekolongouma (EKG) and Itanga (ITG) village sites. Asterisks indicate significance levels for pairwise comparisons (site, depth, moisture): * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, **** $p < 0.0001$.

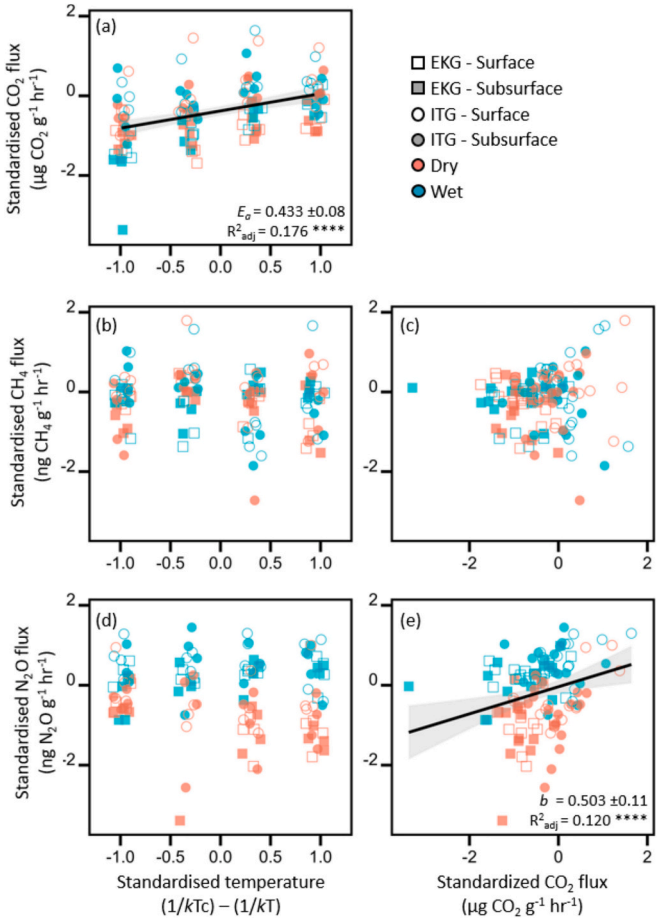


**Fig. 3.** The temperature response of GHG fluxes across two savannah sites (Ekolongouma (EKG): square symbols, Itanga (ITG): circle symbols). Plots show standardised GHG fluxes against standardised Arrhenius temperature (a, b & d) or standardised $CO_2$ flux (c & e) for measurements across the two sites, depths (Surface: open symbols; Subsurface: filled symbols) and moisture (Dry: coral symbols; Wet: turquoise symbols) conditions. Symbols in a, b and d are jittered for visibility across static temperatures (unstandardised values of 20, 25, 30 and 35 °C). Significant linear regression relationships are indicated by black solid lines with the activation energy ($E_a$) or slope ($b$) values presented alongside adjusted $R_2$ fits and significance levels (p < 0.0001: ****).

relationship with other GHG fluxes (Fig. 3c), $N_2O$ fluxes increased significantly with $CO_2$ emissions across all measurements (Fig. 3e).

Interactions between the temperature response of GHG fluxes were tested for site, soil depth and moisture interactions, with the condition that additional explanatory variables have a greater goodness of fit with additional degrees of freedom of $\Delta AIC_{df} < -5$. Few regression models were selected on this basis and were limited to significant relationships between $CO_2$ flux temperature dependence and site (Figs. 4a & b) and between standardised $N_2O$ and $CO_2$ fluxes with moisture (Fig. 4d & e). Greater values for the regression slopes (*Ea* and *b*) in Fig. 4 indicate a greater increase in $CO_2$ flux with an increase in temperature in Fig. 4a & b, and a greater increase in $N_2O$ flux with an increase in $CO_2$ flux in Fig. 4c & d. That is, $CO_2$ emissions were more temperature dependent in Ekolongouma ($Ea = 0.509$, Fig. 4a) than Itanga ($Ea = 0.357$, Fig. 4b) while $N_2O$ fluxes were less sensitive to increasing $CO_2$ emissions in wet soils ($b = 0.148$, Fig. 4d) and more sensitive in dry soils ($b = 0.879$, Fig. 4e).

For the regression models that yielded a significant temperature response we estimated $Q_{10}$ values for $CO_2$ and $N_2O$ fluxes (Table 2). That is, $Q_{10}$ values were not estimated for $CH_4$ fluxes or $N_2O$ fluxes in wet conditions due to the non-significant temperature response across treatments (Fig. 2). $Q_{10}$ estimates for soil respiration were broadly comparable for EKG and ITG (1.92 and 1.58). The estimated $Q_{10}$ for $N_2O$ fluxes in dry conditions were negative, representing a decrease in $N_2O$ fluxes with an increase in temperature.

We investigated non-standardised GHG flux relationships against one another over the experimental temperature range to identify relationships between $CO_2$, and $N_2O$ and $CH_4$ according to additional explanatory variables. We found the relationship between $N_2O$ and $CO_2$ fluxes held for non-standardised measurements (Fig. 5a) and that the key explanatory variable for differences in this relationship was temperature range (Fig. 5b). In contrast to the standardised GHG fluxes (Fig. 3), non-standardised $CH_4$ oxidation showed a significant relationship with $CO_2$ emissions across temperature treatments (Fig. 5c) and showed a significant interaction with soil depth (Fig. 5d).

### 3.4. Principle component analysis

Separate PCAs were run for wet and dry soils. For wet soils, the selected parameters accounted for 79 % of variance (Fig. 6a). The first component separated soils by properties (OI, I index, pH, electrical conductivity, and C:N), while the second component separated soils by GHGs ($N_2O$, $CO_2$, and $CH_4$),. Similarly, in dry soils (Fig. 6c), the selected variables accounted for 80 % of variability, with the first principle component separating soils by soil properties (OI, I index, pH and

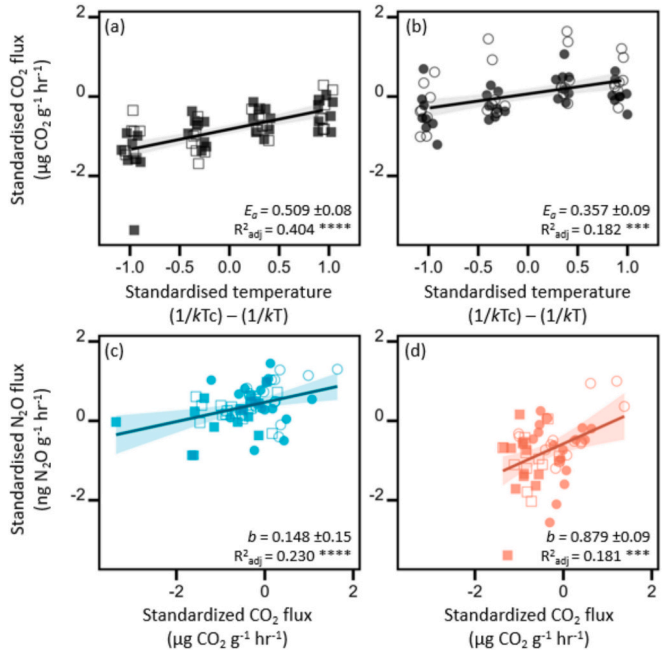


**Fig. 4.** Significantly different GHG flux relationships across sites and moisture treatments. Plots show (a & b) the temperature dependence of standardised $CO_2$ fluxes in Ekolongouma (a) and Itanga (b) and (c & d) relationships between standardised $N_2O$ and $CO_2$ fluxes across both sites (symbol shapes and colours as in Fig. 3) in wet (c) and dry (d) conditions. Slope and significance values as in Fig. 3. Symbols in a and b are jittered for visibility across static temperatures (unstandardised values of 20, 25, 30 and 35 °C).

electrical conductivity), and the second component separating C:N, and GHG exchange ($CH_4$ and $CO_2$).

## 4. Discussion

### 4.1. Soil properties

We identified significant differences in a range of biogeochemical properties between sites, with the exception of the R index, with only limited differences between soil depths. Soils from Itanga were characterised by high organic matter content in both the surface and subsurface and very acidic pH, possibly indicating significant time since the last major fire event (Úbeda et al., 2009), or due to relatively high soil moisture levels (Table 1). Conversely, soils from Ekolongouma have substantially lower organic matter content, and higher (although still acidic) pH. A higher I index and OI may have been driven by relatively recent fresh inputs of litter. High HI and low OI values (e.g. in soils from Ekolongouma) indicate the presence of hydrogen rich compounds which can include celluloses, whereas low HI and high OI values in Itanga soils are broadly indicative of increased presence of aromatic carbon (i.e. increased recalcitrant black carbon and humic substances) (Saenger et al., 2013). Such differences may be accounted for by contrasts in fire regime, which are frequent in savannahs in the region, or through contrasts in soil moisture resulting from flooding regime. In general, fires in savannahs deplete labile soil organic carbon fractions (for example relatively fresh litter inputs), although precise effects are determined by the inherent properties of the litter itself. Oxygen-containing functional groups are particularly vulnerable to loss on heating. In turn, this is associated with a relative increase in humic fractions, with soils heavily affected by fire featuring high quantities of black carbon (González-Pérez et al., 2004). pH increases following burning due to the incorporation of ash are generally reported (Úbeda et al., 2009), although conversely, pH can decrease through nitrification, which is enhanced in the short term following burning due to increased temperatures, and the availability of pyrolysable material (Mohamed et al., 2007), or due to high concentrations of aluminium found in ash produced at low temperatures (Pereira et al., 2017). Conversely, differences may be associated with contrasting moisture regimes between sites, with Itanga featuring higher gravimetric moisture compared to soils from Ekolongouma (Table 1). Increased moisture may be indicative of flooding (and neighbouring peatland sites in the area periodically flooded) (Crezee et al., 2022), which would reduce rates of aerobic decomposition and thus drive the accumulation of organic matter in the profile, and also result in lower pH (Girkin et al., 2019).

### 4.2. Temperature response of greenhouse gas emissions

Baseline rates of soil respiration (4–29 μg $CO_2$ $g^{-1}$ $h^{-1}$), $CH_4$ oxidation, and $N_2O$ fluxes were broadly comparable to values previously reported in the literature (Castaldi et al., 2010; Hao et al., 1988; Livesley et al., 2011; Sanhueza and Santana, 1994; Wachiye et al., 2020), with

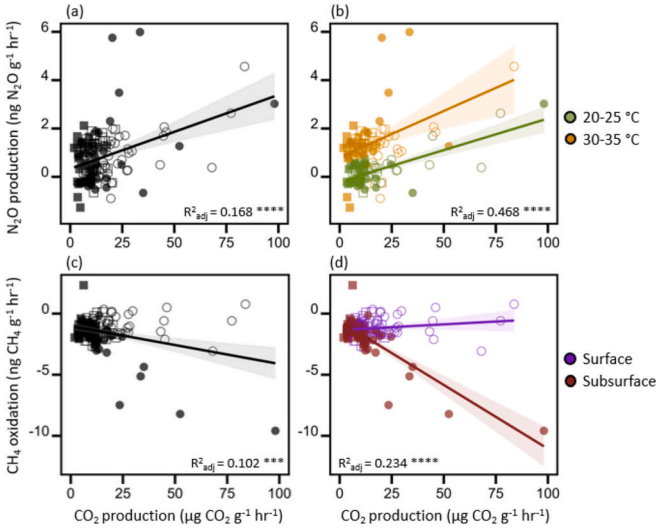


**Fig. 5.** GHG flux relationships with one another across the experimental temperature range, showing non-standardised measurements for (a & b) $N_2O$ and $CO_2$ and (c & d) $CH_4$ and $CO_2$ fluxes. Significant interactions between GHG flux relationships were found for (b) $N_2O$ and temperature range and (d) $CH_4$ and soil depth.

**Table 2**
Regression analysis for the two savannah sites and GHG flux responses to temperature (note $CH_4$ did not show a significant temperature response). $Q_{10}$ values were estimated using the parameters $B$ and $E_a$ from Eq. (1) and calculated for temperatures ranging between 20 and 35 °C. NS indicates a non-significant temperature response for $N_2O$ in wet conditions.

| Site /Moisture treatment | GHG | *B* | *Ea* | F | $R^2_{adj}$ | *p* | Estimated $Q_{10}$ |
|---|---|---|---|---|---|---|---|
| EKG | $CO_2$ | −0.824 ± 0.055 | 0.509 ± 0.077 | 43.73 | 0.404 | **** | 1.92 ± 0.006 |
| ITG | $CO_2$ | 0.066 ± 0.066 | 0.357 ± 0.092 | 15.00 | 0.182 | *** | 1.58 ± 0.004 |
| Wet | $N_2O$ | ns | | | | | |
| Dry | $N_2O$ | −0.709 ± 0.108 | −0.343 ± 0.144 | 5.70 | 0.077 | * | −0.64 ± 0.001 |

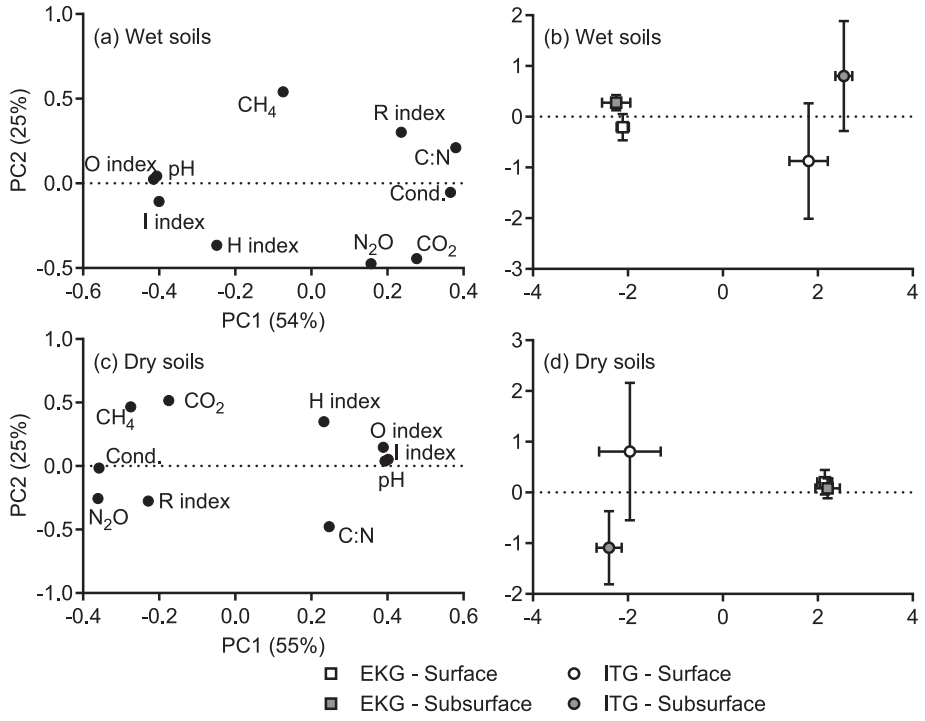


**Fig. 6.** (a & c) PCA loadings and (b & d) PCA scores for wet and dry soils for GHG emissions and soil properties.

the exception that, in this study, soils were consistently a sink for $CH_4$ (i.e. significant methanotrophic activity). Previous studies of the processes underlying the exchange of GHGs have indicated important roles for changes in moisture and burning, although many of these effects can be transitory (Castaldi et al., 2010).

$CO_2$ emissions was strongly influenced by temperature across both sites and all conditions (Fig. 3a), while $CH_4$ oxidation (Fig. 3b) and $N_2O$ production in wet conditions (Fig. 3d, showing wet and dry conditions together) showing a non-significant temperature response. $N_2O$ fluxes were, however, related to $CO_2$ fluxes across experimental temperatures and wet and dry soil conditions (Fig. 3e). Site had a large effect on the temperature dependence (how much of the variation in GHG flux was explained by temperature) and sensitivity (how much the GHG flux increases with temperature) (Fig. 4a & b). That is, temperature explained greater variation in $CO_2$ fluxes ($R^2_{adj} = 0.40$) and $CO_2$ was more temperature dependent ($E_a = 0.51$) for Ekolongouma than Itanga soils ($R^2_{adj} = 0.18$; $E_a = 0.36$) (Table 2). Many of the soil biogeochemical properties measured varied significantly between sites, and in particular soil organic matter and carbon which were substantially higher in both surface and subsurface soils at Itanga; soils from Ekolongouma also featured a higher I index (Table 1). Results from our PCA indicated that O, I and R indices (i.e. the availability of labile and recalcitrant carbon) are important for mediating observed responses. In contrast to the carbon quality hypothesis, the increased presence of aromatic/recalcitrant carbon at the ITG site was not associated with higher $Q_{10}$ values (1.58 for ITG versus 1.92 for EKG). This somewhat surprising finding may reflect one or more of several processes. Physical protection may differ between soils (Davidson and Janssens, 2006; Cooper et al., 2021), with the potential for increased protection of carbon within aggregates at ITG, resulting in apparent substrate limitation at microsites, despite greater total carbon. Other environmental constraints can also be significant, for example the increased presence of clay-sized minerals that can adsorb organic matter, and help retain soil moisture (Davidson and Janssens, 2006).

Soil moisture exerts a strong limitation on GHG fluxes in the dry season (Thomas et al., 2011; Wood et al., 2013), and although we found no evidence for a soil moisture interaction with $CO_2$ or $CH_4$ fluxes, we did observe a significant interaction between $N_2O$ with $CO_2$ in wet vs dry conditions or both Ekolongouma and Itanga soils (Fig. 4c &d). Fig. 4c shows higher $N_2O$ fluxes relative to $CO_2$ fluxes in wet conditions and Fig. 4d shows a greater increase (sensitivity) of $N_2O$ fluxes to increasing $CO_2$ fluxes in dry conditions. This is important in a wider context, as soil moisture is closely coupled to regional climate, particularly precipitation patterns. Based on our findings, extended wet seasons will likely result in higher $N_2O$ fluxes, but $N_2O$ will increase more rapidly in dry conditions. The relationship between $N_2O$ and $CO_2$ fluxes is also higher, although not as sensitive to higher temperature ranges (Fig. 5a & b) making temperature and soil moisture interactions an important consideration for predicting future soil GHG-climate feedbacks.

Under wetter conditions, methanogenesis is likely to have increased in anaerobic microsites, although oxidation remains the dominant process, particularly under dry conditions (Fest et al., 2017). Savannah soils have previously been reported to act as $CH_4$ sources when fully inundated, with emission rates exponentially related to soil temperature (Otter and Scholes, 2000). Savannah ecosystems more broadly can also become substantial $CH_4$ sources through biomass burning (Laris et al., 2021), although in our study we found no evidence of temperature dependence for $CH_4$ oxidation and did not observe $CH_4$ production (Whalen and Reeburgh, 1996). Previous studies have demonstrated substantial temperature dependence of methanogenesis, particularly for high carbon peat soils (Girkin et al., 2020a; Sjögersten et al., 2018). Within this study, subsurface soils are likely to have been exposed to higher concentrations of headspace $CH_4$ than they would have been exposed to in situ due to the role of surface soils as a diffusion barrier for atmospheric $CH_4$ (Murguia-Flores et al., 2021). As a consequence, our estimates for $CH_4$ uptake for subsurface soils are likely an overestimation, as soils will have had increased substrate availability for methanotrophy.

The relatively low $N_2O$ flux rates (and sometimes negative fluxes, particularly under dry, basal conditions) across all temperatures likely reflect the acidic and nutrient-poor soils (Andersson et al., 2004; Castaldi et al., 2006) (Table 1), and match relatively low emissions reported in tropical forest oils elsewhere in the region (Barthel et al., 2022). In the tropics, high production and flux rates in situ are generally only reported

in tropical forests and in soils converted to agricultural use (Weitz et al., 2001). Under moisture limited conditions, low soil water content limits the presence of anoxic microsites required for denitrification (Firestone and Davidson, 1989). Increased WFPS in soils reduces oxygen availability, increasing fluxes of $N_2O$. However, extensive flooding beyond the experimental treatments applied in this study are likely to substantially reduce production because high moisture contents favours the production of $N_2$ rather than $N_2O$ (Ciarlo et al., 2007). During the wet season, in situ soils are likely to emit pulses of $N_2O$ as rainfall will stimulate mineralisation and nitrification (Castaldi et al., 2010). Previous studies of the temperature dependence of $N_2O$ fluxes in temperate environments have strong exponential responses to increasing temperatures (Schindlbacher et al., 2004), but studies in the tropics and in savannahs specifically, are more limited. In general, increasing temperatures drive enhanced nitrification and denitrification, with optima between 25 and 35 °C (Melling et al., 2007). Our results, however, show a comparatively limited response to soil warming. In dry soils, $N_2O$ fluxes are likely greater due to canonical nitrification-denitrification resulting in $N_2O$, but at higher soil moistures there is increased production of $N_2$ as the product of denitrification, resulting in lower $N_2O$ fluxes, although this may be low at 70 % WFPS (Girkin and Cooper, 2023). Soil denitrification can be inhibited under acidic conditions, with denitrification rates decreasing with increasing soil acidity (Ciarlo et al., 2007). pH has previously been identified as important in predicting $Q_{10}$s both within and between land uses (Meyer et al., 2018; Min et al., 2014; Zhou et al., 2013), likely the result of pH-dependent microbial community structure and function (Blagodatskaya and Anderson, 1998). We only identified a significant temperature response for $N_2O$ net production from EKG and not for ITG; moreover, the temperature response for EKG soils was low, collectively suggesting that these soils may be relatively insensitive to changes in soil temperature across the measured ranges, and implying a certain level of resilience to soil warming.

Our $Q_{10}$ values for soil respiration (Table 2) are broadly comparable to findings globally (e.g. 1.9 for a North Australian savannah soil (Chen et al., 2002), and 2.1 in Senegalese savannahs (Elberling et al., 2003), and 1.4 to 2.7 during a 21 day incubation experiment with soils from the Brazilian cerrado (Espíndola et al., 2018). Makhado and Scholes (2011) reported a range of $Q_{10}$ values for soil respiration (0.59–3.07) in *Acacia* and *Combretum* dominated savannah areas in the Kruger National Park across a series of 10 °C temperature gradients. Overall, these values are generally lower than those reported for other tropical ecosystems, potentially indicating some degree of resilience of microbial communities in tropical savannah soils in the region to rising temperatures (Girkin et al., 2020a, 2020b; Sjögersten et al., 2018).

## 5. Conclusion

Here, we show the response of GHG production in Central African savannah soils to changes in temperature and soil moisture. We identified that soil $CO_2$ production can be sensitive to warming under certain circumstances. In contrast, the temperature response of $N_2O$ fluxes was only significant in dry conditions and no significant temperature response of $CH_4$ fluxes was observed. Significant differences in soil properties and GHG production between sites are likely driven by differences in site history and were strong drivers of production, mediating effects through contrasting soil organic matter properties. Overall, our results show that savannah soils can exhibit comparatively limited responses to increasing soil temperatures, which may indicate the potential resilience of soil processes to climate warming.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geodrs.2025.e00934.

## Data availability

Data is available in supplementary materials

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