



# Soil disturbance in wetlands by feral pigs increases greenhouse gas emissions

Maria Fernanda Adame<sup>1</sup>, Alex Pearse<sup>2</sup>, Jack W Hill<sup>2</sup>, Swade Cristo<sup>3</sup>, Jonathan Nadji<sup>4</sup>, Jasmine Malua Hall<sup>1</sup>, Jessa Thurman<sup>1,5</sup>, Valerie Hagger<sup>2</sup>, Catherine E Lovelock<sup>2</sup>

<sup>1</sup>Australian Rivers Institute, Griffith University, QLD, 4111, Australia

<sup>2</sup>School of Environment, The University of Queensland, St Lucia, 4072, Australia

<sup>3</sup>Murrumburr clan, Kakadu National Park, NT, Australia

<sup>4</sup>Bunitj clan, Kakadu National Park, NT, Australia

<sup>5</sup>Agriculture & Food, CSIRO, Dutton Park, QLD, 4102, Australia

Correspondence to: MF Adame (f.adame@griffith.edu.au)

**Abstract.** Multiple approaches are needed to decrease greenhouse gas emissions and reduce the pace of climate change. Wetlands are among the most carbon-rich ecosystems on the planet, and when disturbed, they can generate disproportionately high emissions. Invasive hoofed mammals, such as feral pigs (*Sus scrofa*), cause significant soil disturbances by trampling, grubbing, and digging in wetlands. We tested whether soil disturbances by feral pigs would increase greenhouse gas emissions (carbon dioxide, CO<sub>2</sub>, methane, CH<sub>4</sub>, and nitrous oxide, N<sub>2</sub>O) as a result of reduced soil oxygen and plant cover, and increased nitrogen. Six paired sites were sampled in Kakadu National Park, northern Australia, a site of immense cultural and natural significance. Fluxes of CH<sub>4</sub> were significantly different among treatments, with emissions being higher at disturbed plots ( $663 \pm 740$ , 54 to 4,820  $\mu\text{g m}^{-2} \text{hr}^{-1}$ ) compared to reference plots ( $375 \pm 292$ , -8.6 to 1,785  $\mu\text{g m}^{-2} \text{hr}^{-1}$ ). The most notable differences were observed for N<sub>2</sub>O, with significantly higher emissions at disturbed plots ( $81 \pm 88.7$ , 26.6 to 548  $\mu\text{g m}^{-2} \text{hr}^{-1}$ ), which were up to an order of magnitude higher than those for the reference plots ( $11.9 \pm 3.0$ , 2.7 to 20.4  $\mu\text{g m}^{-2} \text{hr}^{-1}$ ). Soil redox values were correlated with emissions in plots disturbed by pigs, with negative values associated with high CH<sub>4</sub> emissions. The highest emissions were found in recently disturbed sites. This study provides another compelling example of how animal populations can significantly impact the carbon cycle at the landscape scale. It also provides evidence for the viability of a carbon methodology to reduce greenhouse gas emissions through feral pig management, which will support both culture and nature.

## 1 Introduction

As climate change and human impacts on landscapes intensify, multiple approaches are needed to decrease greenhouse gas emissions. First and foremost, reducing fossil fuel use is required; additionally, nature-based solutions that reduce emissions while increasing ecosystem and societal benefits are possible (Matthews et al., 2022). One such solution is the restoration and improved management of wetlands.

Wetlands are one of the most carbon-rich ecosystems on the planet; their high soil carbon content and low oxygen conditions favour sequestration but can also lead to potentially high methane (CH<sub>4</sub>) and nitrous oxide (N<sub>2</sub>O) emissions. These potent



greenhouse gases are emitted in large quantities in wetlands from tropical climates, mostly when they are polluted (Rosentreter et al., 2021; Saunois et al., 2020). Emissions from wetlands increase when soils are disturbed, for example, by the trampling, grubbing, and digging of invasive ungulates or hoofed mammals (O'Bryan et al., 2021). Thus, managing invasive species could decrease greenhouse gas emissions and improve wetland carbon sequestration (Rowland & Lovelock, 2024; Schmitz et al., 2014).

In tropical Australia, the management of invasive ungulates, such as water buffaloes (*Bubalus bubalis*), horses (*Equus caballus*), and feral pigs (*Sus scrofa*), is a huge challenge (Bradshaw et al., 2007a). Pigs are especially abundant, with the latest estimates of around 3.2 million pigs throughout Australia, with a mean density of one pig per square kilometre (Hone, 2020). Feral pigs are common in wetlands, where they cause extensive damage to soils, disperse weeds, and prey on native species (Ballari and Barrios-García, 2014; Waltham and Schaffer, 2018). Introducing feral pigs into Australia has had catastrophic effects on biodiversity and ecosystem functions. For instance, pigs consume large numbers of native animals, such as freshwater turtles (Doupé et al., 2009). Meanwhile, feral pigs have become prey to native saltwater crocodiles (*Crocodylus porosus*), which currently obtain a significant portion of their nutrition from these invasive animals (Adame et al., 2018). Finally, feral pigs are potential carriers of human diseases such as Japanese encephalitis, which is transmitted by mosquitoes (Bradshaw et al., 2007a). To date, controlling the numbers of feral ungulates has been intermittent and controversial, as some people consider them an important food source (Bradshaw et al., 2007). Long-term planning with cost-effective strategies is necessary to effectively mitigate the environmental and human impacts of feral pigs (Hamnett et al. 2024).

Carbon markets can provide long-term funding for projects that reduce greenhouse gas emissions, increase carbon sequestration, and protect carbon stocks. In Australia, a national carbon market exists, allowing for the generation of credits (Australian Carbon Credit Units, ACCUs) from projects in agriculture, energy, landfill and waste management, mining, transport, and vegetation (Clean Energy Regulator, CER, 2024). The latter includes nature-based projects such as vegetating landscapes, restoring tidal wetlands, and managing fires (CER, 2024). A methodology that reduces greenhouse gas emissions by managing invasive ungulates could provide cultural and economic benefits while reducing environmental impacts. However, the emissions from pig disturbance of wetlands are still uncertain (median of 4.9 million MtCO<sub>2</sub> per year and a wide range from -30.3 to 94 million MtCO<sub>2</sub>), and further investigations assessing the climate benefits of feral pig management are required (O'Bryan et al., 2022).

This study was conducted in Kakadu National Park in northern Australia (Fig. 1). The park has immense cultural and natural values, being one of the last unmodified tropical rivers in the world. Kakadu has been home to First Nations People (Traditional Owners) for more than 65,000 years (Clarkson et al. 2017), being the oldest living culture on Earth with a strong spiritual connection to “country”, which refers to the lands, waterways, and seas (physical, cultural, and spiritual) with which they are



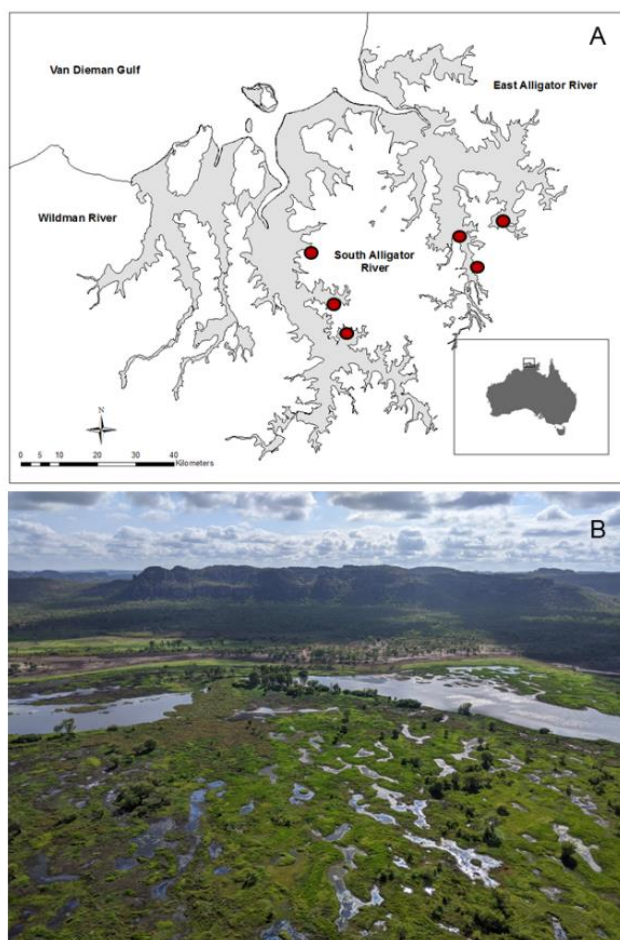
65 associated. The Traditional Owners of Kakadu are the Bininj in the north and Mungguy in the south, and together, they manage and lead research that is connected within the park (Robinson et al., 2022).

We measured the effect of soil disturbance in wetlands by feral pigs on greenhouse gas emissions (carbon dioxide, CO<sub>2</sub>, CH<sub>4</sub>, and N<sub>2</sub>O) by comparing 1) six paired plots distributed across two floodplains with and without soil pig disturbance, 2) variability from time of disturbance (recently and old disturbed), and 3) variability within two seasons: Yekke, the cool post-  
70 monsoon season, and Kunumeleng, the dry and hot pre-monsoon season. We hypothesised that pig disturbance in wetlands would result in changes in the physicochemical properties of the soil. We predict that soil nitrogen and labile carbon will increase due to animal excretion (Krull et al., 2013), and that soil oxygen (and thus its reduction-potential or redox) will decrease due to the increased microbial respiration and the death of fine roots (Doupé et al., 2009; Liu et al., 2020). We expect these changes to result in increased incomplete nitrification-denitrification, which increases N<sub>2</sub>O emissions (Anderson &  
75 Levine, 1986) and an increase in soil decomposition, favouring CO<sub>2</sub> and CH<sub>4</sub> emissions. Finally, we predict that emissions would be highest immediately after disturbance (Liu et al., 2020), especially during the hotter Kunumeleng season, as higher temperatures accelerate CH<sub>4</sub> production (Yvon-Durocher et al., 2014).

## 2 Methods

### 2.1 Study site and sampling design

80 Kakadu National Park is bounded by the Van Dieman Gulf to the north, and the Kakadu escarpment to the south; three main rivers flow through the park, Wildman River, and South and East Alligator (Fig. 1). The region has a monsoonal climate with a total mean rainfall of 1,547 mm, mostly falling between December and March (1,383 mm); annual mean temperature ranges between 22.7 and 34.4°C (1971-2021; Bureau of Meteorology, BM, Jabiru Airport, Station 14198). The climate is classified into six seasons according to traditional knowledge: Kudjewk or monsoon season (December to March), Bangkerreng or storm  
85 season (April), Yekke or cool and humid season (May to mid-June), Wurrkeng or cold season (mid-June to August), Kurrung or hot dry season (mid-August to October), and Kunumeleng or pre-monsoon storm season (mid-October to late December). During the Kudjewk, the rivers that run through Kakadu overflow and inundate adjacent low-lying areas where sediments carried by the river are deposited, and dense vegetation grows (Adame et al., 2017; Erskine et al., 2018). These floodplains can stay inundated for six to eight months of the year (Ward et al., 2016). During the dry season, flooding recedes, and  
90 permanent deep-water holes remain in the floodplain until the next wet season, when they are once again reconnected to the river channel



**Figure 1. (A) Location of Kakadu National Park in northern Australia, and sampling points (north to south): Munmarlay, Coolaboo, Mamukala in the South Alligator and Ubirr, Djabulukgu and Dja Dja in the East Alligator, (B) floodplain wetlands of the Magela Creek adjacent to the East Alligator River. Picture by MF Adame.**

We conducted two field campaigns, one during Yekke (8-14th June 2023) or the cool season and one during Kunumeleng (25-30th October 2023) or the hot, pre-monsoon season. Sampling in other seasons was not possible due to the remoteness of the area, extreme heat, and the dangers posed by saltwater crocodiles (*Crocodylus porosus*) during the wetter seasons of the year. For our first trip, six sites were selected by the Traditional Owners co-authors. The selected sites were Munmarlay, Coolaboo and Mamukala in the South Alligator and Ubirr, Djabulukgu and Dja Dja in the East Alligator (Fig. 1).

The vegetation of the sampling sites included floodplain grassland with scattered broad-leaved paperbark (*Melaleuca viridiflora*) at Dja Dja and Ubirr, paperbark forests at Djabulukgu, Coolaboo, and Munmarlay (*M. viridiflora*, *Melaleuca cajuputi*), and freshwater mangroves (*Barringtonia acutangula*) at Mamukala. Away from the open water, the wetlands were



surrounded by savanna or pandanus (*Pandanus spiralis*) woodland. We sampled a reference plot at each site, either grassland  
or a forest of paperbark forest which was relatively undisturbed and a plot nearby with soil disturbances (Fig. 2). The disturbed  
plots were either “digging areas” that pigs use for finding roots and other underground food (e.g., turtles) or “wallows” which  
were deeper and are used by pigs to cover themselves with mud to avoid overheating (Bracke, 2011). Although the soil  
disturbances were mostly done by pigs, feral water buffalo (*Bubalus bubalis*) may have also contributed, as buffalo wallows  
and tracks were observed at Dja Dja, Ubirr, and Munmarlay.



**Figure 2.** Examples of (A) a reference or undamaged plot at Djabulukgu, (B) a recently disturbed plot by feral pigs at Coolaboo, and (C) an old, disturbed plot that was bare of vegetation and dry (Djabulukgu). Pictures by JM Hall.

On our second trip during the Kunumeleng season, we resampled three of the sites (Munmarlay, Djabulukgu, and Mamukala). But this time, targeting not only reference and disturbed plots but also areas that were previously disturbed and were now  
unvegetated and dry (Fig. 2). The three treatments (reference, recently disturbed and old disturbed) were as close to each other  
as possible, usually less than 50 m away, except for our plot in Munmarlay, where we could not access a recently disturbed  
plot, and was paired with a reference plot in nearby Coolaboo (Fig. 1).

## 2.2 Soil physicochemical characteristics

At each plot, reduction-oxidation potential (redox; 3-5 measurements) and soil temperature (five measurements) were  
determined with a redox meter (HQ 11d ORP- meter, Hach). Redox from reference and old disturbed sites during the  
Kunumeleng season could not be measured as the soil was completely dry. Three soil samples of a known volume were taken





at each plot, weighed, and oven-dried at 50°C. They were then weighed again, from which the water content and bulk density were calculated. The samples were analysed for organic carbon (after testing for inorganic carbon, C, through HCl addition), nitrogen (N),  $\delta^{13}\text{C}$ , and  $\delta^{15}\text{N}$  (EA-IRMS, Serco System at Griffith University). The particle size distribution of surface sediments (0-5 cm deep) was assessed from three subsamples from each plot, which were homogenised into a single sample and sieved through meshes of the following sizes:  $< 20\ \mu\text{m}$  (fine silt and clay),  $>20\ \mu\text{m}$  (medium and coarse silt)  $\leq$ ,  $> 63\ \mu\text{m}$  (very fine sand)  $\leq$ ,  $>125\ \mu\text{m}$  (fine, medium and coarse sand)  $\leq$ , and  $> 2\ \text{mm}$  (gravel). The contents of each sieve were weighed, and their contribution to the total sample was calculated. Finally, soil conductivity was measured with a conductivity meter (ProDSS YSI, OH, USA or HACH) from a solution of soil to water (1:5) adjusted to the dominant grain size class of each plot.

### 2.3 Greenhouse gas emissions

Instantaneous gas fluxes ( $n = 5$  per plot) were measured in dark, closed chambers (Hutchinson & Mosier, 1981) made of polyvinyl chloride (4L, 15 cm diameter and 30 cm in height; Fig. 2). During each experiment, gas samples were collected from the headspace of the chambers with a syringe at 0, 20, 40, and 60 min and transferred into vacuumed containers (Labco, High Wycombe, UK; Brannon et al., 2016). The  $\text{CO}_2$ ,  $\text{CH}_4$ , and  $\text{N}_2\text{O}$  concentrations within each sample were measured in a gas chromatograph (Shimadzu GC-2010 Plus, DESITI, Queensland Government). Linearity of fluxes within each chamber in time was checked. Those who complied were used to calculate fluxes ( $F$ ) per hour from the net changes in gas concentrations ( $N$ , mol) during the incubation time ( $t$ , hours), per volume of the chamber ( $V$ ,  $\text{m}^3$ ), at a given temperature of the soil ( $T$ , °K), assuming a pressure of one atmosphere:

$$F = \frac{N}{RT} \times \frac{V}{t A}$$

Equation 1

where,

$$R = 8.205 \times 10^{-5} \text{ m}^3 \text{ atm}^{-1} \text{ K}^{-1} \text{ mol}^{-1}$$

### 2.4 Root versus soil respiration

Soil  $\text{CO}_2$  fluxes are a combination of the decomposition of organic matter and dead roots and the respiration of live roots, which can contribute up to 79% of the total (Krauss et al. 2012). To test the contribution of root respiration to soil  $\text{CO}_2$  emissions, we measured instantaneous gas fluxes and biomass from roots in reference and disturbed plots by sampling sediment cores at each plot. On the same collection day, the sediments were washed and sieved through a 1 mm mesh, and roots were hand-picked, blotted dry, and weighed. The  $\text{CO}_2$  flux from each pooled sample (coarse and fine roots) was measured in the



dark with a portable gas analyser (Picarro, GasScouter, California, USA). The following week, back in the laboratory, the roots were oven-dried at 60°C and reweighed to measure their biomass.

## 2.5 Emission reduction potential

To estimate the carbon abatement potential of feral pig management, CH<sub>4</sub> and N<sub>2</sub>O fluxes were converted to CO<sub>2eq</sub> by multiplying them by their 100-year warming potential, which is 27 for CH<sub>4</sub> (non-fossil origin) and 273 for N<sub>2</sub>O (IPPC, AR6 Sixth Assessment Report, 2021). Fluxes of CO<sub>2</sub> were also included by correcting for respiration using the differences in emissions (%) from vegetated and unvegetated plots. The rates were extrapolated to annual fluxes per hectare.

## 2.6 Statistical analyses

Data was tested for normality with Shapiro-Wilk and Kolmogorov-Smirnov tests, for datasets that complied with normality, a two-way nested ANOVA with main effects (disturbance: old/new/reference) nested within the site was conducted to test differences between disturbed (recently and old disturbed) and reference plots across the six sites for gas fluxes (CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O) and physicochemical parameters (soil conductivity, temperature, redox, soil C, N, C:N, δ<sup>15</sup>N and δ<sup>13</sup>C). For datasets that did not comply with normality (CH<sub>4</sub> fluxes), comparisons among treatments were conducted with a non-parametric Wilcoxon matched-pairs signed-rank test. A repeated-measurements ANOVA was used to test for differences in gas fluxes between the two seasons. Regression and non-linear model fits were conducted to assess the response of greenhouse gas fluxes to physicochemical parameters. Statistics were analysed with GraphPrims 10.2.3. Values are mean ± standard error (min-max) unless specified otherwise.

## 3 Results

### 3.1 Soil physicochemical characteristics

During Yekke (cool season), soil conductivity, temperature, and redox were significantly higher at the reference plots (180 ± 74.3 μS cm<sup>-1</sup>, 27.8 ± 1.7°C, 206.3 ± 53.6 mV) compared to the disturbed plots (56.7 ± 7.6 μS cm<sup>-1</sup>, 25.3 ± 0.8°C, 67.7 ± 15.5 mV;  $F_{1,24} = 580.6$   $p < 0.001$ ,  $F_{1,47} = 424.7$   $p < 0.001$  and  $F_{1,24} = 26.19$   $p < 0.001$ , respectively; Table 1). In contrast, bulk density and water content were similar between treatments (58.0 ± 4.6 % and 0.46 ± 0.05 g cm<sup>-3</sup> versus 53.2 ± 5.2 % and 0.45 ± 0.08 g cm<sup>-3</sup> for reference and disturbed plots, respectively; Table 1).



**Table 1. Soil physicochemical characteristics of six reference plots paired with six recently disturbed plots by feral pigs during Yekke (cool season). Soil conductivity, temperature, and redox were significantly higher at the reference compared to the disturbed plots ( $F_{1,24} = 513.2$   $p < 0.01$ ,  $F_{1,47} = 424.7$   $p < 0.01$ , and  $F_{1,24} = 26.19$   $p < 0.001$ ). Significant differences are shown as  $p < 0.05^*$  and  $p < 0.001^{**}$ .**

	Conductivity ( $\mu\text{S cm}^{-1}$ )		Redox (mV)	
	Reference	Disturbed	Reference	Disturbed
Ubirr	239 $\pm$ 15	103 $\pm$ 4 <sup>**</sup>	125.3 $\pm$ 13.2	79.9 $\pm$ 44.5
Munmarlay	532 $\pm$ 35	98 $\pm$ 2 <sup>**</sup>	174.6 $\pm$ 17.9	22.0 $\pm$ 68.6*
Mamukala	1,319 $\pm$ 59	216 $\pm$ 12 <sup>**</sup>	445.7 $\pm$ 5.6	89.5 $\pm$ 42.9 <sup>**</sup>
Coolaboo	60 $\pm$ 2	80 $\pm$ 3	61.3 $\pm$ 15.6	16.9 $\pm$ 58.4
Djaja	126 $\pm$ 7	103 $\pm$ 10	210.8 $\pm$ 90.8	99.2 $\pm$ 67.1
Djabulukgu	128 $\pm$ 3	65 $\pm$ 3*	220.0 $\pm$ 22.0	98.5 $\pm$ 21.4
	Temperature ( $^{\circ}\text{C}$ )		Water content (%)	
	Reference	Disturbed	Reference	Disturbed
Ubirr	35.0 $\pm$ 0.0	24.0 $\pm$ 0.0 <sup>**</sup>	43.8 $\pm$ 1.8	39.2 $\pm$ 3.6
Munmarlay	24.5 $\pm$ 0.0	26.0 $\pm$ 0.0 <sup>**</sup>	61.7 $\pm$ 2.8	54.5 $\pm$ 2.8
Mamukala	24.7 $\pm$ 0.0	24.0 $\pm$ 0.0*	73.4 $\pm$ 1.4	73.5 $\pm$ 1.2
Coolaboo	31.0 $\pm$ 0.5	29.0 $\pm$ 0.0 <sup>**</sup>	48.9 $\pm$ 1.6	61.1 $\pm$ 1.9
Dja Dja	26.0 $\pm$ 0.0	24.0 $\pm$ 0.0 <sup>**</sup>	67.0 $\pm$ 1.3	49.3 $\pm$ 1.1
Djabulukgu	25.6 $\pm$ 0.4	25.0 $\pm$ 0.0*	53.5 $\pm$ 1.2	41.9 $\pm$ 1.6

Surface soil C and N, and molar C:N were also similar between reference (8.1  $\pm$  1.1% C and 0.63  $\pm$  0.09% N, 9.7  $\pm$  0.9) and disturbed plots (8.5  $\pm$  1.4% C and 0.68  $\pm$  0.10% N, 10.8  $\pm$  0.7;  $p = 0.480$ ,  $p = 0.312$ , and  $p = 0.251$ , respectively). Soil  $\delta^{15}\text{N}$  did not differ between treatments, with 2.73  $\pm$  0.60‰ for reference compared to 2.74  $\pm$  0.17‰ for disturbed plots (Table 2). However,  $\delta^{13}\text{C}$  was slightly but significantly higher at the reference plots (-22.6  $\pm$  1.7‰) compared to the disturbed ones (-21.4  $\pm$  1.7‰;  $F_{1,24} = 8.66$ ,  $p = 0.007$ ; Table 2).

All sites had different sediment grain size composition; Mamukala, Dja Dja and Djabulukgu were dominated by sand (fine, medium and coarse), Ubirr was dominated by silt (medium and coarse), while Munmarlay and Coolaboo were dominated by fine silt and clay (Table 3).





**Table 2. Soil carbon, nitrogen, molar C:N, isotopic composition ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) and bulk density of six reference plots paired with six recently disturbed plots by feral pigs. Reference and disturbed plots were similar for all parameters except for  $\delta^{13}\text{C}$ , which was significantly lower in the disturbed plots ( $F_{1,24} = 8.66, p = 0.007$ ). Significant differences are shown as  $p < 0.05^*$  and  $p < 0.001^{**}$ .**

	C (%)		N (%)		C:N	
	Reference	Disturbed	Reference	Disturbed	Reference	Disturbed
Ubirr	9.7 ± 0.5	11.6 ± 2.5	0.9 ± 0.1	0.9 ± 0.1	9.7 ± 0.3	10.7 ± 0.7
Munmarlay	7.4 ± 0.8	8.2 ± 1.8	0.6 ± 0.1	0.7 ± 0.1	9.8 ± 0.2	9.9 ± 0.7
Mamukala	6.3 ± 0.8	4.2 ± 0.5	0.4 ± 0.0	0.3 ± 0.0	15.0 ± 1.4	13.1 ± 0.6
Coolaboo	8.3 ± 1.0	6.1 ± 0.5	0.7 ± 0.1	0.5 ± 0.0	9.6 ± 0.2	10.1 ± 0.0
Dja Dja	12.3 ± 1.5	13.2 ± 0.9	0.8 ± 0.1	0.9 ± 0.1	12.9 ± 0.3	12.5 ± 0.2
Djabulukgu	4.3 ± 0.3	7.8 ± 0.3	0.4 ± 0.0	0.8 ± 0.0	10.3 ± 0.4	8.6 ± 0.1
	$\delta^{13}\text{C}$ (‰)		$\delta^{15}\text{N}$ (‰)		Bulk density (g cm <sup>-3</sup> )	
	Reference	Disturbed	Reference	Disturbed	Reference	Disturbed
Ubirr	-17.9 ± 1.5	-17.4 ± 0.4	1.2 ± 0.5	2.2 ± 0.7	0.30 ± 0.02	0.27 ± 0.03
Munmarlay	-23.4 ± 0.6	-21.1 ± 0.9*	3.6 ± 0.5	2.6 ± 0.6	0.50 ± 0.04	0.45 ± 0.05
Mamukala	-28.8 ± 0.5	-26.7 ± 0.7	3.0 ± 0.5	3.2 ± 0.5	0.56 ± 0.06	0.79 ± 0.08
Coolaboo	-21.1 ± 0.6	-18.1 ± 0.8**	1.8 ± 0.1	3.2 ± 0.3	0.35 ± 0.02	0.55 ± 0.02
Dja Dja	-25.3 ± 0.2	-26.1 ± 0.4	1.7 ± 0.6	2.9 ± 0.1	0.63 ± 0.02	0.39 ± 0.03
Djabulukgu	-19.2 ± 0.5	-19.0 ± 0.2	5.1 ± 0.5	2.3 ± 0.2	0.44 ± 0.02	0.27 ± 0.01

**Table 3. Soil grain size composition (%) of six reference plots (R) paired with six recently disturbed plots by feral pigs (D). Bold values highlight the dominant grain size per plot (reference/disturbed) and site.**

	Gravel		Fine, medium, coarse sand		Very fine sand		Medium and coarse silt		Fine silt and clay	
	R	D	R	D	R	D	R	D	R	D
Ubirr	4.0	0.9	3.8	4.9	29.0	26.4	<b>35.6</b>	19.9	27.5	<b>47.9</b>
Munmarlay	1.2	1.2	8.8	28.9	10.5	6.0	15.0	13.7	<b>64.4</b>	<b>50.1</b>
Mamukala	6.9	6.5	<b>61.3</b>	<b>63.7</b>	11.0	7.8	10.8	6.1	10.0	15.9
Coolaboo	5.3	0.0	17.2	1.8	25.4	0.0	17.2	2.4	<b>35.0</b>	<b>95.8</b>
Dja Dja	4.2	1.2	<b>46.2</b>	<b>51.6</b>	15.5	12.7	11.0	17.0	23.1	17.5
Djabulukgu	12.4	0.5	<b>55.3</b>	31.9	7.5	18.5	6.7	9.9	18.1	<b>39.2</b>

### 3.2 Greenhouse gas emissions

#### 3.2.1 Impact of pig disturbance

During Yekke or the cool season, CO<sub>2</sub> emissions were significantly different among sites ( $F_{5,48} = 3.871$   $p = 0.005$ ) and slightly, but not significantly, lower at the reference (mean of the six sites of  $462 \pm 101$  (286 to 921) mg m<sup>-2</sup> hr<sup>-1</sup>) compared to disturbed plots ( $523 \pm 43$  (468 – 743) mg m<sup>-2</sup> hr<sup>-1</sup>;  $F_{1,48} = 2.87$   $p = 0.097$ ; Fig.3A). Fluxes of CH<sub>4</sub> were significantly different among treatments ( $W = 248$ ,  $p = 0.0037$ ,  $n = 29$ ) with emissions being higher at disturbed plots ( $663 \pm 740$ , 54 to 4,820 µg m<sup>-2</sup> hr<sup>-1</sup>) compared to reference plots ( $375 \pm 292$ , -8.6 to 1,785 µg m<sup>-2</sup> hr<sup>-1</sup>) at all sites except Coolaboo (Fig. 3B), where the reference plot was not a *Melaleuca* forest but a grass-dominated wetland. The most significant differences were observed for N<sub>2</sub>O, with higher emissions at disturbed plots ( $F_{1,48} = 41.5$   $p < 0.01$ ) with a mean of  $81 \pm 88.7$  (26.6 to 548) µg m<sup>-2</sup> hr<sup>-1</sup>, which were up to an order of magnitude higher than those for the reference sites with  $11.9 \pm 3.0$  (2.7 to 20.4) µg m<sup>-2</sup> hr<sup>-1</sup> (Fig. 3C).

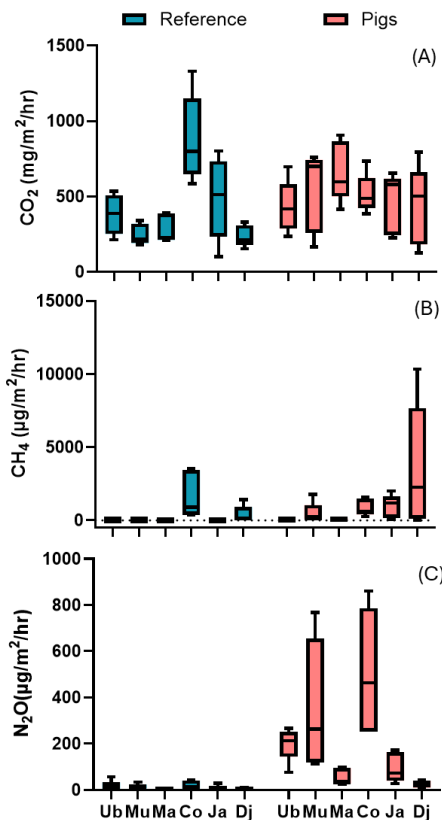


Figure 3. Greenhouse gas emissions (CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O) from reference plots (blue-left) and plots disturbed by feral pigs (red-right) for six sites across the floodplains in Kakadu National Park: Ub = Ubirr, Mu = Munmarlay, Ma = Mamukala, Co = Coolaboo, Ja = Djaja, Dj = Djabulukgu. Values of the box plots represent the mean and standard error; whiskers represent the minimum and maximum values.



### 3.2.2 Variability from the time of disturbance

The time since soil disturbance, whether the plot was old or recently used by pigs, was assessed during Kunumleng or the pre-monsoon season. At this time, CO<sub>2</sub> emissions were highest at the reference plots, compared to old and new disturbed plots (220 ( $F_{2,36} = 6.84$   $p = 0.003$ ; Fig. 4A). The time of disturbance significantly affected the CH<sub>4</sub> emitted, with higher emissions at the newly disturbed plots ( $F_{2,36} = 3.60$   $p = 0.038$ ) compared to old plots or reference sites (Fig. 4B). Finally, N<sub>2</sub>O emissions were similar among treatments ( $F_{2,36} = 1.07$   $p = 0.354$ ). However, there was a trend of N<sub>2</sub>O uptake (negative values) at the reference plots compared to emissions at the old and disturbed plots (Fig. 4C).

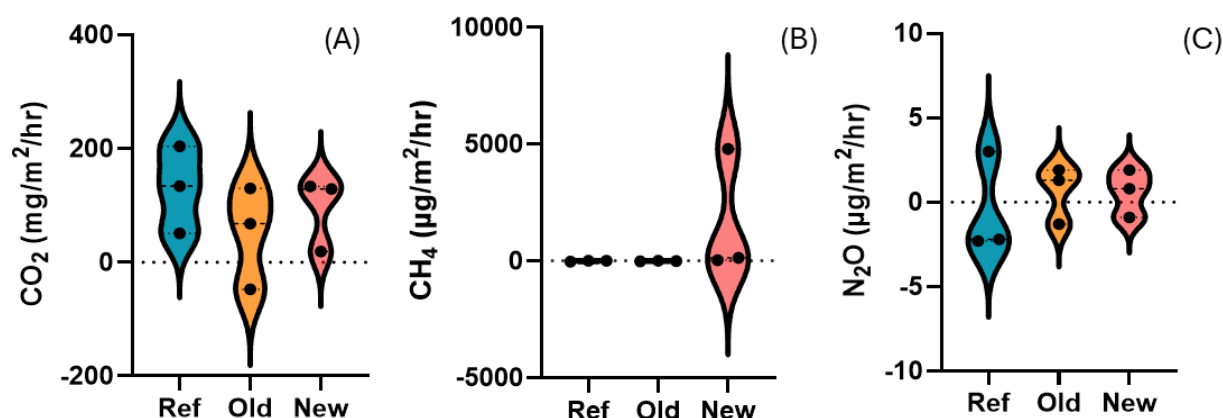
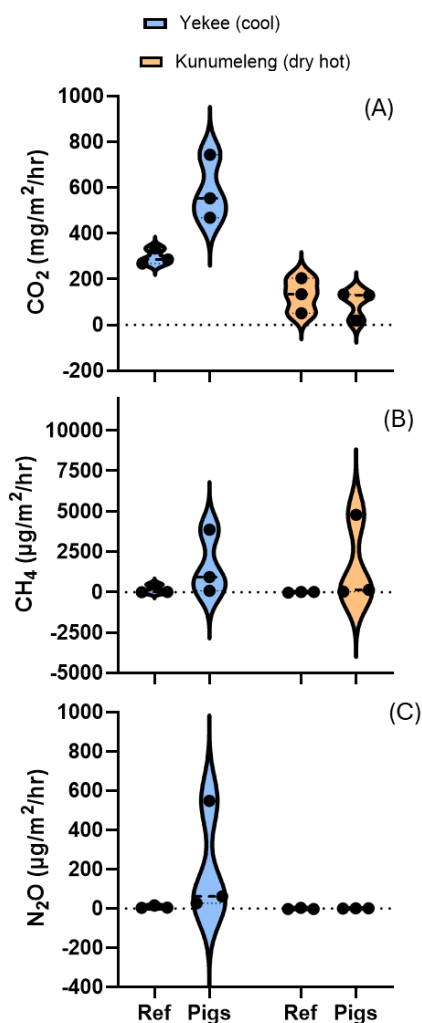


Figure 4. Greenhouse gas (CO<sub>2</sub>, CH<sub>4</sub>, and N<sub>2</sub>O) fluxes of reference sites (Ref- blue), sites previously used by pigs (Old- orange), and recently used by pigs (New-red). Violins represent the distribution of the mean fluxes (five chambers) within each treatment at three sites (Djabulukgu, Mamukala and Munmarlay) during Kunumleng (pre-monsoon) season.

### 3.2.3 Variability between seasons

The CO<sub>2</sub> emissions were significantly lower during the Kunumeleng (pre-monsoon) season compared to the Yekke (cool) season ( $F_{1,8} = 42.29$   $p = 0.0002$ ; Fig. 5A). The CH<sub>4</sub> emissions were similar ( $F_{1,13} = 00.148$   $p = 0.71$ ) but N<sub>2</sub>O emissions were significantly lower during Kunumeleng at the disturbed sites ( $F_{1,14} = 8.10$   $p = 0.013$ ; Fig. 5B, C). Redox potential in the disturbed plots was lower during Kunumleng (mean of three sites of  $12.2 \pm 44.3$  mV) than during Yekke (mean of five sites of 235  $67.7 \pm 15.5$  mV).



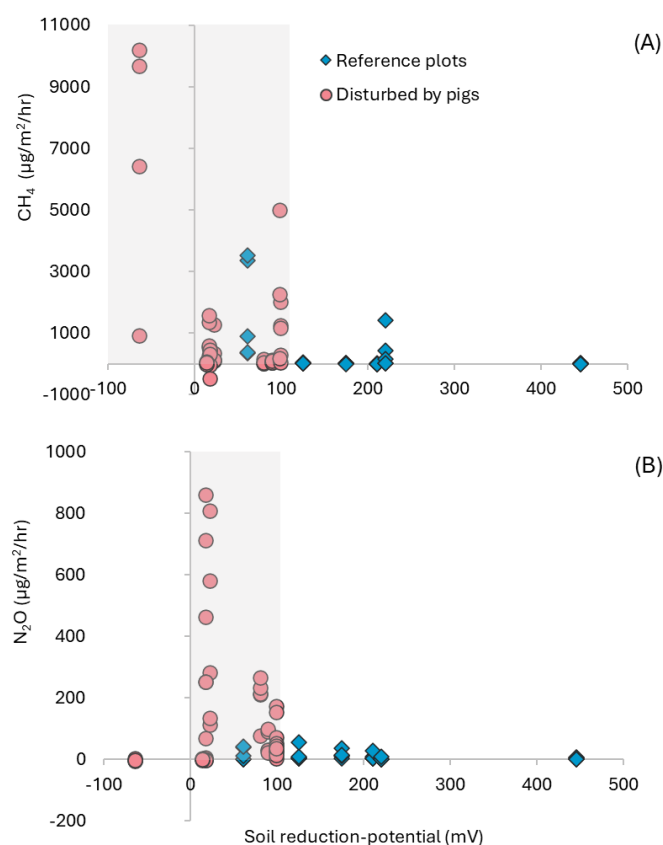
**Figure 5. Greenhouse gas ( $\text{CO}_2$ ,  $\text{CH}_4$  and  $\text{N}_2\text{O}$ ) fluxes for two seasons: Yekke or cool season (blue-left) and Kunumleng or pre-monsoon season (orange-right), for three plots without (Ref) and with feral pig disturbance (Pigs). Violins represent the distribution of the mean fluxes for five chambers per treatment and three sites (Djabulukgu, Mamukala and Munmurlay).**

### 3.2.4 Physicochemical factors associated with emissions

Only two parameters analysed strongly predicted greenhouse gas fluxes: pig disturbance and soil redox. Soils disturbed by pigs had lower redox than reference or old disturbed plots. Low redox values were correlated with high  $\text{CH}_4$  emissions, and although the correlation was significant, the regression was poorly fitted to a linear trend (Fig. 4;  $R^2 = 0.087$   $p = 0.012$ ).



Additionally, redox values between 0-100mV were associated with increased N<sub>2</sub>O emissions (Fig. 6B), a response that was best fitted to a Gaussian curve; however, the fit was modest and had low statistical confidence ( $R^2 = 0.21$   $n = 45$ , Fig. 6). Nevertheless, a clear pattern was observed between redox and emissions; anaerobic soil with redox values lower or close to zero promoted CH<sub>4</sub> emissions and soils with values between 0-100 mV promoted N<sub>2</sub>O emissions, but only in plots disturbed by pigs (Fig. 6).



**Figure 6. Relationship between soil redox (reduction-potential, mV) and (A) CH<sub>4</sub> and (B) N<sub>2</sub>O fluxes (µg m<sup>-2</sup> hr<sup>-1</sup>) from reference (blue diamonds) and disturbed (red circles) plots by feral pigs. Lower redox values were associated with higher CH<sub>4</sub> emissions, and values between 0 and 100 mV were associated with higher N<sub>2</sub>O emissions, but only at plots disturbed by pigs.**

### 3.2.5 Root versus soil respiration

Root biomass was variable, but on average, higher at the reference plots compared to those disturbed by pigs ( $84 \pm 63$  vs  $17 \pm 3$  mg cm<sup>-3</sup>; Table 3). Root respiration was similar or even higher than soil respiration, suggesting that most of the soil CO<sub>2</sub> emissions in the reference plots originated from root respiration (Table 4). This assumption was further supported when



comparing vegetated and unvegetated plots during the Kunumleg season, with 61% higher emissions in the vegetated plots  
260  $(130 \pm 44 \text{ (51-204) mg m}^{-2} \text{ h}^{-1})$  compared to the unvegetated plots  $(50 \pm 52 \text{ (-47 to 129) mg m}^{-2} \text{ h}^{-1})$ .

**Table 4. Root biomass, root respiration, and soil respiration of reference and disturbed plots by feral pigs.**

	Root biomass (mg cm <sup>-3</sup> )		Root respiration (mg m <sup>-2</sup> hr <sup>-1</sup> )		Soil respiration (mg m <sup>-2</sup> hr <sup>-1</sup> )	
	<i>Reference</i>	<i>Disturbed</i>	<i>Reference</i>	<i>Disturbed</i>	<i>Reference</i>	<i>Disturbed</i>
Ubirr	26.4 ± 0.7	12.9 ± 8.1	2,953 ± 546	802 ± 195	1,000 ± 49	369 ± 58
Munmarlay	22.9 ± 0.8	24.8 ± 13.1	501 ± 7.7	747 ± 114	300 ± 66	351 ± 48
Coolaboo	337	18.5	2,293	1,799 ± 580	203 ± 1	363 ± 1
Djadja	16.5	n.a.	2,808 ± 546	n.a.	1,066 ± 302	n.a.
Djabulukgu	14.6 ± 4.4	13.5 ± 8.5	1,193 ± 286	1,073 ± 322	2,062 ± 96	993 ± 355

### 3.2.6 Emission reduction potential

The potential reduction of greenhouse gas emissions through feral pig management was estimated per site during sampling in  
265 Yekke, where the most spatially comprehensive sampling occurred. We found that avoiding soil disturbance could result in  
potential CO<sub>2</sub> reductions (corrected for root respiration by 61%) at all six sites, CH<sub>4</sub> reductions in five out of six sites, and N<sub>2</sub>O  
reductions at all sites (Table 3). When transforming the gases by their warming potential (CO<sub>2-eq</sub>), reductions were highest for  
CO<sub>2</sub> with  $33 \pm 240 \text{ MgCO}_{2\text{eq}} \text{ ha}^{-1} \text{ yr}^{-1}$ , followed by N<sub>2</sub>O with  $2.0 \pm 0.2 \text{ MgCO}_{2\text{eq}} \text{ ha}^{-1} \text{ yr}^{-1}$  and CH<sub>4</sub> with  $1.7 \pm 1.7 \text{ MgCO}_{2\text{eq}} \text{ ha}^{-1}$   
yr<sup>-1</sup> (Table 5).

270

275





**Table 5. Greenhouse gas emissions (CO<sub>2</sub>, CH<sub>4</sub>, and N<sub>2</sub>O) and emission reduction potential from reference plots compared to disturbed plots by pigs in six sites in Kakadu NP. Values are mean ± standard error for five chambers within each plot and median ± propagated error for the six sites. The soil CO<sub>2</sub> emissions were corrected for root respiration (CO<sub>2-resp</sub>), which contributed approximately 61% of the emissions.**

	CO <sub>2-resp</sub> mg m <sup>-2</sup> h <sup>-1</sup>		CH <sub>4</sub> μg m <sup>-2</sup> h <sup>-1</sup>		N <sub>2</sub> O μg m <sup>-2</sup> h <sup>-1</sup>	
	Reference	Pigs	Reference	Pigs	Reference	Pigs
Ubirr	161 ± 25	463 ± 93	14.1 ± 7.3	53.5 ± 25.1	17.6 ± 10.9	210 ± 32.6
Munmarlay	111 ± 11	592 ± 117	5.2 ± 6.9	394 ± 225	15.7 ± 5.5	384.7 ± 135
Mamukala	129 ± 18	743 ± 93	0.4 ± 4.9	79.1 ± 23.0	4.2 ± 1.6	61.8 ± 18.3
Coolaboo	355 ± 49	554 ± 56	1,785 ± 751	932 ± 283	20.4 ± 9.6	548 ± 132
Djaja	209 ± 52	491 ± 99	-8.6 ± 4.6	1,024 ± 385	10.6 ± 5.5	100 ± 29.1
Djabulukgu	104 ± 14	468 ± 124	453 ± 295	4,819 ± 2,160	2.7 ± 2.0	26.6 ± 7.8
Median ± SE	178 ± 39	523 ± 43	10 ± 292	663 ± 740	11.9 ± 3.0	155 ± 84
MgCO <sub>2eq</sub> ha <sup>-1</sup> yr <sup>-1</sup>	13 ± 7	46 ± 21	0.02 ± 1.9	1.6 ± 5.3	0.3 ± 0.4	3.7 ± 4.7
Emission reductions (by difference)						
MgCO <sub>2eq</sub> ha <sup>-1</sup> yr <sup>-1</sup>	33 ± 23		1.5 ± 5.6		3.4 ± 4.7	
TOTAL emission reductions						
MgCO <sub>2eq</sub> ha <sup>-1</sup> yr <sup>-1</sup>			38 ± 24			

## 4 Discussion

The iconic wetlands of Kakadu National Park have been managed for millennia by the Bininj and Mungguy peoples. However, they currently face multiple challenges, including rising sea levels, erratic rainfall patterns, and the impacts of invasive species (Bradshaw et al., 2007b; Pettit et al., 2018). In this study, we found that beyond the known impacts of feral pigs on biodiversity (Risch et al. 2021), they also increase soil CO<sub>2</sub>, CH<sub>4</sub>, and N<sub>2</sub>O emissions, confirming that feral pigs pose a serious threat to soil carbon (O'Bryan et al., 2021). This study provides another compelling example of animal populations significantly affecting the carbon cycle at the landscape scale (Schmitz et al., 2014)

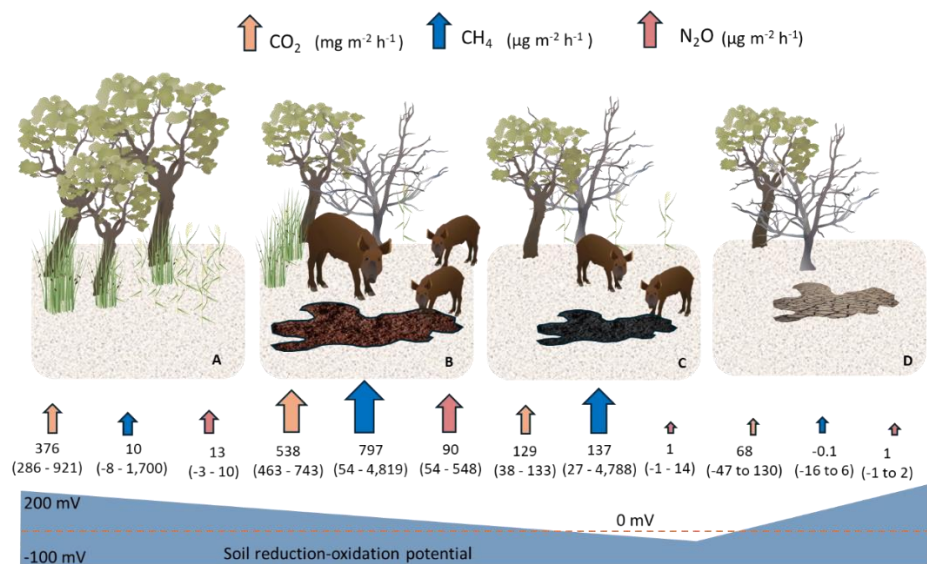
The effect of feral pigs was evident and widespread at all sites, where the soil was turned over and mostly devoid of vegetation. The disturbed plots were also colder and filled with fresh groundwater, as pigs used some of these areas to wallow or coat themselves with mud to avoid overheating (Bracke, 2011). The soil redox potential at all disturbed plots was significantly



reduced, indicating low oxygen conditions. Low oxygen or anoxic soils favour microbial respiration through nitrification-denitrification when nitrate ( $\text{NO}_3^-$ ) is available. This process produces  $\text{N}_2\text{O}$  as a byproduct, especially when the soil is high in nitrogen, such as in soils enriched with pig excreta (Krull et al., 2013). However, soil nitrogen concentrations in our plots were similar in reference and disturbed plots, suggesting that nitrogen enrichment from feral pigs was sporadic and was rapidly removed, potentially through denitrification, which can result in  $\text{N}_2\text{O}$  emissions. Due to low oxygen and potentially high nitrogen loads, the emissions of  $\text{N}_2\text{O}$  during the Yekke season were up to an order of magnitude higher than those in the reference plots.

As the dry season progresses, the weather becomes hotter, and the soil becomes drier. Consequently, pigs move closer to the waterhole fringes to exploit resources at the edge of the open water (Froese et al., 2017). The wallows left behind were highly anaerobic, with redox values close to or below zero (mV). The lack of oxygen in the soil during this time of the year resulted in high  $\text{CH}_4$  emissions, but low  $\text{N}_2\text{O}$  emissions. This result can be explained by the thermodynamics of respiration; nitrogen is more energetically favoured than carbon, but once nitrogen is exhausted and oxygen is depleted, methanogenesis becomes the dominant respiration pathway (Reddy & DeLaune, 2008). The disturbed soils showed slightly reduced  $^{13}\text{C}$  values, indicating methanogenesis. Methane has a negative isotopic value of around -60‰; thus, when produced, it significantly lowers the  $^{13}\text{C}$  value of the soil (Fry, 2006).

Once the disturbed site was completely dried up and devoid of vegetation, the carbon and nitrogen from the soil were exhausted, and fluxes decreased (Fig. 7). At this point, the  $\text{CO}_2$  emissions reached their minimum values because  $\text{CO}_2$  is the net result of two processes: root respiration and soil organic matter decomposition. During the Yekke season, reference sites were fully vegetated and had large amounts of litter accumulated on the soil surface (See Fig. 2A); thus, root respiration and litter decomposition caused high  $\text{CO}_2$  emissions. The disturbed plots had low vegetation cover and little standing litter, but likely had high decomposition rates, arising from dead root material and exposed soil organic matter, resulting in similar or higher  $\text{CO}_2$  emissions compared to the reference plots. During the Kunumleng season, the plots had dried up and had little vegetation or standing litter, resulting in the lowest  $\text{CO}_2$  emissions measured. Finally, we expect that during Kudjewk, or the monsoon season, the floodplains will overflow again, providing fresh habitat for feral pigs, which will continue to disturb the soil and release the carbon accumulated during the wetter months (Fig. 7).



**Figure 7. Schematic diagram on the greenhouse gas emission changes in a floodplain wetland (A) before pig disturbance; (B) during pig disturbance as vegetation is lost, soil redox decreases, and soil decomposition and nitrogen inputs increase, resulting in very high CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O emissions; (C) as the site is less used as animals move closer to the remaining waterholes during drier months, N<sub>2</sub>O emissions decrease but CH<sub>4</sub> emissions remain high as oxygen is very low; (D) finally, once the site is abandoned, the soil is depleted of carbon and nitrogen, redox potential increases, and fluxes are minimal. The red hashed line represents oxido-reduction potential values of zero; values close to or below this line significantly increase CH<sub>4</sub> emissions.**

Despite the strong evidence of increased emissions from pig disturbance in this study, we acknowledge some limitations. First, greenhouse gas emissions could not be measured during the wettest months due to the hazardous conditions at the location, particularly the presence of saltwater crocodiles. Emissions during these wet periods could be higher than our measurements, although seasonal differences in greenhouse gas emissions in tropical Australia tend to be relatively low (Iram et al. 2022). Second, the contribution of root versus soil respiration remains unresolved, given the confounding effect of CO<sub>2</sub> production from root respiration and soil decomposition (O'Bryan et al. 2022). We used an approximate value of 62% contribution of root respiration to our measurements, which is consistent with other studies (79%, Krauss et al. 2012), although it does not incorporate the potential absorption of CO<sub>2</sub> as it travels from the sediment to the atmosphere. However, future studies could refine this estimation, facilitating the inclusion of CO<sub>2</sub> in carbon emissions from soil disturbance.

In conclusion, we demonstrate that feral pigs pose a significant threat to the integrity of soil carbon in tropical floodplains in Australia, and likely globally. The physical activity on the soil and the increase in nitrogen through their excreta are significantly increasing emissions, especially of CH<sub>4</sub> and N<sub>2</sub>O. Tackling these two potent greenhouse gases has the potential to significantly contribute to climate change mitigation (Ocko et al., 2021), while also improving biodiversity and human health.



### Author contributions

MFA, CS, JN, VH, and CEL designed the study; MFA, AP, JMH, JT, CS, and JN carried out field experiments; MFA and JH  
345 analysed the data; MFA wrote the original manuscript, and all co-authors contributed to the editing, interpretation, and  
conclusions.

### Competing interests

The contact author has declared that none of the authors has any competing interest.

### 350 References

- Adame, M., Jardine, T., Fry, B., Valdez, D., Linder, G., Nadji, J., & Bunn, S. (2018). Estuarine crocodiles in a tropical coastal  
floodplain obtain nutrition from terrestrial prey. *PLoS ONE*, 13, 6.
- Adame, M., Pettit, N., Valdez, D., Ward, D., Burford, M., & Bunn, S. (2017). The contribution of epiphyton to the primary  
production of tropical floodplain wetlands. *Biotropica*, 49, 461–471.
- 355 Anderson, I. C., & Levine, J. (1986). Relative rates of nitric oxide and nitrous oxide production by nitrifiers, denitrifiers and  
nitrate respirers. *Applied and Environmental Microbiology*, 51(5), 938–945.
- Ballari, S. A., & Barrios-García, M. N. (2014). A review of wild boar *Sus scrofa* diet and factors affecting food selection in  
native and introduced ranges. *Mammal Review*, 44(2), 124–134. <https://doi.org/10.1111/mam.12015>
- Bracke, M. B. M. (2011). Review of wallowing in pigs: Description of the behaviour and its motivational basis. *Applied Animal*  
360 *Behaviour Science*, 132(1–2), 1–13. <https://doi.org/10.1016/j.applanim.2011.01.002>
- Bradshaw, C. J. A., Field, I. C., Bowman, D. M. J. S., Haynes, C., & Brook, B. W. (2007a). Current and future threats from  
non-indigenous animal species in northern Australia: A spotlight on World Heritage Area Kakadu National Park. *Wildlife*  
*Research*, 34(6), 419–436. <https://doi.org/10.1071/WR06056>
- Brannon, E. Q., Moseman-Valtierra, S. M., Rella, C. W., Martin, R. M., Chen, X., & Tang, J. (2016). Evaluation of laser-  
365 based spectrometers for greenhouse gas flux measurements in coastal marshes. *Limnology and Oceanography: Methods*,  
14(7), 466–476. <https://doi.org/10.1002/lom3.10105>
- Clean Energy Regulator, Australian Government, 2024. [ACCU Scheme methods | Clean Energy Regulator \(cer.gov.au\)](https://www.cer.gov.au/accu-scheme-methods)
- Doupé, R., Schaffer, J., Knott, M., & Dicky, P. (2009). A description of freshwater turtle habitat destruction by feral pigs in  
Tropical North-eastern Australia. *Herpetological Conservation and Biology*, 4, 331–339.
- 370 Erskine, W. D., Saynor, M. J., Boyden, J. M., & Evans, K. G. (2018). Sediment fluxes and sinks for Magela Creek, Northern  
Territory, Australia. *Marine and Freshwater Research*, 69(7), 1018–1025. <https://doi.org/10.1071/MF16107>
- Froese, J.G., C.S. Smith, P. A. Durr, C.A. McAlpine, R.D. van Klinken. 2017. Modelling seasonal habitat suitability for wide-  
ranging species: Invasive wild pigs in northern Australia. *PlosOne*, 12(5), e0177018.
- Fry, B. (2006). *Stable isotope ecology*. Springer Sc+ Business Media LLC.



- 375 Hamnett, P.W., F. Saltre, B. Page, M. Tarran, M. Korcz, K. Fielder, L. Andrews, & C.J.A. Bradshaw. (2024). Stochastic population models to identify optimal and cost-effective harvest strategies for feral pig eradication. *Ecopshere*, 15:e70082.
- Hone, J. (2020). How many feral pigs are in Australia? An update. *Australian Journal of Zoology*, 67(4), 215–220. <https://doi.org/10.1071/ZO20077>
- 380 Hutchinson, G. L., & Mosier, A. R. (1981). Improved soil cover method for field measurement of nitrous oxide fluxes. *Soil Science Society of America Journal*, 45(2), 311–316. <https://doi.org/10.2136/sssaj1981.03615995004500020017x>
- Intergovernmental Panel on Climate Change (IPCC). 6th assessment. United Nations. Geneva, Switzerland
- Iram, I.N., K.E. Kavechi, D. Maher, S. Bunn, R. Rashti M., B. Farahani, M.F. Adame (2021) Soil greenhouse gas fluxes from tropical coastal wetlands and alternative agricultural land uses. *Biogeosciences* 18(18) 5085-5096
- 385 Krauss, K.W., Whitbeck, J. L., Howard, R. J. (2012). On the relative roles of hydrology, salinity, temperature, and root productivity in controlling soil respiration from coastal swamps (freshwater). *Plant Soil* 358: 265-274
- Krull, C. R., Choquenot, D., Burns, B. R., & Stanley, M. C. (2013). Feral pigs in a temperate rainforest ecosystem: Disturbance and ecological impacts. *Biological Invasions*, 15(10), 2193–2204. <https://doi.org/10.1007/s10530-013-0444-9>
- Liu, Y., Liu, X., Yang, Z., Li, G., & Liu, S. (2020). Wild boar grubbing causes organic carbon loss from both top- and sub-
- 390 soil in an oak forest in central China. *Forest Ecology and Management*, 464(December 2019), 118059. <https://doi.org/10.1016/j.foreco.2020.118059>
- Matthews, H. D., Zickfeld, K., Dickau, M., MacIsaac, A. J., Mathesius, S., Nzotungicimpaye, C.-M., & Luers, A. (2022). Temporary nature-based carbon removal can lower peak warming in a well-below 2 °C scenario. *Communications Earth & Environment*, 3(1), 1–8. <https://doi.org/10.1038/s43247-022-00391-z>
- 395 O’Bryan, C. J., Patton, N. R., Hone, J., Lewis, J. S., Berdejo-Espinola, V., Risch, D. R., Holden, M. H., & McDonald-Madden, E. (2021). Unrecognized threat to global soil carbon by a widespread invasive species. *Global Change Biology*, 28(3), 877-882
- O’Bryan, C. J., Patton, N. R., Hone, J., Lewis, J. S., Berdejo-Espinola, V., Risch, D. R., Holden, M. H., & McDonald-Madden, E. (2022). Invasive wild pigs (*Sus scrofa*) as a human-mediated source of soil carbon emissions: Uncertainties and future
- 400 directions. *Global Change Biology*, 28(3), e1–e3. <https://doi.org/10.1111/gcb.15992>
- Ocko, I.B., T. Sun, D. Shindell, M. Oppenheimer, A.N. Hristov, S.W. Pacala, D. L. Mauzerall, Y. Xu & S.P. Hamburg. (2021). Acting rapidly to deploy readily available methane mitigation measures by sector can immediately slow global warming. *Environmental Research Letters*. 16, 054042.
- Pettit, N. E., Bayliss, P., & Bartolo, R. (2018). Dynamics of plant communities and the impact of saltwater intrusion on the floodplains of Kakadu National Park. *Marine and Freshwater Research*, 69(7), 1124–1133. <https://doi.org/10.1071/MF16148>
- Reddy, K. R., & DeLaune, R. D. (2008). *Biogeochemistry of Wetlands*. CRC Press, Taylor and Francis Group.



- Risch, D.R., J. Ringma, & M. Price. (2021). The global impact of wild pigs (*Sus scrofa*) on terrestrial biodiversity. *Scientific Reports* 11, 13256
- 410 Robinson, C. J., Macdonald, J. M., Douglas, M., Perry, J., Setterfield, S., Cooper, D., Lee, M., Nadji, J., Nadji, S., Nayinggul, A., Nayinggul, A., Mangiru, K., Hunter, F., Coleman, B., Barrowei, R., Markham, J., Alderson, J., Moyle, F., May, K., & Bangalang, N. gangila. (2022). Using knowledge to care for country: Indigenous-led evaluations of research to adaptively co-manage Kakadu National Park, Australia. *Sustainability Science*, 17(2), 377–390. <https://doi.org/10.1007/s11625-021-01015-9>
- 415 Rosentreter, J. A., Borges, A. V., Deemer, B. R., Holgerson, M. A., Liu, S., Song, C., Melack, J., Raymond, P. A., Duarte, C. M., Allen, G. H., Olefeldt, D., Poulter, B., Battin, T. I., & Eyre, B. D. (2021). Half of global methane emissions come from highly variable aquatic ecosystem sources. *Nature Geoscience*, 14(4), 225–230. <https://doi.org/10.1038/s41561-021-00715-2>
- Rowland, P. I., & Lovelock, C. E. (2024). Global impacts of introduced ungulates on wetland carbon and biodiversity: A review. *Biological Conservation*, 290(October 2023), 110432. <https://doi.org/10.1016/j.biocon.2023.110432>
- 420 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>
- 425 Schmitz, O. J., Raymond, P. A., Estes, J. A., Kurz, W. A., Holtgrieve, G. W., Ritchie, M. E., Schindler, D. E., Spivak, A. C., Wilson, R. W., Bradford, M. A., Christensen, V., Deegan, L., Smetacek, V., Vanni, M. J., & Wilmers, C. C. (2014). Animating the carbon cycle. *Ecosystems*, 17(2), 344–359. <https://doi.org/10.1007/s10021-013-9715-7>
- Waltham, N., & Schaffer, J. (2018). Thermal asphyxia exposure risk to freshwater fish in feral-pig damaged tropical wetlands. *Journal of Fish Biology*, 93, 723–728.
- 430 Ward, D. P. P., Pettit, N. E. E., Adame, M. F., Bunn, S. A. E. S. E., Douglas, M. M. M., Setterfield, S. E. A. S. A., & Bunn, S. A. E. S. E. (2016). Seasonal spatial dynamics of floodplain macrophyte and periphyton abundance in the Alligator Rivers region (Kakadu) of northern Australia. *Ecohydrology*, 9(8), 1675–1686. <https://doi.org/10.1002/eco.1757>
- Yvon-Durocher, G., Allen, A. P., Bastviken, D., Conrad, R., Gudas, C., St-Pierre, A., Thanh-Duc, N., & Del Giorgio, P. A. (2014). Methane fluxes show consistent temperature dependence across microbial to ecosystem scales. *Nature*, 507(7493), 488–491. <https://doi.org/10.1038/nature13164>
- 435