Soil disturbance in wetlands by feral pigs increases greenhouse gas emissions

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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_2, methane, CH_4, and nitrous oxide, N_2O) 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_4 were significantly different among treatments, with emissions being higher at disturbed plots (median (IQR) of 663 (845) µg m^{-2} hr^{-1}) compared to reference plots (10 (342) µg m^{-2} hr^{-1}). The most notable differences were observed for N_2O, with significantly higher emissions from disturbed plots (155 (270) µg m^{-2} hr^{-1}), which were up to an order of magnitude higher than those from the reference plots (13 (11) µg m^{-2} hr^{-1}). Soil surface redox values were correlated with emissions in plots disturbed by pigs, with negative values associated with high CH_4 emissions. The highest emissions were found in recently disturbed sites. This study provides a compelling example of how animal populations can significantly impact greenhouse gas fluxes at the landscape scale. It also provides evidence for the viability of a carbon methodology to reduce greenhouse gas emissions through feral pig management, supporting both culture and nature.

1 Introduction

As climate change and other 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 potential 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_4) and nitrous oxide (N_2O) emissions. These potent greenhouse gases are emitted in large quantities in wetlands, 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; Traby and Grover 2023). 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 across Australia and a mean density of one pig per square kilometre (Hone, 2020). Feral pigs are common in wetlands, where they cause extensive soil damage, 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 their environmental and human impacts (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 $MtCO_2$ per year and a wide range from -30.3 to 94 million $MtCO_2$), 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 associated. The Traditional Owners of Kakadu are the Bininj in the north and Mungguy in the south, and together, they manage and lead research 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_2, CH_4, and N_2O) by comparing 1) six paired sites distributed across two floodplains with and without soil pig disturbance, 2) variability from time of disturbance (recent and past), and 3) variability within two seasons: Yekke, the cool post-monsoon season, and Kunumeleng, the dry and hot pre-monsoon season. We hypothesised that pig disturbance in wetlands would alter soil physicochemical properties. We predict that nitrogen inputs 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 removal of vegetation and increased microbial activity (Doupé et al., 2009; Liu et al., 2020). We expect these changes to result in increased soil CH_4 emissions and incomplete nitrification-denitrification, which increases N_2O emissions (Anderson & Levine, 1986). 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_4 production (Yvon-Durocher et al., 2014).

2 Methods

2.1 Study site and sampling design

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 season (April), Yekke or cool and humid season (May to mid-June), Wurrkeng or cold season (mid-June to mid-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 rivers are deposited, and dense vegetation grows (Ward et al. 2016, Erskine et al., 2018). These floodplains remain inundated for about five months per year (Ward et al., 2014). During the dry season, flooding recedes, and permanent deep-water holes remain in the floodplain until the next wet season, when they are once again reconnected to the river channel

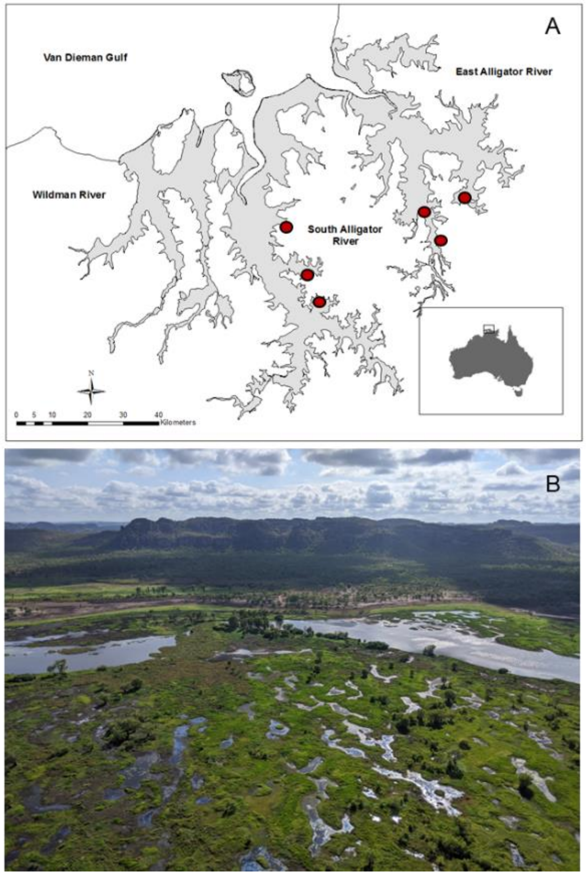


Figure 1. (A) Location of Kakadu National Park in northern Australia, and sampling sites (north to south): Munmarlay, Coolaboo, Mamukala in the South Alligator and Ubirr, Djabulukgu and Dja Dja in the East Alligator, (B) floodplain wetlands of the Magela Creek adjacent to the East Alligator River. Grey areas represent the extent of the floodplain (modified from Ward et al. 2014). Picture by MF Adame.

We conducted two field campaigns: one during Yekke (8-14th June 2023), the cool season, and one during Kunumeleng (25-30th October 2023), the hot, pre-monsoon season. Both sampling trips were preceded by dry conditions with no precipitation in the previous 30 days and mean daily temperatures ranging from 33-36 °C during sampling in Yekke and 38-40 °C in Kunumeleng (Jabiru Airport Station, 14198, Australian Bureau of Meteorology). 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. For our first trip, six sites were selected by the Traditional Owners (co-authors of this study). 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 two plots at each site: a reference plot, either a paperbark forest or a grass-dominated area (Coolaboo) 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 caused by pigs, feral water buffalo (*Bubalus bubalis*) may have also contributed, as buffalo wallows and tracks were observed at Dja Dja, Ubirr, and Munmarlay.

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 treatment plots (reference, recent, and past disturbance) 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).

Reference | Recent disturbance | Past disturbance

Figure 2. Examples of (A) a reference or undamaged plot at Djabulukgu, (B) a plot with recent disturbance at Coolaboo, and (C) plots with past disturbance, which were dry and unvegetated (Djabulukgu). Pictures by JM Hall.

2.2 Soil physicochemical characteristics

At each plot, surface (0-2 cm deep) reduction-oxidation potential (redox; 3-5 measurements) and soil temperature were determined with a redox meter (HQ 11d ORP- meter, Hach, calibrated against ZoBell's Solution). Redox from reference and past disturbed sites during the Kunumeleng season could not be measured as the soil was completely dry. Three surface (0- 5 cm) 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 (C, after testing for inorganic carbon, through HCl addition), nitrogen (N), $\delta^{13}C$, and $\delta^{15}N$ (from acidified and unacidified samples, respectively; 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 µm (fine silt and clay), >20 µm (medium and coarse silt) $\leq$, > 63 µm (very fine sand) $\leq$, >125 µm (fine, medium and coarse sand) $\leq$, and > 2 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 soil-to-water (1:5) solution 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). The chambers were installed right before the measurements, hammered into the soil at least 3 cm deep, acknowledging some disturbance to the soil. After 15 minutes of deployment, gas samples were collected from the headspace of the chambers using a plastic 30 mL syringe with a 26G needle and transferred to 12mL vacuumed glass containers (flat-bottom, 103 mm length, 15.5 mm diameter, Labco Exetainer). The air samples were collected at 0 and 60 min at all chambers and at 0, 20, 40, and 60 min in one chamber per plot. During each sampling, the headspace was mixed with the syringe three times before the air sample was retrieved.

Back in the laboratory, the CO_2, CH_4, and N_2O concentrations within each sample were measured in a gas chromatograph (Shimadzu GC-2010 Plus, DESITI, Queensland Government). The analyses had accuracies of 0.2%, 0.5%, and 1.5% for CO_2, CH_4, and N_2O, respectively. Air temperature next to the chambers was monitored throughout the experiment with a handheld thermometer. The chamber with continuous measurements was checked for linearity using a regression of time for each gas within each plot. Coefficients for each regression are shown in Table S1; chambers with poor fit ($R^2 < 50$) were identified at sites with very low N_2O fluxes or very high CH_4 emissions. Because CH_4 is characterised by nonlinearity and spikes due to ebullition, outliers were retained in the calculations, although median values along with interquartile ranges were used to provide conservative estimates. Only one emission value of CH_4 in a disturbed site by pigs, which was three orders of magnitude higher than the rest of the chambers within the same plots, was removed from calculations (Coolaboo, chamber D, during Kunumeleng season). Fluxes (F) were calculated per hour from the net changes in gas concentrations (N, mol) during the incubation time (*t*, hours), per volume of the chamber (*V*, m3), at a given air temperature (*T*, °K), assuming a pressure of one atmosphere:

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

Equation 1

where,

R = 8.205 × 10-5 m3 atm^{-1} K^{-1} mol^{-1}

2.4 Root respiration

Soil CO_2 fluxes are a combination of the decomposition of organic matter and dead roots and the respiration of live roots, the latter contributing up to 79% of the total (Krauss et al. 2012). To test the contribution of root respiration to soil CO_2 emissions, we compared CO_2 emissions from the unvegetated and vegetated plots measured during the Kunumeleng season. Additionally, we measured root biomass at each reference and disturbed plot by sampling the surface (top 10cm) with a sediment corer (7.3 cm diameter). 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 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. Root respiration was converted to aerial emissions, considering the area of root sampled (22.9 cm^2). We acknowledge the limitations of this approach, as root respiration was measured once roots were extracted from the soil, without accounting for the effects of the aboveground vegetation and the soil profile vegetation, which could consume CO_2 through photosynthesis and other non-photosynthetic pathways (Rodriguez *et al* 2025). Furthermore, direct root respiration cannot be distinguished with certainty from organic matter decomposition without the use of additional tracers, such as ^{14}C (Trumbore *et al* 2006). Thus, our estimations on root respiration contributions to CO_2 emissions should be interpreted as a first-step calculation.

2.5 Emission reduction potential

To estimate the carbon abatement potential of feral pig management, CH_4 and N_2O fluxes were converted to CO_{2eq} by multiplying them by their 100-year warming potential, which is 27 for CH_4 (non-fossil origin) and 273 for N_2O (IPPC, AR6 Sixth Assessment Report, 2021). Fluxes of CO_2 were included after being corrected for root respiration.

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) nested within site was conducted to test differences between disturbed (recent and past) and reference plots across the six sites for gas fluxes (CO_2 and N_2O) and physicochemical parameters (soil conductivity, temperature, redox, soil C, N, C:N, $\delta^{15}N$ and $\delta^{13}C$). For datasets that did not comply with normality (CH_4 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^{-1}, 27.8 ± 1.7°C, 206.3 ± 53.6 mV) compared to the disturbed plots (56.7 ± 7.6 µS cm^{-1}, 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^3 versus 53.2 ± 5.2 % and 0.45 ± 0.08 05 g cm^{-3} for reference and disturbed plots, respectively; Table 1).

Surface soil C and N, and molar C:N were also similar between reference (8.1 ± 1.1% C and 0.63 ± 0.09% N, 9.7 ± 0.9) and disturbed plots (8.5 ± 1.4% C and 0.68 ± 0.10% N, 10.8 ± 0.7; $p = 0.480$, $p = 0.312$, and $p = 0.251$, respectively). Soil $\delta^{15}N$ did not differ between treatments, with 2.73 ± 0.60‰ for reference compared to 2.74 ± 0.17‰ for disturbed plots (Table 2). However, $\delta^{13}C$ was slightly but significantly lower at the reference plots (-22.6 ± 1.7‰) compared to the disturbed ones (-21.4 ± 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, coarse and fine) and clay, while Munmarlay and Coolaboo were dominated by fine silt and clay (Table 3).

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

Table 2. Soil carbon, nitrogen, molar C:N, isotopic composition ($\delta^{15}N$ and $\delta^{13}C$) 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 $\delta^{13}C$, which was significantly lower in the reference 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

	$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)		Bulk density (g cm^{-3})	
	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	**35.6**	19.9	27.5	**47.9**
Munmarlay	1.2	1.2	8.8	28.9	10.5	6.0	15.0	13.7	**64.4**	**50.1**
Mamukala	6.9	6.5	**61.3**	**63.7**	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	**35.0**	**95.8**
Dja Dja	4.2	1.2	**46.2**	**51.6**	15.5	12.7	11.0	17.0	23.1	17.5
Djabulukgu	12.4	0.5	**55.3**	31.9	7.5	18.5	6.7	9.9	18.1	**39.2**

3.2 Greenhouse gas emissions

3.2.1 Impact of pig disturbance

During Yekke or the cool season, CO_2 emissions were significantly different among sites ($F_{5,48}$ = 3.88 p = 0.005) and similar between disturbed and reference plots ($F_{1,48}$ = 2.90 p = 0.095; Fig.3A). Fluxes of CH_4 were highly variable, but marginally higher (W = 15: n = 49, p = 0.063) at disturbed plots (1,219 ± 740, 54 to 4,823 µg m^{-2} hr^{-1}) compared to reference plots (93 ± 90, -8.6 to 454 µg m^{-2} hr^{-1}), 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_2O, with emissions at disturbed plots ($F_{1,48}$ = 32.2, $p < 0.001$) of 222 ± 84.1 (26.6 to 549) µg m^{-2} hr^{-1}, which were up to an order of magnitude higher than those for the reference sites with 11.9 ± 3.0 (2.7 to 20.4) µg m^{-2} hr^{-1} (Fig. 3C).

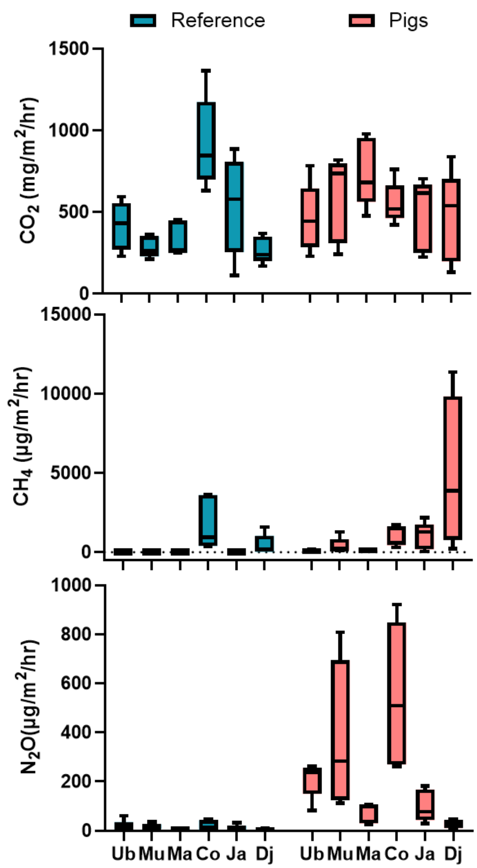


Figure 3. Greenhouse gas emissions (CO_2, CH_4 and N_2O) from reference plots (blue-left) and plots disturbed by feral pigs (red-right) for six sites across the floodplains during the Yekke season in Kakadu National Park: Ub = Ubirr, Mu = Munmarlay, Ma = Mamukala, Co = Coolaboo, Ja = Djaja, Dj = Djabulukgu. The box plots show the mean and standard error for five chambers at five plots within five sites; 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 past or recently used by pigs, was assessed during Kunumeleng or the pre-monsoon season. At this time, CO_2 emissions were highest at the reference plots, compared to those that were past and recently disturbed ($F_{2,36}$ = 6.84 p = 0.003; Fig. 4A). The time of disturbance significantly affected the CH_4 emitted, with higher emissions, although not significantly different, at the newly disturbed plots ($F_{2,35}$ = 2.0; p = 0.15) compared to plots with past disturbance and reference sites (Fig. 4B). Finally, N_2O emissions were similar among treatments ($F_{2,36}$ = 0.93; p = 0.40). However, there was a trend of higher N_2O emissions at the recently disturbed sites (Fig. 4C).

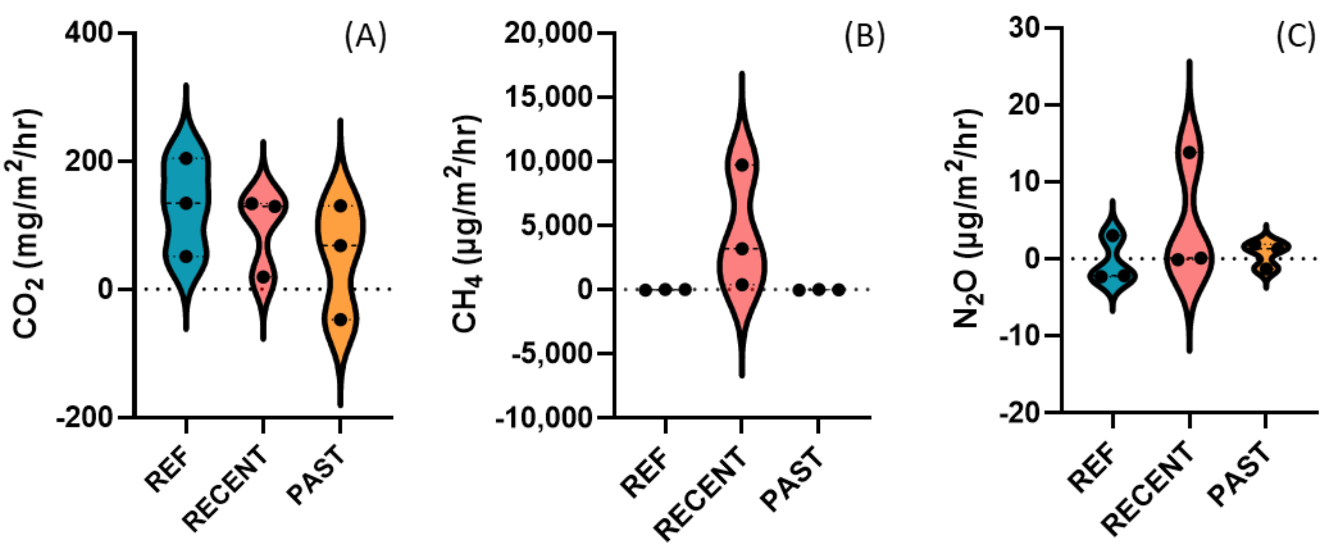
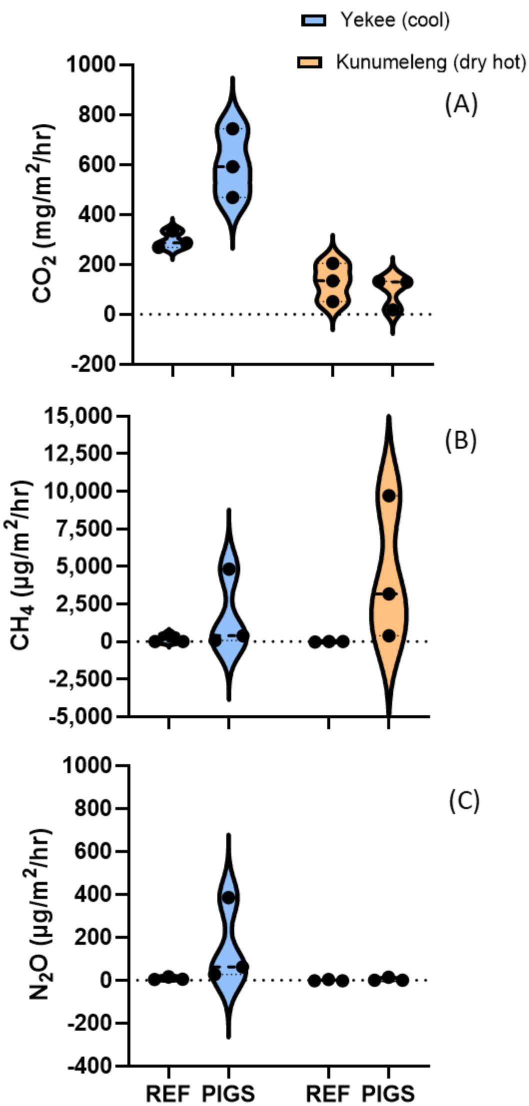


Figure 4. Greenhouse gas (CO_2, CH_4, and N_2O) fluxes of reference sites (REF- blue), sites previously used by pigs (PAST- orange), and recently used by pigs (RECENT-red). Violins represent the distribution of the average of five chambers of three plots within three sites (Djabulukgu, Mamukala, and Munmarlay) during Kunumeleng (pre-monsoon) season.

3.2.3 Variability between seasons

The CO_2 emissions were significantly lower during the Kunumeleng (pre-monsoon) season compared to the Yekke (cool) season ($F_{1,8}$ = 45.1; p = 0.0001; Fig. 5A). However, CH_4 and N_2O emissions were not significantly different ($F_{1,8}$ = 3.66; p = 0.0 and $F_{1,8}$ = 1.85; p = 0.21, respectively; Fig. 5B, C). Redox potential in the disturbed plots was lower during Kunumeleng (mean of three sites of 12.2 ± 44.3 mV) than during Yekee (mean of five sites of 67.7 ± 15.5 mV).



265 **Figure 5. Greenhouse gas (CO_2, CH_4 and N_2O) fluxes for two seasons: Yekke or cool season (blue-left) and Kunumeleng or pre-monsoon season (orange-right), for three plots without (REF-reference) and with feral pig disturbance (PIGS). Violins represent the distribution of the average of five chambers at three plots within three sites (n = 3; Djabulukgu, Mamukala, and Munmurlay-Coolaboo).**

3.2.4 Physicochemical factors associated with emissions

Two parameters analysed were strongly associated with greenhouse gas fluxes: pig disturbance and soil redox. Soils disturbed by pigs had lower redox potential than reference soils or soils from plots with past disturbance. Low redox values were correlated with high CH_4 emissions, and although the correlation was significant, the regression was poorly fitted to a linear trend (Fig. 6; R^2 = 0.087, p = 0.012). Additionally, redox values between 0-100mV were associated with increased N_2O 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 soil redox and emissions; anaerobic soil with redox values lower or close to zero promoted CH_4 emissions and soils with redox values between 0-100 mV promoted N_2O emissions, but only in plots disturbed by pigs (Fig. 6).

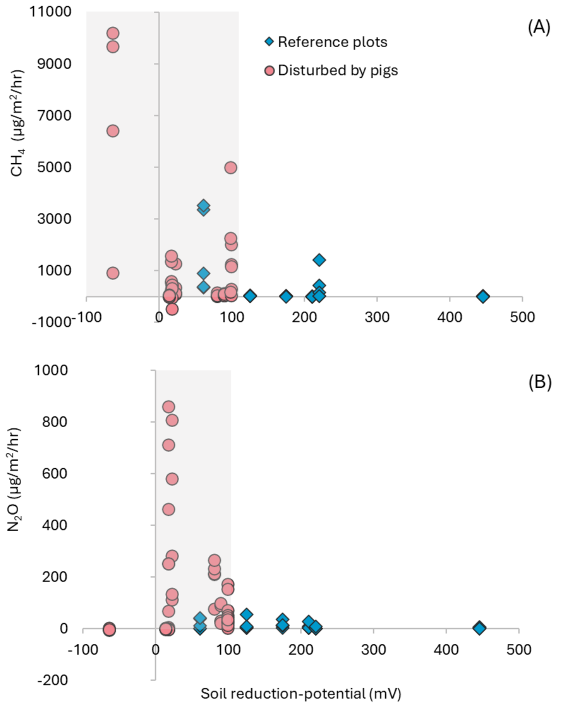


Figure 6. Relationship between soil redox (reduction-potential, mV) and (A) CH_4 and (B) N_2O fluxes (µg m^{-2} hr^{-1}) from reference (blue diamonds) and disturbed (red circles) plots by feral pigs. Lower (< 100 mV) redox values were associated with higher CH_4 emissions, and values between 0 and 100 mV were associated with higher N_2O emissions, but only at plots disturbed by pigs. Shaded areas represent redox conditions that favoured CH_4 (< 100 mV; A) and N_2O (0-100 mV; B) emissions.

3.2.5 Root versus soil respiration

Root biomass was variable, but, on average, higher in the reference plots than in those disturbed by pigs (84 ± 63 vs 17 ± 3 mg cm^{-3}; Table 4). Root respiration was higher than soil CO_2 emissions measured directly in the field, suggesting that most of the soil CO_2 emissions in the reference plots originated from root respiration (Table 4). This assumption was further supported when comparing vegetated and unvegetated plots during the Kunumeleng season, with 61% higher emissions in the vegetated plots (130 ± 44 (51-204) mg CO_2 m^{-2} h^{-1}) compared to the unvegetated plots (50 ± 52 (-47 to 129) mg CO_2 m^{-2} h^{-1}).

Table 4. Root respiration and biomass from the top 10 cm during the Kunumeleng in reference and disturbed plots by feral pigs.

	Root respiration ($mg\ m^{-2}\ hr^{-1}$)	Root biomass ($mg\ cm^{-3}$)	
		Reference	Disturbed
Ubirr	2,953 ± 546	26.4 ± 0.7	12.9 ± 8.1
Munmarlay	501 ± 7.7	22.9 ± 0.8	24.8 ± 13.1
Coolaboo	2,206	337	18.5
Djadja	2,808 ± 546	16.5	n.a.
Djabulukgu	1,193 ± 286	14.6 ± 4.4	13.5 ± 8.5

3.2.6 Emission reduction potential

The potential reduction in greenhouse gas emissions from feral pig management was estimated per site during Yekke, when the most spatially comprehensive sampling was conducted. We found that avoiding soil disturbance could result in potential CO_2 reductions (corrected for root respiration by 61%) at all six sites, CH_4 reductions in five out of six sites, and N_2O reductions at all sites (Table 5). When transforming the gases by their warming potential (CO_{2-eq}), reductions (propagated error) were highest for CO_2 with 378 ± 136 $mgCO_{2eq}\ m^{-2}\ hr^{-1}$, followed by N_2O with 39 ± 74 $mgCO_{2eq}\ m^{-2}\ hr^{-1}$ and CH_4 with 18 ± 25 $mgCO_{2eq}\ m^{-2}\ hr^{-1}$.

Table 5. Greenhouse gas emissions (CO_2, CH_4, and N_2O) and emission reduction potential from reference plots compared to disturbed plots by pigs in six sites in Kakadu NP during the Yekke season. Values are mean ± standard error for five chambers within each plot and median (IQR, interquartile range) for the six sites. The soil CO_2 emissions were corrected for root respiration ($CO_{2\text{-resp}}$), which contributed approximately to 61% of the emissions.

	$CO_{2\text{-resp}}$ mg m^{-2} h^{-1}		CH_4 µg m^{-2} h^{-1}		N_2O µg m^{-2} h^{-1}	
	Reference	Pigs	Reference	Pigs	Reference	Pigs
Ubirr	161 ± 26	463 ± 93	14.1 ± 7.3	53.5 ± 25.1	17.5 ± 10.7	210 ± 32.6
Munmarlay	110 ± 11	591 ± 117	5.2 ± 6.9	394 ± 225	15.7 ± 5.5	385 ± 135
Mamukala	129 ± 18	743 ± 93	0.4 ± 4.9	79.3 ± 23.0	4.2 ± 1.6	61.8 ± 18.3
Coolaboo	355 ± 49	555 ± 56	1,785 ± 751	932 ± 283	20.4 ± 9.6	549 ± 132
Djaja	209 ± 52	491 ± 99	-8.6 ± 4.6	1,027 ± 386	10.6 ± 5.5	100 ± 29.1
Djabulukgu	104 ± 14	468 ± 124	454 ± 296	4,823 ± 2,161	2.7 ± 2.0	26.6 ± 7.8
Median (IQR)	145 (82)	523 (108)	10 (342)	663 ± 845	13 ± 11	155 ± 270

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 greenhouse gas emissions, confirming that feral pigs pose a serious threat to soil carbon and other biogeochemical cycles (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, suggesting low oxygen conditions. Low redox soils favour microbial respiration through nitrification-denitrification when nitrate (NO_3^-) is available. This process produces N_2O as a byproduct, especially in soils high in nitrogen, such as those 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 N_2O emissions. Due to potential low oxygen and high nitrogen loads, N_2O emissions during the Yekke season were up to an order of magnitude higher than those from 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). During this season, understorey vegetation and litter were scarce, limiting organic carbon inputs into the soil and potentially causing reduced CO_2 fluxes compared to Yekke. The wallows left behind had soils with redox values near or below zero (mV). The lack of oxygen in the soil during this time of the year resulted in high CH_4 emissions, but low N_2O 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). These results complement previous studies showing the effect of hoofed animals in increasing CH_4 emissions in wetlands (Treby and Grover, 2023).

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 CO_2 emissions reached their minimum values because 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 CO_2 emissions. The disturbed plots had low vegetation cover and little standing litter but likely had high decomposition rates, driven by dead root material and exposed soil organic matter, resulting in CO_2 emissions similar to or higher than those of the reference plots. During the Kunumeleng season, the plots had dried up and had little vegetation or standing litter, resulting in the lowest 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).

Despite the strong evidence of increased emissions from pig disturbance in this study, there are limitations for extrapolating our results to annual rates. 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 from *Melaleuca* wetlands during flooding periods in the region are higher for CH_4 but lower for CO_2 (Bass et al. 2014), and year-to-year variations in emissions are likely under different pre-flooding conditions, with lower emissions in floods preceded by dry periods (Jeffrey et al. 2019). Second, the contribution of root versus soil respiration remains unresolved, given the confounding effects of CO_2 production from root respiration and soil decomposition (O'Bryan et al. 2022). We used an approximate value of 62% contribution of root respiration in our measurements, consistent with other studies (79%; Krauss et al. 2012). However, future studies could refine this estimate, facilitating the inclusion of CO_2 in carbon emissions from soil disturbance.

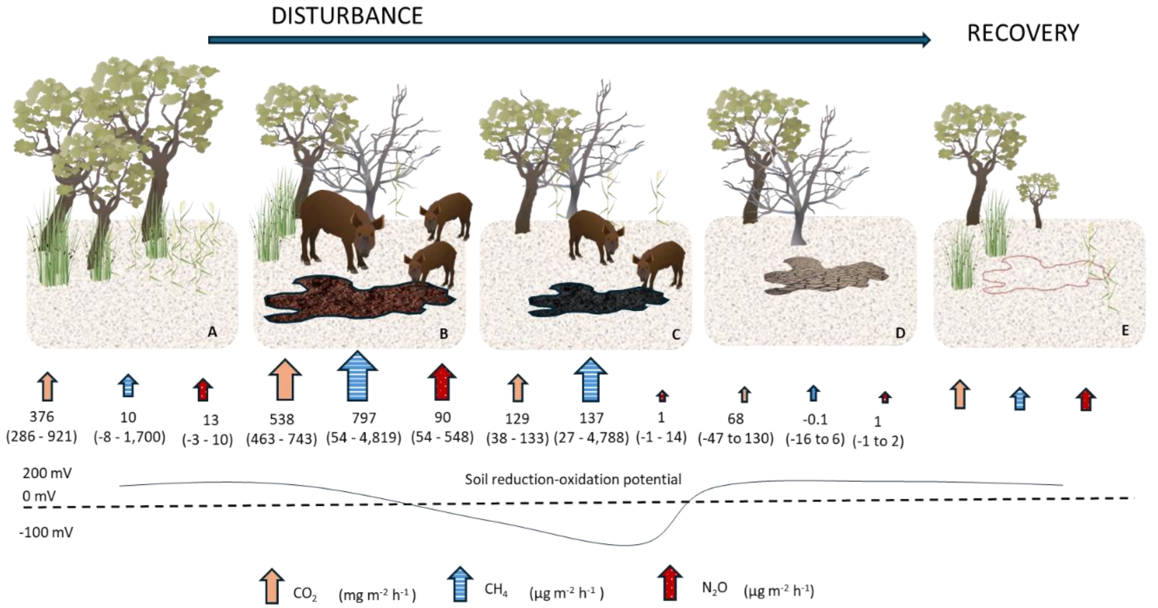


Figure 7. Schematic diagram on the greenhouse gas emission changes in a floodplain wetland (A) before pig disturbance; (B) during pig disturbance as vegetation is lost, soil redox decreases, and soil decomposition and nitrogen inputs increase, resulting in very high CO_2, CH_4 and N_2O emissions; (C) as the site is less used as animals move closer to the remaining waterholes during drier months, N_2O emissions decrease but CH_4 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; (E) potential pathway of recovery if feral pigs are managed. The hashed line represents oxido-reduction potential values of zero; values close to or below this line significantly increase CH_4 emissions.

We cautiously estimate annual emissions from pig disturbance using our data, supplemented by published estimates of emissions during flooding (Bass et al. 2014). We consider emissions from flooded *Melaleuca* swamps to be representative of reference sites and open-water areas without vegetation to represent sites damaged by pigs. Seasonal differences were included in our estimations, considering that the wet seasons Kudjewk and Bangkerrent seasons span from 20 Dec- 30 April, the cool seasons, Yekke and Wurrkeng, from 1st May- 15th August (data from this study), and the hot dry seasons, Kurrung and Kunumeleng seasons, span from 16th Aug to 19th December (data from this study). We estimate that annual emission reductions by comparison (reference vs disturbed) are 13.2 Mg CO_2 ha^{-1} yr^{-1}, 1.1 Mg CH_4 ha^{-1} yr^{-1}, and 0.004 Mg N_2O ha^{-1} yr^{-1}, equivalent to reductions of 43.4 Mg $CO_{2\text{-eq}}$ ha^{-1} yr^{-1}. We can then extrapolated these emissions to the Kakadu and adjacent river floodplains (See Fig 1; 356,800 ha, Ward et al. 2014) considering that about 10% of the area is disturbed by pigs (unpublished data). We estimate emissions of 0.47, 1.04, and 0.04 Mt $CO_{2\text{-eq}}$ yr^{-1} for CO_2, CH_4, and N_2O, respectively, or a total of 1.5 Mt $CO_{2\text{-eq}}$ yr^{-1}. These levels of emissions are equivalent to 5.6% of the Northern Territory's emissions in Australia, or 57.4% of the Territory's agricultural emissions. Although we have acknowledged the limitations of our calculations and the challenge of removing the thousands of pigs inhabiting these wetlands, it is clear that there is significant potential to reduce greenhouse gas emissions through feral pig control.

In conclusion, we demonstrate that feral pigs pose a significant threat to soil carbon integrity and significantly modify soil biogeochemical processes, increasing greenhouse gas emissions. These effects, measured in this study in tropical floodplains in Australia, are likely to occur in wetlands worldwide. Physical activity in the soil and the increase in nitrogen from pig excreta are significantly increasing emissions, especially of CH_4 and N_2O. Tackling these two potent greenhouse gases exacerbated by feral pigs has the potential to significantly contribute to climate change mitigation (Ocko et al., 2021), while also improving biodiversity and culture.

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 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.

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Supplementary Material

Table S1.Regression coefficients for greenhouse gas emission for reference plots and plots with pig damage during the Kunumeleng season.

	Reference			**Pigs**			**Reference**			**Pigs**		
	CO_2						**CH_4**					
SITE	*b*	*m*	R^2	*b*	*m*	R^2	*b*	*m*	R^2	*b*	*m*	R^2
UB	577	28.5	1.00	528	14.9	0.93	1.8	0.0002	0.10	1.7	0.006	0.90
MU	562	14.2	0.94	596	13.2	0.50	1.7	0.002	0.83	2.2	0.11	0.60
MA	539	11.0	1.00	612	33.6	1.00	1.8	0.002	0.83	1.9	0.003	0.52
CO	599	24.2	0.98	487	21.2	0.99	1.9	0.06	0.99	5.3	0.36	0.92
JA	553	15.1	0.99	457	24.8	1.00	2.0	-0.002	0.96	2	0.01	0.92
DJ	462	14.2	1.00	514	33.3	1.00	1.7	0.004	0.87	11.4	1.0	0.92
	N_2O											
UB	0.34	0.0002	0.42	0.35	0.009	0.99						
MU	0.33	0.002	0.94	0.38	0.005	0.63						
MA	0.34	0.0001	0.12	0.35	0.001	0.89						
CO	0.34	0.0001	0.79	0.43	0.036	1.00						
JA	0.32	0.0001	0.50	0.32	0.007	1.00						
DJ	0.32	0.0001	0.29	0.31	0.001	0.95						

Table S2 Regression coefficients for greenhouse gas emission for reference plots and plots with recent and past pig damage during the Yekee season.

	Reference			**PIGS Recent**			**PIGS Past**		
	CO_2								
SITE	*b*	*m*	R^2	*b*	*m*	R^2	*b*	*m*	R^2
MU	560	-0.7	0.64	619	7.9	1.00	553	3.0	0.93
MA	655	0.27	0.01	620	3.6	0.40	544	3.4	0.99
DJ	889	1.3	0.02	571	7.2	0.78	828	4.6	0.72
	CH_4								
MU	1.8	0.002	0.71	2.6	0.042	0.98	1.9	-0.002	0.72
MA	1.9	0.001	0.26	328	2.3	0.08	2.2	-0.002	0.50
DJ	1.9	-0.001	0.15	54	0.85	0.33	1.7	-0.003	0.79
	N_2O								
MU	0.35	-0.0001	0.40	0.36	0.002	0.99	0.34	0.0001	0.10
MA	0.34	0.0001	0.22	0.32	0.001	0.01	0.35	-0.00001	0.35
DJ	0.35	-0.0002	0.54	0.35	-0.0002	0.72	0.34	0.0001	0.54