Key Points:
- Feral ungulate damage resulted in a 4-fold increase in combined CO_2 and CH_4 emissions during the early dry season compared with undamaged sites
- Wetland GHG emissions declined significantly from the early to late dry season as soils dried and salinity increased
- Ungulate exclusion plots had higher belowground biomass, but changes to soil organic carbon (SOC) and total nitrogen (TN) were not detected

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Feral Ungulate Impacts on Carbon Cycling in a Coastal Floodplain Wetland in Tropical Northern Australia

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Abstract Coastal wetland ecosystems play critical roles in mitigating climate change by sequestering substantial amounts of carbon in vegetation and sediments. The Laynhapuy Indigenous Protected Area, northern Australia, includes culturally significant floodplains that support diverse coastal wetlands. The Yirralka Rangers and Yolŋu Traditional Owners who manage this region have identified invasive ungulates as a key threat to wetlands. Paperbark forests, with species known to Yolŋu as *raŋan* (*Melaleuca viridiflora*) and *nämbarra* (*Melaleuca cajuputi*), have experienced ungulate damage combined with dieback due to saltwater intrusion. Sedgelands, dominated by culturally significant *räkay* (*Eleocharis dulcis*), suffer annual soil and vegetation damage caused by invasive pigs (*Sus scrofa*) and buffalo (*Bubalus bubalis*). The Rangers and Macquarie University scientists established an ungulate exclusion fenced plot array in 2018 across a supratidal paperbark forest and sedgeland on the Gurrumuru floodplain. To assess carbon cycle impacts, belowground carbon stocks in sediments and biomass were quantified, along with greenhouse gas (GHG) emissions across the plot array. Our findings revealed fourfold higher GHG emissions (combined CO_2 and CH_4) in locations damaged by invasive ungulates compared to undamaged sites in the early dry season. Belowground biomass increased by 21%–104% within exclusion plots compared with damaged plots. No significant differences in soil organic carbon (SOC) and total nitrogen (TN) stocks or rates of litter decomposition were found between damaged and undamaged plots. This study contributes to potential carbon crediting methods focused on reducing feral ungulate impacts to wetlands, that could help fund coastal floodplain wetland management.

Plain Language Summary Northern Australian wetlands attract feral pigs and buffalo leading to damaged soils and vegetation as well as reduced water quality. The Yolŋu Traditional Owners of the Laynhapuy Indigenous Protected Area have long seen and noted these impacts. These disturbances can affect wetland carbon cycles, increase CO_2 and CH_4 emissions, reduce soil carbon, and change plant composition above- and belowground. In this study, we used fences to keep pigs and buffalo out of parts of a floodplain wetland in northeast Arnhem Land to measure the difference between damaged and undamaged areas. Our results showed that the damage these animals cause increases greenhouse gas emissions from wetlands, particularly during the early dry season when wet season floodwaters slowly subside. They also likely reduced root biomass and the thickness of the organic soil layer near the ground surface. These findings highlight the importance of managing feral ungulates that will in turn reduce greenhouse gas emissions.

1. Introduction

Despite offering critical and unique ecosystem services, global coastal wetland ecosystems are increasingly threatened (White & Kaplan, 2017). Ecosystem services provided by coastal wetlands, including flood hazard mitigation, cultural and spiritual values, and the regulation of carbon and nitrogen cycles (Clarke et al., 2021; Costanza et al., 2021; Engle, 2011), greatly outweigh the total landmass they occupy (Costanza et al., 2021; Davidson et al., 2019; Hopkins et al., 2018). The monetary value of these ecosystem services is estimated to be among the highest of any biome (Costanza et al., 2014). However, coastal wetlands face many stressors. Their location in proximity to the marine environment makes them attractive locations for coastal development and resource extraction, and puts them at high risk of climate-related disturbances including sea level rise and coastal flooding (Kirwan & Gedan, 2019; Newton et al., 2020; Waltham et al., 2019). These pressures jeopardize the health of coastal wetlands and the ecosystem services they provide.

Coastal wetlands are productive, waterlogged environments often manifesting in anoxic conditions with slow microbial decomposition of organic material (Kelleway et al., 2016; Macreadie et al., 2017). Significant carbon is stored below ground as soil organic carbon (SOC), in addition to below and aboveground biomass (Alongi et al., 2016; Kauffman et al., 2020; Meng et al., 2021). These coastal wetlands are recognized as "blue carbon" ecosystems (Adame, Kelleway, et al., 2024; Lovelock & Duarte, 2019). Global estimates for mangrove ecosystems, for example, suggest that belowground carbon stocks may be more than six times greater than aboveground stock (Kauffman et al., 2020). This ability of blue carbon ecosystems to sequester carbon has become a significantly valuable ecosystem service, with the global wealth generated from sequestration alone being estimated at approximately US $191 billion annually (Bertram et al., 2021; Friess et al., 2022). However, the ability of blue carbon ecosystems to sequester and store carbon can be impacted by disturbances turning them from carbon sinks to potential sources (Lovelock et al., 2017). Therefore, management of these systems using the voluntary carbon market has begun (Friess et al., 2022; Lovelock et al., 2022).

Diverse fauna, including many invasive species, utilize coastal wetlands (Ens et al., 2017; Sloane et al., 2021; Whitehead et al., 1990), resulting in wetland degradation (Rowland & Lovelock, 2024). In northern Australian coastal wetlands, invasive ungulates such as buffalo (*Bubalus bubalis*), pigs (*Sus scrofa*), and cattle (*Bos taurus*) are of particular concern (Bradshaw et al., 2007). These large bodied, hard-hooved ungulates heavily disturb Australian wetland soils that have evolved in the absence of large hard-hooved species, and are therefore vulnerable to their grazing, trampling, pugging, and wallowing activities (Bradshaw et al., 2007; Cherubin et al., 2019; Treby & Grover, 2023, 2024; Waltham et al., 2023). These behaviors can interrupt biogeochemical cycles, resulting in SOC loss and reductions in above and belowground biomass (Bradshaw et al., 2007; Cherubin et al., 2019; Skeat et al., 1996). Soil disturbance by ungulates can also increase soil compaction, oxygen availability, and temperature, which can reduce carbon sequestration and storage capacity, and alter rates of greenhouse gas (GHG) release (Bragazza et al., 2016; Treby & Grover, 2023). In northern Australia, feral ungulates have also impacted inundation regimes, further affecting natural hydrological and ecological cycles of coastal floodplains (Finlayson et al., 1997; Saintilan et al., 2019).

Notwithstanding the invasive ungulate impacts, coastal floodplains of northern Australia have largely avoided intensive land use change and development, and remain relatively intact ecologically compared with coastal wetlands elsewhere in Australia (Renwick et al., 2017; Whitehead et al., 1990). As a result, northern Australian coastal wetlands continue to play important roles for Indigenous Peoples, providing essential provisioning and cultural ecosystem services as they have for millennia (Bayliss & Yeomans, 1990; Cowie et al., 2000; Jackson, 2005). For example, the Yolŋu of northeast Arnhem Land have strong kinship, spiritual and cultural connections to wetlands for example, through ceremony, songlines, and customary harvest of species such as *räkay* (water chestnut, *Eleocharis dulcis*), *gurrumaṯtji* (magpie goose, *Anseranas semipalmata*) and *minhala* (northern snake-necked turtle, *Chelodina rugosa*) (Campbell et al., 2022; Mitsch et al., 2015; Yunupingu et al., 1995). Indigenous landowners also generate income from coastal wetlands through tourism, crocodile egg harvesting, and fisheries (Barber, 2010; Corey et al., 2018). However, ungulates threaten these cultural and provisional uses. The Yolŋu Yirralka Rangers and Traditional Owners of the Laynhapuy Indigenous Protected Area (IPA) have identified the ongoing pervasive threat of feral ungulates to the health of coastal floodplains and associated cultural practice and livelihoods (Sloane et al., 2019). Research has shown that *räkay*, *gurrumaṯtji,* and *minhala* are negatively impacted by buffalo, pigs, or both (Fordham et al., 2006; Russell et al., 2023; Traill & Brook, 2011). Damage to land, water, or species can affect human-country relationships and Indigenous Peoples' health, livelihoods, and cultural maintenance (Burgess et al., 2005; Putnis et al., 2008; Russell et al., 2021).

Despite documented negative impacts of invasive ungulates on northern Australia's coastal wetlands, ongoing control efforts have been limited due to a lack of sustainable funding, potential income from ungulate tourism and harvesting, and sociocultural attachments across the region's diverse land tenures (Albrecht et al., 2009; Robinson et al., 2005). A widespread buffalo eradication campaign did occur in the 1980s, driven by concerns about brucellosis and tuberculosis outbreaks (More et al., 2015). However, new carbon market opportunities are touted as offering additional income for Indigenous groups and other land managers for feral ungulate management (Davies et al., 2023; Davis et al., 2023), although estimates of the actual carbon storage or greenhouse gas emissions reductions following ungulate removal are currently lacking.

This study contributes to this data gap by exploring wetland carbon cycling following five years of feral ungulate exclusion on a coastal floodplain in the Laynhapuy (IPA), northern Australia. The objectives of this study were to
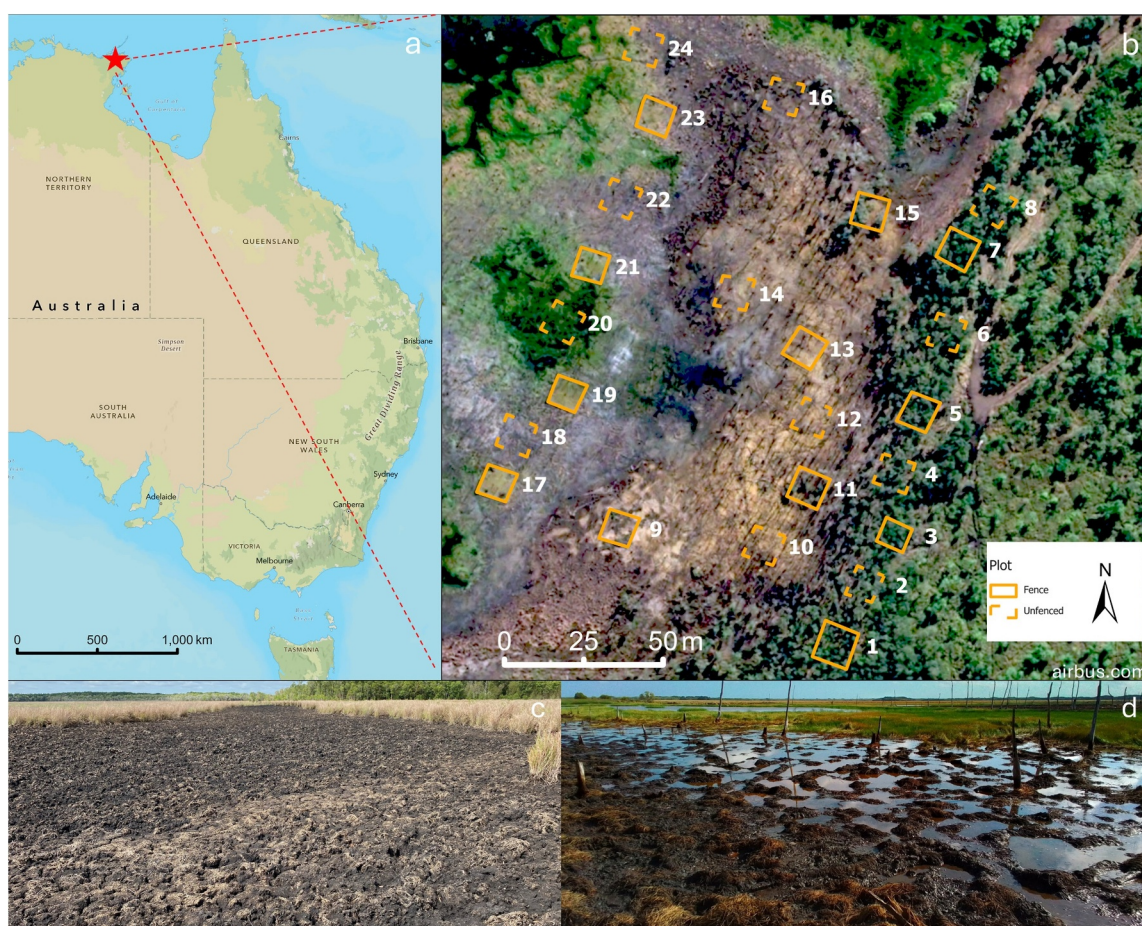
Figure 1. Site location in northern Australia (a) with inset showing satellite imagery of the fence plot array (b). Fences are indicated by closed orange boxes and control plots with broken orange boxes. Damage within the wetland caused by both feral buffalo and pigs (c), and by feral pig alone (d).

(a) evaluate whether feral ungulates affect the carbon cycling in northern Australia's floodplain wetlands, and (b) to determine whether feral ungulate removal could enhance soil carbon sequestration or reduce greenhouse gas (GHG) emissions from these ecosystems. We predicted higher GHG emissions and litter decomposition in damaged sites due to increased soil temperature and microbial activity through mixing and aeration (Treby & Grover, 2023). Root biomass and SOC were expected to be lower in damaged locations through plant disturbance and increased organic matter breakdown (Treby & Grover, 2024), while total nitrogen (TN) was expected to increase via ungulate excretions (McKergow et al., 2012).

2. Materials and Methods

2.1. Site Description and Fenced Plots

The site location was Gurrumuru *ninydjiya* (floodplain) in the Laynhapuy IPA, northeast Arnhem Land in the Northern Territory (NT), Australia (12.3°S, 136.1°E) (Figure 1). Gurrumuru is home to the Dhaḻwaŋu clan of the Yolŋu People and contains many sacred sites and songlines of cultural significance. The site hosts part of a long-term collaborative partnership program between the Yolŋu and Macquarie University scientists (Sloane et al., 2019, 2021). The sediment profile of the site and wider floodplain includes tidally influenced shelly sands, silts, and clays associated with the main river channel and black soils derived from vegetated coastal deposits across the floodplain (Pietsch et al., 1997; Rawlings et al., 1997). Gurrumuru and the surrounding region experiences a tropical monsoonal climate according to the Köppen-Geiger climate classification (Beck et al., 2018). The nearest climate monitoring stations are at Gove Airport (station ID 014508; ~73 km NE; 22.6–30.8°C, 1,461 mm annual rainfall) (Bureau of Meteorology, 2024), and Gapuwiyak/Lake Evella (station ID 014515;

~47 km W; 1,736 mm annual rainfall, no temperature data) (Bureau of Meteorology, 2025). The study site is typical of northern Australia coastal floodplains, with *Eleocharis* sedgeland, floodplain grassland and open-water communities at lower elevations, supratidal *Melaleuca* spp., open forest, and fringing savanna woodland to the east (Finlayson, 2005; Finlayson et al., 1997; Sloane et al., 2024; Whitehead et al., 1990).

This study centered on an ungulate exclusion fence plot array erected by the Yirralka Rangers and Macquarie University scientists in 2018 (Sloane et al., 2024). The array ($n = 24$) includes 12 fenced plots with 12 adjacent unfenced control plots, each 10×10 m. Fenced plots are undamaged by feral ungulates, while the unfenced plots are visibly damaged, henceforth referred to as "undamaged" and "damaged." The array spans three vegetation communities. Plots 1–8 to the east (Figure 1) are located below a *Melaleuca cajuputi* and *Melaleuca viridiflora* supratidal forest, species locally known by Yolŋu as *räŋan* and *nämbarra*, respectively. Plots 9–16 span across a dieback zone of *Melaleuca* spp. and sparsely vegetated area, including sedge *Fimbristylis acuminata*. Plots 17–24 are located within the *räkay* sedgeland. These three vegetation communities will henceforth be referred to as "*Melaleuca* forest," "sparsely vegetated," and "*räkay* sedgeland." For further information on the array, see Sloane et al. (2024). Sampling was undertaken in the early dry season (EDS; June–July) and late dry season (LDS; October–November) of 2023 and 2024. Water quality in the wetland varied markedly, with salinity ranging from 0–16 ppt in the EDS to 28–42 ppt in the LDS, and pH ranging from 6.5 to 7.2.

2.2. Root Biomass

Root biomass and belowground detrital plant material was collected to a depth of 10 cm using a 5 cm diameter stainless steel root corer during the EDS of 2024. Roots and detrital plant material were separated from soil and sediment using a 250 µm sieve, with rocks and charcoal visually separated. Root material was then dried at 65°C for a minimum of 24 hr to obtain a dry biomass weight. Dry biomass was converted to Mg C ha^{-1} by first scaling root biomass from g corer^{-1} to g m^{-2}, followed by conversion of g to Mg and m^{-2} to ha^{-1}.

2.3. Greenhouse Gas (GHG) Flux

Soil CO_2 and CH_4 gas fluxes were measured in each plot using a Picarro G4301 portable GHG analyser (Picarro Inc., California, USA). The GHG analyser measures concentrations of CH_4, CO_2, and H_2O based on laser absorption (cavity ring-down) spectroscopy. Two sampling rounds occurred: in the EDS (June) and LDS (November), 2023. Measurements were taken in all plots plus some additional opportunistic locations in nearby observable damaged and undamaged areas to increase sample size (Table S1 in Supporting Information S1).

The GHG analyser was connected to PVC chambers using air tubing with a drying agent to create a non-steady state through-flow chamber system, also known as a closed dynamic chamber (Maier et al., 2022; Pavelka et al., 2018; Rochette et al., 1997). At each sampling point, the PVC chamber was inserted 2–3 cm into the soil and left for at least 5 min to allow recovery of soil disturbance (Pavelka et al., 2018). The chamber was then connected to the GHG analyser and air circulated through the system at 1.0 L min^{-1}, recording CO_2 and CH_4 concentrations every 3 s for a period of 8 min. Once the GHG measurements were complete, four measurements of the height of the chamber were taken from the soil (or water) surface to the top of the chamber to calculate chamber volume. Between sampling points, the chamber and the GHG analyser were purged with air.

Soil GHG flux was estimated following Zaman et al. (2021). A linear regression was fitted for GHG concentration over time to estimate the flux rate (ppm s^{-1}) of each gas at each sampling point. The flux rate was then multiplied by the system volume to calculate the volume of gas in the system, which was converted to mass using the ideal gas law (Hutchinson & Mosier, 1981). Regressions with an R^2 of <0.7 were discarded for quality control purposes (Treby & Grover, 2023). This resulted in 29 CH_4 measurements being removed from the analysis, while three measurements for CH_4 and CO_2 were lost due to machine malfunction. Many of those data points removed had CH_4 flux rates at or near background. For transparency, all analyses were also performed on the full CH_4 data set ($n = 71$), which can be found in Supporting Information S1. The total combined CO_2 and CH_4 emissions based on a 100-year time horizon were estimated to provide the total carbon emissions as CO_2 equivalent (CO_2-e). Total emissions were estimated using the CO_2 and CH_4 warming potentials relative to CO_2 over 100-year time, which are 1 and 27 times, respectively (IPCC, 2023).

Air temperature (°C), soil temperature (°C), soil oxidation reduction potential (ORP; mV), soil EC (µS/cm), soil pH (pH$_w$), and plant cover (%) were also recorded in conjunction with GHG measurements. Air temperature was

recorded at the start and the end of each GHG measurement period using a digital thermometer (model: IC7209, Digitech Australia, NSW, Australia) installed on the inside of the GHG chamber. Soil temperature was measured using a portable soil probe (model: RS40, RS Components Australia, NSW, Australia) inserted 10 cm into the soil adjacent to the chamber. ORP (mV) was measured using a multimeter (model: DM-5300, A.W. Sperry Instruments Inc., New York, USA) attached to an Ag/AgCl reference electrode and five platinum electrodes inserted approximately 15 cm into the soil adjacent to the GHG chamber (Rabenhorst et al., 2009). Soil EC (EC) and pH (pH_w) measurements were obtained from 0-10 cm depth, where 5 g of soil was mixed with 25 mL of deionized water for a 1:5 weight to volume soil/water suspension, following methods suggested by Rayment and Lyons (2011). Both pH_w and EC were measured using a PCTestr 35 multiparameter handheld probe (Eutech Instruments), with 10 replicates averaged per plot. Plant cover was estimated using the point intercept transect method (Sloane et al., 2024).

A substantial proportion of soil CO_2 emissions originate from root respiration (R_{root}) (Kuzyakov & Larionova, 2005). Therefore, total CO_2 flux from soils includes both autotrophic (plant roots) and heterotrophic (microbial) respiration (Kuzyakov & Larionova, 2005; Schmitz et al., 2018). The total CO_2 respiration from the soil is described by R_{soil}, while R_{root} is the contribution of CO_2 respiration by roots to R_{soil} with R_h being the other heterotrophic component. Because R_{root} is a byproduct of photosynthesis and is balanced by plant uptake of CO_2, it should be excluded from total soil CO_2 flux estimates. Noh et al. (2024) found that R_{root} contributed 24% of the total CO_2 respiration (R_{soil}) in a *Melaleuca* forest of southeast Australia. Holt et al. (1990) found that R_{root} was responsible for approximately 40% of the R_{soil} in a tropical semiarid *Eucalyptus* and *Melaleuca* woodland of northeastern Australia (50 km south of Townsville). Given that the latter study was done in similar climatic conditions to the present study, we attributed 40% of the measured CO_2 flux to R_{root} and subtracted this from the total CO_2 flux, estimating CO_2 emissions from microbial decomposition of organic matter as 60% of the CO_2 fluxes assessed in the *Melaleuca* and sparsely vegetated plots.

No studies were found on the contribution of R_{root} to the R_{soil} in *räkay* sedgeland or any other *Eleocharis* spp. In rice fields, R_{root} contributed 81%–90% of R_{soil} (Neogi et al., 2020), and grass systems contributed 53% (Borden et al., 2021), while in tropical grasslands R_{root} contributed 12%–56% (Kumari et al., 2022) across different stages of the monsoon season. A review of 14 studies of nonforest species (Hanson et al., 2000) found that the average annual R_{root} contributed 60% of the R_{soil} while global modeling estimated mean contributions of ∼45% for tropical climates and ∼52% for wetland ecosystem contributions of R_{root} to the R_{soil} (Jian et al., 2022). Given the wide range of estimates for different wetland and herbaceous plants, a conservative estimate of 40% was selected for R_{root} in *räkay* sedgelands and subtracted from the CO_2 flux to estimate CO_2 emissions from microbial decomposition (equivalent to the other communities in the study).

2.4. Soil Parameters

Soil cores were collected in the EDS using an open-faced gouge auger in the center of each damaged and undamaged plot ($n = 24$) to a depth of 0.5 m. This depth sampled across the organic-rich sediment layer that extended to a maximum of 0.42 m below ground across the site. The depth of disturbance by feral ungulates has not been observed to exceed 0.3 m at the site. Following sampling, excess water was drained from the cores, which were then split into 10 cm intervals across the depth of the core (0–10, 10–20, 20–30, 30–40, and 40–50 cm). The depth of the organic-rich soil layer, found from the surface to 0.11–0.42 m belowground, was also measured in each soil core. Samples were preserved in sealable low-density polyethylene bags and stored at 4°C prior to analysis.

Each core section was oven dried at 50°C for at least 48 hr until a constant mass was reached. This temperature, being lower than the 65°C for similar methods suggested by Rayment and Lyons (2011), was chosen to avoid volatilizing elemental nitrogen from the samples. Dry weights of each section were used to calculate dry bulk density (DBD) and soil gravimetric water content (GWC). Organic material including pieces of charcoal, root material, and leaf litter were removed from the dried subsamples. Dried subsamples were homogenized using a Rocklabs SRM standard ring mill with 500 mL zirconium oxide bowl and balls, operated at 400 revolutions per min for 3 min. Any remaining fibrous organic material was removed using a 2 mm sieve. Pedogenic carbonates were not observed in soils or sediments of the floodplain site; however, to confirm absence, a few drops of hydrochloric acid were added to an aliquot of each subsample followed by visual inspection for effervescence

(Schlacher & Connolly, 2014). No effervescence was observed, confirming limited carbonate material within samples.

Both SOC and total nitrogen (TN) in soil were determined using high temperature combustion with an automated CHNS elemental analyser (Elementar vario MICRO, Elementar Analysensysteme GmbH). In the CHNS analyser, SOC and TN were combusted at 1150°C and converted into CO_2 and N_2 gases, which were then both detected by thermal conductivity (Bansal et al., 2023; Chatterjee et al., 2009). All subsamples had duplicate aliquots analysed using a peak-picking algorithm (Python 3.11), which were then averaged to provide SOC and TN as percentages of the soil, herein referred to as SOC% and TN%, respectively. Both SOC% and TN% were subsequently converted to units of Mg ha^{-1} using Equations 1 and 2.

$$SOC_{density} \text{ or } TN_{density} = DBD \times \frac{SOC\% \text{ or } TN\%}{100} \qquad (1)$$

$$SOC_{stock} \text{ or } TN_{stock} = \left(SOC_{density} \text{ or } TN_{density} \times C_t\right) \times 100 \qquad (2)$$

In Equation 1, $SOC_{density}$ and $TN_{density}$ are the SOC (g C cm^{-3}) and TN (g N cm^{-3}), respectively, while DBD of soil was measured in g cm^{-3}. In Equation 2, SOC_{stock} and TN_{stock} (Mg ha^{-1}) is the SOC and TN content of a given soil sample per hectare. C_t refers to the core/sample thickness (cm). There were 19 measurements of TN that fell below instrument detection limits. These were imputed using multiple imputation by chained equations with five imputed data sets, using the "mice" package in R (Van Buuren & Groothuis-Oudshoorn, 2011). Imputations were performed using predictive mean matching based on the variables pH, depth, vegetation community, and fencing and were constrained between the instrument detection limit (TN% = 0.05) and 0.

Other parameters analysed across the soil core included GWC (%), DBD (g cm^{-3}), pH, and soil EC (μS/cm). Soil EC and pH were measured from each core section using the same methods described above. Both pH$_w$ and soil EC analyses were conducted using a Thermo Fisher Scientific Inc. Orion Star A329 portable pH/ISE/conductivity/RDO/DO meter.

2.5. Leaf Litter Decomposition

To estimate litter decomposition rates in the three vegetation communities, litter bags were purpose-made containing representative local plant material from corresponding vegetation. Live plant material was harvested in June 2023 from each of the three plot array vegetation communities: *M. cajuputi* and *M. viridiflora* leaves from *Melaleuca* forest, *F. acuminata* leaves from sparsely vegetated, and *E. dulcis* leaves from *räkay* sedgeland. Plant material was air dried at 65°C for 24 hr to a constant weight to remove water.

Litter bags were 10 × 10 cm nylon bags with a mesh size of 1 mm. The *räkay* sedgeland and sparse vegetation litter bags were filled with 4 g of corresponding dried material while 3 g of *Melaleuca* spp. was used for the *Melaleuca* litter bags as it has a lower mass to volume ratio. Four replicate litter bags were buried at 10 cm per plot. Half of the replicates were retrieved in the October 2023 after the progression of the dry season (112 days for *räkay* sedgeland and sparsely vegetated communities and 111 days for *Melaleuca* forest). The others were left in situ for 355 days and collected in June 2024 following the 2023/24 wet season.

2.6. Data Analysis

Separate generalized linear models (GLM) were used to analyse the GHG fluxes using the R Package "MASSExtra" (Venables, 2023). GLMs were chosen given the non-normal GHG data sets, confirmed using the Shapiro-Wilk test. For CO_2, CH_4 and total emissions, a negative binomial distribution was chosen given the overdispersed data (where variance exceeded the mean). Both feral ungulate damage (damaged vs. undamaged) and season (EDS or LDS) were fixed factors for both CH_4 and total emissions. For CO_2, each of feral ungulate damage, season, and vegetation community (*Melaleuca* forest, sparsely vegetated or *räkay* sedgeland) were considered fixed factors. The additional fixed factor used in the CO_2 model was possible due to the greater sample size and distribution. Models were selected based on Akaike's information criterion (AIC) with the lowest AIC value used to help determine which model was used (Tables S2–S4 in Supporting Information S1). Analysis of deviance was used to evaluate the significance of the main effects. Pairwise comparisons of the means for the different variable

combinations were performed using the Tukey HSD post hoc comparisons with the "emmeans" R package (Lenth, 2024).

A linear mixed-effect model was used for both SOC and TN with the core locations (Plot ID) set as a random effect. Depth, feral ungulate damage (damaged or undamaged), and vegetation community (*Melaleuca* forest, sparsely vegetated or *räkay* sedgelands) were considered fixed effects. A linear mixed-effect model was appropriate for analysis of SOC given the plot array could be considered pseudoreplication due to the replicates (four in each community) being in the same wetland (given accessibility problems and remoteness of the field site). Linear mixed-effect models are an appropriate way to deal with such sampling design problems (Millar & Anderson, 2004). Two-way interactions between the main effects were also tested as it is possible that feral ungulates may only have had a significant effect on the *Melaleuca* forest layers of soil (0–10 and 10–20 cm) or a particular community category given greater observed feral damage in the *räkay* sedgelands plots. ANOVA was used to test the effects of fixed factors, and Tukey's HSD post hoc pairwise comparisons were performed to assess differences between variable means. Model residuals were visually inspected and met normality assumptions using the Shapiro-Wilk test. The homogeneity of variance assumption was also met, being examined using Levene's test. A linear mixed-effect model was employed for root biomass with core locations (Plot ID) as a random effect and feral damage and vegetation community as fixed effects. The same approach as above was used to evaluate model fixed effects and post hoc comparisons.

For leaf litter decomposition, an exponential decay model (Equation 3) was adopted to estimate the decay rate (k) of litter from each plot (Smith et al., 2024; Wider & Lang, 1982).

$$M_t = M_0 * \exp^{-kt} \tag{3}$$

This approach is used to determine k, which is the decay constant or the proportion faction of mass lost per day (day^{-1}). Here M_t is defined as the mass remaining at t (time) with M_0 as the initial mass. A two-way ANOVA was used to test the main effects (feral ungulate damage, vegetation community/litter type, and the interaction) on k. Model assumptions of equal variance and normality of residuals were met. A post hoc Tukey HSD test was used to conduct pairwise comparisons between groups.

Spearman rank correlation tests were conducted on the additional environmental variables measured in conjunction with CO_2 and CH_4 fluxes as well as SOC and TN in soil. A p-value of <0.05 was used to determine if the correlation between variables was significant. A two-way ANOVA following the same procedure for leaf litter decomposition above was also used to test the same effects on the thickness of the organic layer in each soil core.

All analyses were undertaken using R version 4.3.3 (R Core Development Team, 2024). Data were cleaned and manipulated using "tidyverse" (Wickham et al., 2019) and extended with "readxl" (Wickham & Bryan, 2023). Data were plotted with "ggplot2" (Wickham, 2016).

3. Results

3.1. Root Biomass

For all vegetation communities, root biomass was higher on average in undamaged plots than damaged plots: *Melaleuca* averaged 21% higher biomass in undamaged (42.8 ± 7.2 Mg C ha^{-1}) than damaged plots (38.9 ± 4.8 Mg C ha^{-1}); sparsely vegetated was 44% higher in undamaged (35.5 ± 13.0 Mg C ha^{-1}) versus damaged plots (26.8 ± 5.8 Mg C ha^{-1}); and *räkay* sedgeland root biomass in undamaged plots (11.1 ± 2.6 Mg C ha^{-1}) was double that of damaged plots (5.5 ± 1.2 Mg C ha^{-1}). However, none of the differences between groups were significant given the small sample size and high variation across samples.

The root biomass of the vegetation communities (combined damaged and undamaged data) significantly differed ($F_{(2, 18)} = 20.6$ and $P < 0.001$) from each other. Pairwise comparisons revealed that *räkay* sedgeland had significantly lower root biomass than the sparsely vegetated (mean difference = −8.66, $t = −3.04$, and $P = 0.018$) and *Melaleuca* communities (mean difference = −12.63, $t = −4.44$, and $P < 0.001$; Figure 2). There was no difference in root biomass between the *Melaleuca* and sparsely vegetated plots (Figure 2).
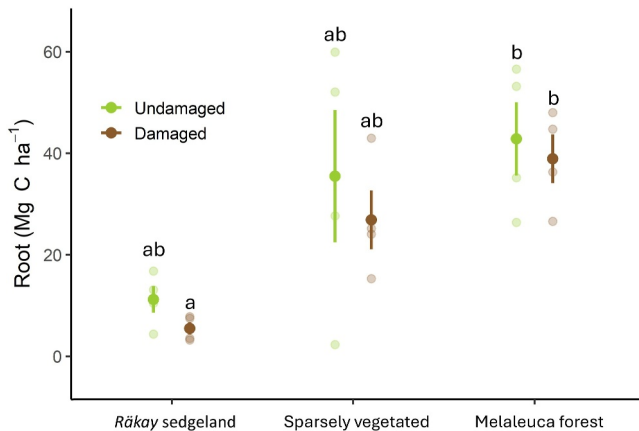
Figure 2. Mean root biomass across different communities and fencing effects. Error bars represent one standard error. Faded circles represent individual data points. Letters above lines represent Tukey post hoc results. Mean values that share the same letter are not significantly different at the 5% level.

3.2. Soil GHG Emissions

3.2.1. Carbon Dioxide

There was a significant interactive effect of feral damage, vegetation type, and season (LR Chisq = 9.9, df = 2, and $P = 0.007$) on soil CO_2 emissions (Figure 3a; Table S5 in Supporting Information S1). In both *räkay* sedgeland and sparsely vegetated communities, CO_2 emissions from the damaged and undamaged groups did not differ in either season, while in *Melaleuca* forest, there were greater emissions in undamaged (37.0 ± 5.03 Mg CO_2 ha^{-1} yr^{-1}) than damaged locations (11.6 ± 2.62 Mg CO_2 ha^{-1} yr^{-1}) in the EDS.

Emissions from undamaged locations did not differ between seasons in any vegetation community. However, CO_2 emissions in damaged locations were significantly higher in the EDS than LDS in both the *räkay* sedgeland and sparsely vegetated communities (Figure 3a). There was no difference in CO_2 emissions from damaged *Melaleuca* forest locations between seasons.

3.2.2. Methane

Methane data across vegetation communities were pooled to increase sample size for analyses. Methane emissions in damaged locations averaged 2.82 ± 1.49 Mg CH_4 ha^{-1} yr^{-1} compared to undamaged locations 0.11 ± 0.07 Mg CH_4 ha^{-1} yr^{-1}, a significant difference (LR Chisq = 14.2;
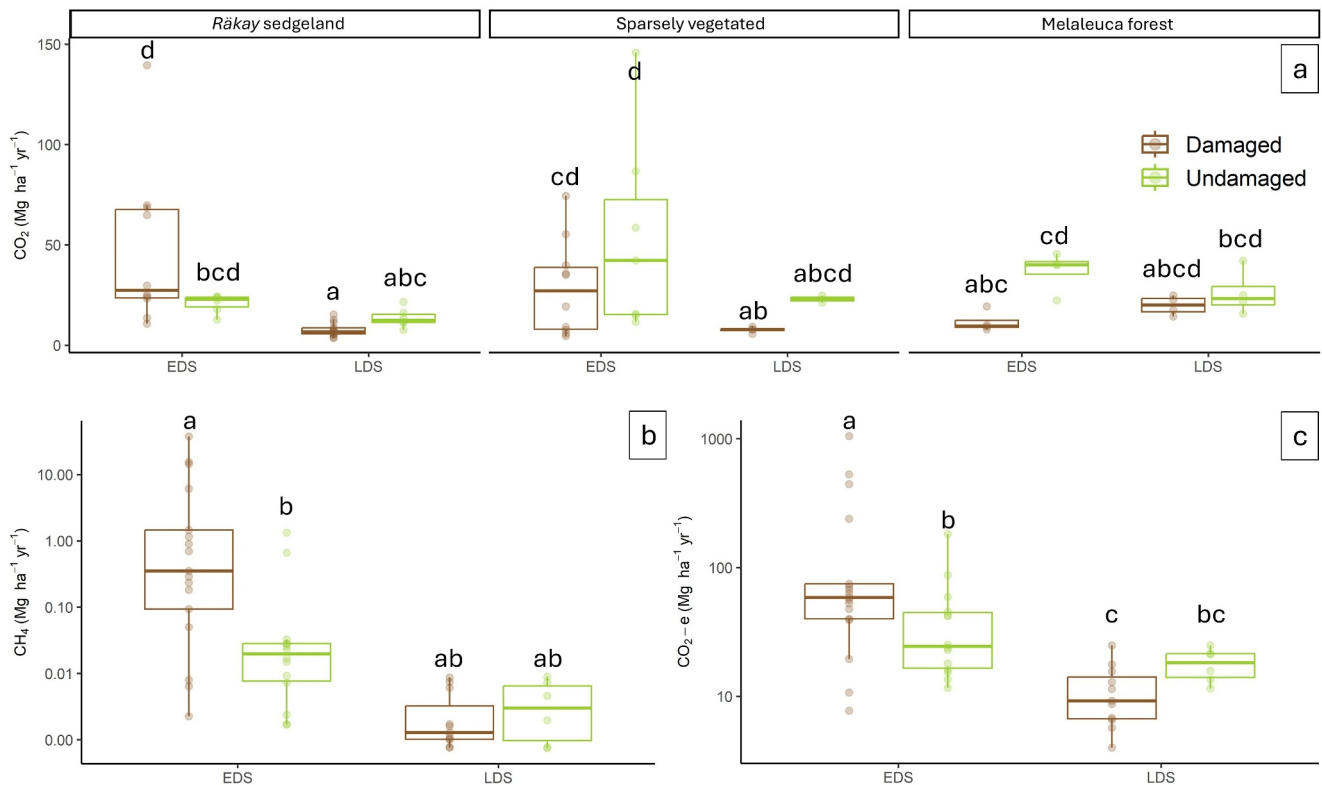
Figure 3. Greenhouse gas emissions from fenced plot arrays and surrounds separated into feral damaged (brown) and undamaged (green) plots broken into seasons with EDS (early dry season) and LDS (late dry season). Boxes represent the interquartile range (IQR), with the central line indicating the median. Whiskers extend to the smallest and largest values within 1.5 times the IQR from the lower and upper quartiles. Circles represent individual data points. The plots have been separated into (a) carbon dioxide (CO_2) emissions, which are shown by feral damage, season, and vegetation community, (b) methane (CH_4) emissions split by feral damage and season, and (c) total emissions as CO_2 equivalents (CO_2-e) shown for feral damage and season. Both CH_4 (b) and CO_2-e (c) have been plotted on a logscale. Letters above boxes represent the Tukey post hoc results. Mean values that share the same letter are not significantly different at the 5% level.

Table 1
Spearman Rank Correlations of GHG Fluxes With Environmental Parameters

	CO_2	CH_4	Total CO_2-e	ORP	Air temp.	Soil temp.	DBD	GWC	pH_w	Soil EC	Plant
CO_2	1										
CH_4	**0.64**	1									
Total CO_2-e	**0.94**	**0.79**	1								
ORP	−0.12	**−0.51**	−0.26	1							
Air temp.	−0.1	−0.26	−0.01	−0.02	1						
Soil temp.	**−0.34**	**−0.56**	**−0.46**	0.06	**0.42**	1					
DBD	**−0.39**	0.23	0.09	**−0.67**	0.34	−0.02	1				
GWC	**0.32**	**0.66**	**0.53**	−0.19	**−0.39**	**−0.81**	−0.01	1			
pH_w	−0.11	**0.58**	0.13	**−0.77**	0.31	−0.24	**0.71**	**0.36**	1		
Soil EC	**−0.52**	0.15	0.14	**−0.44**	0.26	**0.46**	**0.41**	−0.27	**0.3**	1	
Plant	0.14	0.26	0.13	**−0.37**	0	−0.09	**0.42**	0.11	**0.59**	0	1

Note. Color gradients range from blue (indicating positive correlation) to white (no correlation) to red (negative correlation). Bold numbers denote significant correlation ($p < 0.05$) between variables.

df = 1; $P < 0.001$). Emissions also differed by season (LR Chisq = 17.5, df = 1, and $P < 0.001$), with EDS emissions averaging 2.62 ± 1.35 Mg CH_4 ha^{-1} yr^{-1} and LDS averaging 0.003 ± 0.001 Mg CH_4 ha^{-1} yr^{-1} in the LDS. There was no significant interactive effect of feral damage and season on CH_4 emissions (LR Chisq = 0.12, df = 1, and $P = 0.073$). The results of the pairwise comparisons across both effects can be seen in Figure 3b. Model results are presented for both the filtered ($n = 48$) and unfiltered ($n = 71$) data sets in Tables S6 and S7 in Supporting Information S1, respectively.

3.2.3. Total GHG Emissions From Feral Ungulate Damage

In the EDS, total GHG emissions significantly differed averaging 168.7 ± 66.0 Mg CO_2-e ha^{-1} yr^{-1} in damaged locations compared to 43.2 ± 12.1 Mg CO_2-e ha^{-1} yr^{-1} in undamaged locations ($P < 0.001$). There was no difference in damaged and undamaged locations in the LDS, which averaged 11.2 ± 1.9 Mg CO_2-e ha^{-1} yr^{-1} and 18.1 ± 2.1 Mg CO_2-e ha^{-1} yr^{-1}, respectively ($P = 0.74$). There was a significant interaction between feral damage and season (LR Chisq = 10.7, df = 1, and $P = 0.001$) with total GHG emissions being higher in damaged compared to undamaged plots in the EDS but were similar in the LDS (Figure 3c). Model results are presented for both the filtered ($n = 48$) and unfiltered ($n = 71$) data sets in Tables S8 and S9 in Supporting Information S1, respectively.

3.2.4. Environmental Variables and GHG Fluxes

There were several significant correlations between GHG emissions and environmental variables (Table 1). CO_2 emissions declined with increasing soil temperature ($P = 0.004$), soil EC ($P < 0.001$), and DBD ($P = 0.009$) while they increased with increasing GWC ($P = 0.024$). CH_4 emissions were positively correlated with soil pH ($P = 0.006$) and GWC ($P = 0.002$) while CH_4 emissions declined with increasing ORP ($P < 0.001$) and soil temperature ($P < 0.001$). Summary statistics of environmental variables have been provided in Supporting Information S1 (Tables S10 and S11).

3.3. Soils

3.3.1. Soil Organic Carbon (SOC)

There was no significant difference in SOC stocks between the damaged and undamaged plots, and no significant interaction between depth, ungulate damage, and vegetation community on SOC stocks (Table S12 in Supporting Information S1). For all cores, SOC declined with depth intervals in the core ($F_{(4, 72)} = 107.9$ and $P < 0.001$).

When SOC was summed over the core to 50 cm, SOC was similar in the damaged *Melaleuca* forest (148 ± 16 Mg C ha^{-1}) and sparsely vegetated (161 ± 8 Mg C ha^{-1}) compared to the undamaged conditions (*Melaleuca* forest: 146 ± 16 Mg C ha^{-1}; sparsely vegetated 157 ± 24 Mg C ha^{-1}). In the *räkay* sedgeland, there
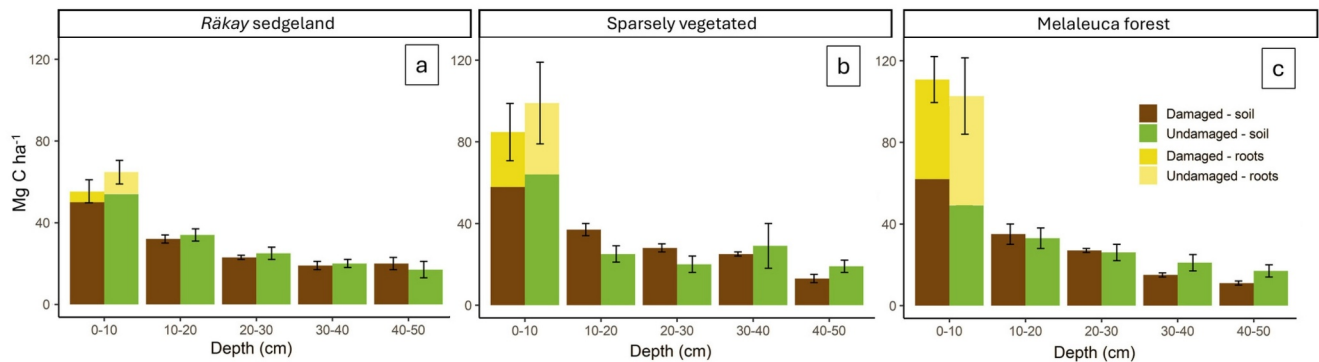
Figure 4. Stacked bar charts of SOC (0–50 cm) and root biomass carbon (0–10 cm) across three vegetation communities: (a) *räkay* sedgeland, (b) sparsely vegetated, and (c) *Melaleuca* forest.

was slightly higher (4%) SOC aggregated over the core (0–50 cm) in undamaged (150 ± 11 Mg C ha^{-1}) than damaged (144 ± 8 Mg C ha^{-1}) plots (Table S13 in Supporting Information S1; Figure 4).

3.3.2. Total Nitrogen (TN)

The damaged *Melaleuca* forest (10.0 ± 0.5 Mg N ha^{-1}) had slightly higher (14.8%) TN than undamaged plots (8.6 ± 1.1 Mg N ha^{-1}). This was also the case with the sparsely vegetated community, where damaged plots (8.8 ± 0.5 Mg N ha^{-1}) had marginally higher average TN than undamaged plots (8.3 ± 1.9 Mg N ha^{-1}). In the *räkay* sedgeland, undamaged plots (9.1 ± 0.7 Mg N ha^{-1}) had marginally higher TN than damaged plots (8.8 ± 0.6 Mg N ha^{-1}). None of these differences were statistically significant at the 5% level.

TN was highest in surface soils (0–10 cm) and declined with core depth (Table S13 in Supporting Information S1). As with SOC, there was no significant interaction of depth, ungulate damage, and vegetation community on TN. A significant interaction between depth and vegetation community on TN was found ($F_{(4, 72)} = 2.47$; $P = 0.01$) where TN was higher in surface soils and declined with depth more rapidly in the *Melaleuca* forest than sparsely vegetated and *räkay* sedgeland communities.

3.3.3. Environmental Variables and SOC and TN

SOC and TN were highly correlated ($P < 0.001$; Table 2). SOC was also significantly positively correlated with soil EC ($P < 0.001$) and GWC ($P < 0.001$), while being significantly negatively correlated with DBD ($P < 0.001$).

3.3.4. Organic Soil Layer Depth

In the community with the greatest observed damage, *räkay* sedgeland, undamaged plots (0.33 ± 0.02 m) had greater organic soil depth (59%) than damaged plots (0.18 ± 0.03 m). Conversely, in the sparsely vegetated community, damaged plots (0.24 ± 0.06 m) tended to have higher organic soil depth (40%) than undamaged plots (0.16 ± 0.04 m). The undamaged *Melaleuca* forest (0.32 ± 0.04 m) had slightly higher (16%) TN than undamaged plots (0.28 ± 0.01 m). All comparisons were not statistically significant at the 5% level.

There was a significant interactive effect of damage and vegetation community on the depth of soil organic layer ($F_{(2, 18)} = 4.67$ and $P < 0.02$). Mean depths and ANOVA results are provided in Supporting Information S1 (Table S14 and S15).

3.4. Leaf Litter Decomposition

There was a significant difference in k across the vegetation communities ($F_{(2, 18)} = 7.58$ and $P = 0.0041$). Tukey HSD post hoc tests indicated significant differences between sparsely vegetated and *räkay* sedgeland plots

Table 2
Spearman Rank Correlations of Environmental Parameters, SOC, and TN

	SOC	TN	DBD	pH$_w$	Soil EC	GWC
SOC	1.0					
TN	**0.96**	1.0				
DBD	**−0.66**	**−0.67**	1.0			
pH$_w$	0.07	0.02	0.16	1.0		
Soil EC	**0.31**	0.2	−0.02	**0.42**	1.0	
GWC	**0.68**	**0.7**	**−0.7**	0.01	**0.23**	1.0

Note. Color gradients range from blue (indicating positive correlation) to white (no correlation) to red (negative correlation). Bold numbers denote significant correlation ($p < 0.05$) between variables.

Table 3
Decomposition Rates of Dominant Ground Level Vegetation and/or Litter Type Across Each of the Three Communities With Pairwise Comparison Between Fenced and Unfenced Locations (Tukey-Adjusted p-Values)

Plant tissues	Feral damage (n =)	k (±se)	t-ratio, p-value
Melaleuca spp. leaves	Undamaged (4)	0.00195 ± 0.0010	$-0.005, p = 0.996$
	Damaged (4)	0.00196 ± 0.0002	
F. acuminata leaves	Undamaged (4)	0.00098 ± 0.0004	$-0.744, p = 0.467$
	Damaged (4)	0.00144 ± 0.0012	
E. dulcis leaves	Undamaged (4)	0.00289 ± 0.0010	$-0.067, p = 0.947$
	Damaged (4)	0.00293 ± 0.0010	

($P = 0.003$, Table 3), with no other differences between groups. There was no significant interactive effect of vegetation community and ungulate damage on k ($F_{(2, 18)} = 0.17$ and $P = 0.85$); similarly, feral damage had no effect on k ($F_{(1, 18)} = 0.22$ and $P = 0.64$).

The highest average k (± one se) was found for the *räkay* leaves in *räkay* sedgeland plots (0.0029 ± 0.0009). The average k of *Melaleuca* spp. leaves from *Melaleuca* forest plots was 0.0020 ± 0.0007, which was double that of the *F. acuminata* leaves from the sparsely vegetated plots averaged 0.0012 ± 0.0009.

4. Discussion

This study found that carbon cycling in northern Australian coastal floodplain wetlands is impacted by feral ungulates, particularly in the early dry season (EDS), when total emissions (CO_2-e) were significantly greater in damaged than undamaged wetland locations (Figure 5). Similar impacts of ungulates on wetland GHG emissions have been observed in Central Asia, southeastern Australia, and the United Kingdom (Hirota et al., 2005; Limpert et al., 2021; Olsen et al., 2011; Treby & Grover, 2023). Emissions were higher in the EDS than the LDS, consistent with dependencies of ecological and biogeochemical processes, specifically biomass availability and microbial activity, on seasonal water availability and temperature in monsoonal climates (Beringer et al., 2013;
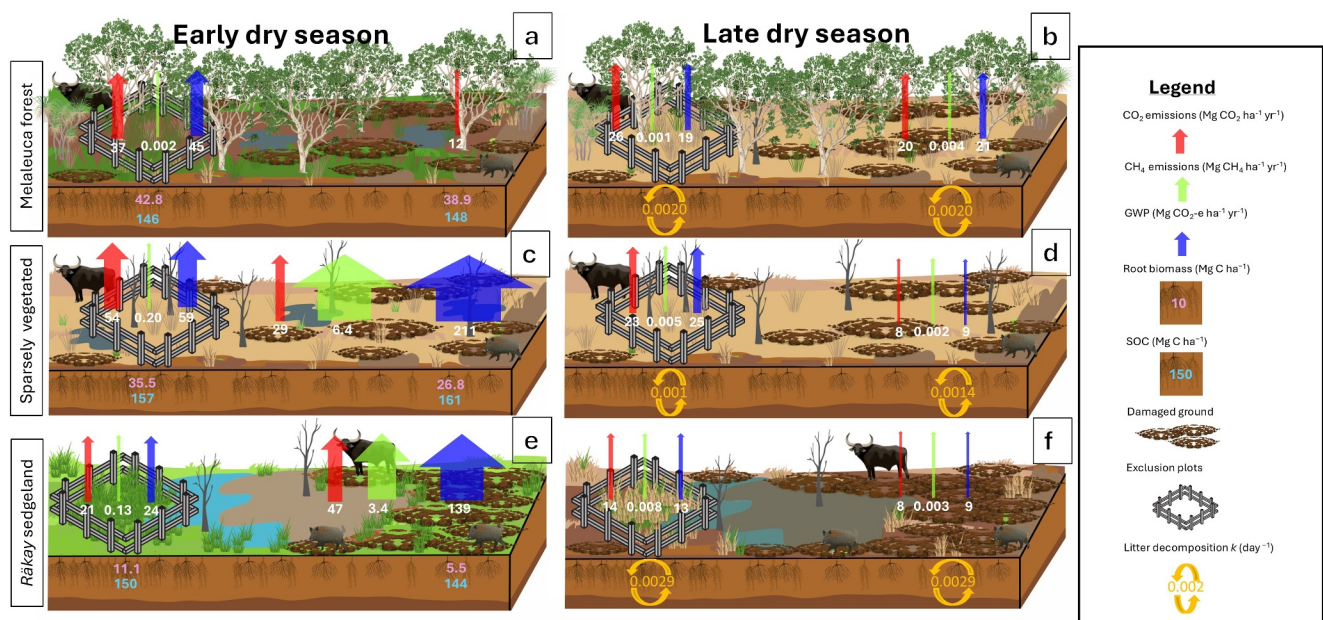
Figure 5. Conceptual model of carbon dynamics from northeast Arnhem Land coastal floodplain wetlands across vegetation communities: (a and b) Melaleuca forest, (c and d) sparsely vegetated, and (e and f) *räkay* sedgeland. The arrows indicating GHG emissions are approximately proportional to the CO_2-e of each except for all CH_4 emissions below 1.0 Mg CH_4 ha^{-1} yr^{-1}, which were capped for visualization purposes. No CH_4, and therefore GWP, measurements were available for damaged Melaleuca forest locations in the EDS due to QA/QC filtering.

Chen et al., 2023; Padhy et al., 2020). In the most intensively damaged vegetation community, the *räkay* sedgelands, there was less root biomass, a reduced thickness of the organic-rich soil layer (Table S14 in Supporting Information S1), and minor reductions in the SOC, although these reductions were not significant (Figure 5). Few studies have assessed carbon cycle impacts from invasive ungulates in Australia, particularly in coastal floodplain ecosystems of northern Australia such as the site examined in this study. The evidence provided here suggests that the removal of feral ungulates from the coastal floodplains of northern Australia would reduce soil disturbance and GHG emissions.

4.1. Belowground Biomass

Root biomass was reduced by ungulates which overturn soils and consume roots and rhizomes (M. A. Ford & Grace, 1998; Wang et al., 2018). While not significant, average belowground biomass was lower in damaged sites across each of the vegetation communities, likely correlated with reduced herbaceous vegetation in damaged plots (Jones, 2024). The *räkay* sedgelands had twofold more root biomass in undamaged locations than damaged locations where feral pig herbivory was most concentrated due to their preference for *räkay* corms (Barrios-Garcia & Ballari, 2012; Jones, 2024). Other vegetation communities in the study showed more similar root biomass distributions between damaged and undamaged plots, likely related to lower feral ungulate damage in these communities. In contrast, some studies in eastern Canada, North West England, and the Netherlands have shown increases in root biomass in wetlands because of ungulate grazing (Elschot et al., 2015; H. Ford et al., 2012; Yu & Chmura, 2009). These studies, all in cooler climate salt marshes, reported increased soil compaction and belowground biomass because of large ungulate disturbance—patterns not observed in this study. Also, these sites were grazed by domestic livestock (sheep or cattle), which do not generally display the soil overturning or wallowing behaviors exhibited by pigs and buffalo in northern Australia.

4.2. Greenhouse Gas Fluxes

Annualized total GHG emissions were fourfold higher in feral ungulate-damaged locations than undamaged locations in the EDS. This was primarily a result of higher CH_4 flux. Increasing evidence indicates links in elevated wetland emissions due to feral ungulate disturbance. In the peatlands of the Australian Alps, feral horse damage converted wetlands from net GHG sinks (-7.4 Mg CO_2-e ha^{-1} yr^{-1} in undamaged sites) into sources, emitting 5.3 Mg CO_2-e ha^{-1} yr^{-1} in damaged sites with vegetation and 10.2 Mg CO_2-e ha^{-1} yr^{-1} in damaged sites without vegetation (Treby & Grover, 2023). These emissions were much lower than those in this study. While GHG emissions were reduced when disturbance was removed at our sites, the system did not revert to an overall GHG sink; rather, greater emissions were avoided. In the drier Wimmera district, also in southeastern Australia, exclusion plots had 35% lower CO_2 emissions than livestock grazed plots (Limpert et al., 2021). Other studies in southeastern Australia have found no effect of feral exclusion on GHG emissions (Bonetti et al., 2021; Treby et al., 2020). Outside of Australia, Olsen et al. (2011) demonstrated that increased soil respiration occurred in grazed sites compared to ungrazed. Similarly in Tibetan Plateau wetlands, combined CO_2 and CH_4 fluxes were 5.6- to 11.3-fold greater in livestock grazed conditions than ungrazed (Hirota et al., 2005).

In the present study, total LDS emissions were lower and not significantly different between damaged and undamaged plots. The CH_4 flux was ~3 orders of magnitude lower in the LDS than the EDS leading to a major reduction in total emissions. Average total emissions in damaged locations were 15-fold lower in the EDS compared to the LDS, and 2.4-fold less in undamaged locations between seasons. Higher CH_4 emissions in the EDS reflect greater water availability, which was positively correlated with CH_4 fluxes, whereas emissions declined in the LDS as soils became drier (Table 1, Tables S10 and S11 in Supporting Information S1; Beringer et al., 2013; Bridgham et al., 2013). Similar seasonal differences in CH_4 emissions were observed elsewhere in northern Australia, unless the soil remained saturated (Beringer et al., 2013), indicating that soil water content rather than seasonality is a primary driver of CH_4 emissions. In northern Australian LDS, there is a lack of rainfall and freshwater runoff. At the time of study, <10 mm rain had fallen across the previous 3 months (Bureau of Meteorology, 2024). CH_4 fluxes were highly variable, particularly in damaged locations in the EDS, indicative of ebullition (Tokida et al., 2005; Yang et al., 2023). Plant productivity has been found to be negatively correlated with methane production, so vegetation loss may enhance methanogenesis in damaged areas (Sutton-Grier & Megonigal, 2011). R_{root} might also decrease with increased salinity, which suppresses plant and microbial productivity (Krauss et al., 2012). Similarly, increased salinity also directly reduces CH_4 emissions (Iram et al., 2021; Poffenbarger et al., 2011). The inclusion of data previously omitted due to variable linear trends (low R^2) did not

substantially alter mean CH_4 emission rates, and model results still indicate higher emissions in damaged than undamaged locations (Tables S6 and S7 in Supporting Information S1).

The mean total emissions of damaged locations in the EDS (169 Mg CO_2-e ha^{-1} yr^{-1}) were similar to that observed in freshwater floodplain wetlands in southeastern Australia (165 Mg CO_2-e ha^{-1} yr^{-1}), although that study did not correct CO_2 emissions for R_{root} when estimating overall emissions (Treby & Carnell, 2023). The wetlands studied by Treby and Carnell (2023) had similar conditions (e.g., soil water content and temperature) to the EDS of the study site when significant freshwater was still present in wetlands. However, in the present study, we found total emissions from undamaged locations during the EDS (43 Mg CO_2-e ha^{-1} yr^{-1}) were fourfold less than damaged locations, while in southeastern Australia, there was no significant difference between total emissions from the different locations (Treby & Carnell, 2023). In contrast, Treby and Carnell (2023) found unseasonal hydrological conditions, rather than ungulate damage, was the main driver of emissions, while differences in ungulate species—cattle, horses, deer, and pigs in southeastern Australia versus pigs and buffalo in Arnhem Land—may also explain variation in impacts.

While CH_4 and total emissions were greater in EDS damaged locations of this study, the CO_2 flux was generally higher in the undamaged locations, except for the *räkay* sedgelands where the highest density of feral damage occurred. While this conflicted with the hypothesis that damaged sites would have higher fluxes, higher CO_2 in undamaged locations has also been identified elsewhere (Treby & Carnell, 2023). This has been attributed to higher root biomass in undamaged plots with enhanced R_{root}, given greater root biomass is highly correlated to R_{root} (Krauss et al., 2012; Pregitzer et al., 2008; Treby & Carnell, 2023). In the *räkay* sedgeland, root biomass was twofold higher in undamaged than damaged plots, indicating that at least in this vegetation type, higher CO_2 emissions in undamaged plots can be explained by increased decomposition of soil organic matter. The high litter decomposition rate in damaged *räkay* sedgeland plots and soil overturning occurring because of pig predation on *räkay* corms (Jones, 2024) may also contribute to high CO_2 emissions.

This study applied a correction factor of 40% to all CO_2 flux measurements to account for CO_2 emissions from R_{root}. However, the proportion of root biomass was not measured in the field for each CO_2 measurement, and therefore, variation in root biomass among sample points was not incorporated into the correction factor. Feral damage had reduced the amount of herbaceous biomass in damaged plots at the site (Jones, 2024). Root biomass was higher on average in undamaged plots across all vegetation communities, though not significantly due to high variance and small sample size. Thus, the 40% reduction in CO_2 emissions may lead to overestimates of emissions in undamaged plots and underestimates in damaged plots, effectively reducing our capacity to detect differences in CO_2 emissions among treatments.

4.3. Feral Disturbance to Soil Carbon Stocks

Contrary to our hypothesis, the results suggest that soil disturbance caused by feral pigs and buffalo did not significantly affect SOC stocks within the wetland. The most concentrated ungulate damage within this study was observed in the *räkay* sedgeland plots. Here, SOC was slightly higher in undamaged plots, but not significantly. Additionally, the organic-rich soil layer did appear to have reduced thickness (59%) in *räkay* sedgeland damaged plots compared with undamaged plots. There was marginally higher SOC in damaged plots in *Melaleuca* forest and sparsely vegetated communities. The sparsely vegetated community had 40% greater thickness of the organic soil layer in damaged than undamaged plots, although this community sees the least feral damage, and therefore, results may be influenced by the small sample size and high data variability.

Impacts of feral ungulates on SOC stocks in the literature have been variable, with some studies suggesting ungulate disturbance increases SOC, while others suggest no effect or decreased SOC. In the inland marsh floodplains of southeastern Australia, there was no significant difference in SOC or corrected TN between feral ungulate damaged and undamaged treatments (Treby & Carnell, 2023). Similar findings were made in other ungulate-damaged wetlands (Barrios-Garcia et al., 2014; Don et al., 2019; M. A. Ford & Grace, 1998). Don et al. (2019) reported that wild boars can transfer forest floor carbon into mineral soils through bioturbation. However, in the peatlands of the Australian Alps, SOC concentrations were 45% greater in undamaged sites than sites damaged by feral horses (Treby & Grover, 2024). Limpert et al. (2021) found that soil carbon was 30% higher in undamaged exclusion plots than grazed sites in the Wimmera district of southeastern Australia. In Denmark, SOC stocks were 29% higher in ungrazed sites than those grazed by cattle and sheep livestock (Morris & Jensen, 1998). In the Laynhapuy IPA exclusion plots, 5 years of exclusion may have been insufficient time to

detect change in SOC. Soil carbon in *Melaleuca* wetlands accumulates at rates of ~0.6 Mg C ha^{-1} yr^{-1} (Adame et al., 2020). Over 5 years, this would be on the order of 3.0 Mg C ha^{-1}, which is much smaller than the variability observed in SOC stocks here (Figure 4), possibly making an ungulate exclusion effect difficult to be detected in the time frame of this experiment.

TN in soil was expected to potentially increase from feral ungulates (McKergow et al., 2012). However, like SOC, there was no significant difference between damaged and undamaged plots, although more TN in damaged Melaleuca and sparsely vegetated areas maybe emerging. Both TN and SOC were highly correlated in the present study, as has been found in other studies of wetland soils (Davidsson & Ståhl, 2000; Qi et al., 2021), suggesting that the main contribution of nitrogen to the soil was from plant organic matter and not through excretions from ungulates. Furthermore, the primary nitrogen compounds excreted by ungulates are nitrate (NO_3^-) and ammonia (NH_4^+) (Singer & Schoenecker, 2003), both of which are soluble and prone to leaching (Rayment & Lyons, 2011). As a result, nitrogen additions from ungulates are unlikely to accumulate over time in the same way that SOC does. This pattern has been observed at other sites, where TN levels increased immediately following livestock grazing but declined with prolonged absence (Mesa et al., 2015). In northern Australian wetlands can be heavily utilized by ungulates for only a short portions of the year. Consequently, due to these "pulse"-type utilization events, it may be difficult to detect elevated TN levels in a single sampling event. Finally, increases in TN have been observed in water rather than soil in response to ungulate presence, suggesting this maybe a valuable focus for future research (Bohlen & Gathumbi, 2007; Mesa et al., 2015).

4.4. Leaf Litter Decomposition

Based on the evidence from this study, damage by ungulates in Arnhem Land wetlands does not appear to significantly alter decomposition rates of leaf detritus in the timescales measured. Guo et al. (2023) found that cattle grazing caused a 15.1% increase in *k* in semi-natural wetlands and a 23.6% reduction in *k* in intensively managed land use, indicating complex controls on leaf litter decomposition in wetlands. In East Asia, salt marsh *k* was also reduced as a result of grazing (Tang et al., 2020). Decomposition rates of graminoid species litter were higher when exposed to heavier grazing regimes (Olofsson & Oksanen, 2002).

Litter decomposition rates were similar to other similar vegetation communities and wetland locations. The highest *k* rates were found in *räkay* sedgelands, which was unexpected given this is the lowest elevation and is inundated the longest annually. However, *räkay* is the most palatable tissue for herbivory by ungulates in the studied wetland, suggesting low lignin and other compounds, which may slow decomposition; similarly, *Eleocharis* spp. contains higher litter quality and tissue nutrients contributing to high decomposition rates (Pisani et al., 2018; Rubio & Childers, 2006). The decomposition rate of *räkay* leaves ($k = 0.0029$ day^{-1}) was similar to the common reed *Phragmites australis* in submerged environments ($k = 0.0024$ day^{-1}) in southeastern Australia (Wallis & Raulings, 2011). These authors attributed their higher *k* to leaching of soluble materials. In this study, the *räkay* sedgeland vegetation community had more neutral pH (pH 5.05) than the *Melaleuca* forest (pH 3.65) and the sparsely vegetated plots (pH 3.75). In soils with lower pH, microbial activity can be inhibited (Malik et al., 2018), which may explain some differences in *k* among communities.

Melaleuca leaf litter bags had the second highest rate of decomposition among the three litter types. The decay rate of 0.002 day^{-1} was similar to that of recalcitrant tea bags ($k = 0.0017$ day^{-1}) measured in *Melaleuca* forests across Queensland with similar temperature but slightly wetter climatic conditions (Adame, Iram, et al., 2024). *Melaleuca k* rates were also similar to the upper range ($k = 0.0015$ day^{-1}) of *Melaleuca ericifolia* litter decay in more temperate Gippsland, Australia (Wallis & Raulings, 2011).

The lowest *k* rates were measured in sparsely vegetated plots with *F. acuminata* leaves. Such low *k* rates maybe partly explained by the poor tissue quality of these leaves. However, high salinity and low soil pH within these plots also likely inhibited plant material decomposition. Local litter quality, ecosystem types, soil conditions, climate, and other factors contribute to the variable nature of litter decomposition (García-Palacios et al., 2016; Ochoa-Hueso et al., 2019). Also, root tissues are known to have different rates of decomposition (Freschet et al., 2013; Ma et al., 2016), and are yet to be assessed at this site. At this site, feral ungulate disturbance had little short-term (<1 year) effect on litter decomposition, suggesting it contributes to CO_2 variation among vegetation types but not between treatments.

4.5. Implications for Management and Potential Carbon Markets

This study found that feral ungulates significantly increased GHG emissions during the EDS and substantially reduced root biomass. Assuming emissions are elevated for half the year, given no difference was measured in the LDS, damaged sites may emit approximately 62 Mg CO_2-e ha^{-1} yr^{-1} more on average than undamaged sites. At the current Australian Carbon Credit Unit price of AU \$35 per Mg CO_2-e (as of 7 July 2025), this equates to a potential return of AU \$2,170 per restored hectare. Additionally, after 5 years of fencing, root biomass in undamaged areas increased by an average of approximately 6 Mg C ha^{-1}. This is equivalent to ∼22 Mg ha^{-1} when converted to CO_2-e (using a factor of 3.67), yielding an additional AU \$776 per hectare, after 5 years. While simplified, these estimates highlight the strong potential for carbon emissions reduction and sequestration, and the likely high return on investment from feral ungulate management in northern Australia.

Management of feral ungulates from wetlands for reducing GHG emissions has the potential for many co-benefits. Lowering feral animal densities would contribute to healing Country for Traditional Owners through improved water quality, reduced predation of culturally important species, and increased aesthetic values (Ens et al., 2016; Russell et al., 2020, 2021). Successful implementation of savanna burning methods in the Australian Carbon Credit Unit Scheme is an example of a reduced emissions method that has delivered significant co-benefits to local Indigenous communities (Russell-Smith et al., 2015).

Indigenous groups in Australia are major landholders with 28% of the Australian land area in exclusive possession via native title, Indigenous owned, or held for Indigenous purposes (Russell-Smith et al., 2024). This includes 85% of the coastline in the NT (Groom et al., 2022). On these lands, Australian Indigenous Peoples have legal rights to conduct carbon projects and receive associated carbon credits (Russell-Smith et al., 2024). Indigenous participation in Australia's tidal reintroduction for blue carbon crediting projects remains limited (Grace & Holmes, 2024). The *tidal restoration of blue carbon ecosystems* method, which is most appropriate for agricultural land where tides have been excluded, is the only currently approved method that applies to coastlines (Lovelock et al., 2022; Russell-Smith et al., 2024). More intact Indigenous-managed coastlines, especially those in northern Australia, therefore, cannot benefit from the tidal restoration method. A feral ungulate management method could create future carbon credit opportunities for Indigenous groups.

4.6. Study Limitations

The site's remote location and wet season inundation limited monitoring frequency, creating study limitations. Both CO_2 and CH_4 fluxes were collected in the dry season during daytime periods. Future studies could benefit from capturing wet season and nighttime measurements (Treby & Grover, 2023). Nitrous oxide (N_2O), a much more potent GHG than either CO_2 or CH_4, is also produced in wetlands and can be affected by ungulate disturbance (Koops et al., 1997). Quantification of N_2O in future studies would improve the understanding of overall net ecosystem GHG flux. Also, future studies may benefit from directly measuring R_{root} in the field via root exclusion from soil, isotopic analysis, or the measurement of excised roots (Kuzyakov & Larionova, 2005). This would confirm whether higher root biomass leads to higher R_{root} and therefore explains the increased CO_2 in some undamaged sites, found in this study.

Impacts of feral ungulate damage on SOC could be further investigated by obtaining chronological sequences, which could account for processes including erosion and SOC accumulation to estimate differences in SOC stocks between damaged and undamaged sites. Similarly, measurement of SOC concentrations and SOC stocks within the soil after a longer period of fencing could allow damaged soil to recover. Soils can take hundreds to thousands of years to develop, and 5 years of feral exclusion may not be enough time to detect effects on SOC stocks (Bansal et al., 2023). Additionally, the presence of other native species that also disturb the soil surface in northern Australian wetlands, particularly the *gurrumatji* or invertebrates, might also influence SOC stocks (Traill & Brook, 2011). Further elucidation of soluble nitrogen compounds and other nutrients in floodwaters could also further clarify the impacts of feral ungulate to the ecological character of these wetlands.

The fence plot array is limited to a single wetland within a single floodplain. Other floodplains across the Laynhapuy IPA have similar wetlands and differing densities of invasive ungulate populations and could potentially host further exclusion plots to enhance the geographic distribution of the study. Similarly, the wetland site itself is constrained to a *Melaleuca* supratidal forest and a *räkay* sedgeland. There are other wetland ecosystem communities on the floodplain, such as coastal and subcoastal floodplain grass, sedge, and herb

swamps, which are heavily utilized by ungulates for wallowing and grazing, and the impacts on these ecosystems and their carbon cycles could also be assessed (Department of Environment, Science and Innovation, Queensland, 2013).

5. Conclusions

This study provides evidence of impacts of feral ungulates to the carbon cycle of tropical floodplain wetlands in northern Australia. These coastal wetlands make up a significant part of the blue carbon ecosystems in Australia (Groom et al., 2022). Due to the environmental stewardship of Traditional Owners and land managers, these floodplains have remained largely intact despite 200 years of European colonization. However, ongoing degradation by high densities of large feral ungulates threatens the ecosystem services that these wetlands provide. Further evidence in other geographic locations, wetland types, timescales, and ungulate communities will further solidify scientific understanding of feral animal impacts on wetland carbon cycles and carbon storage capacity.

Global Research Collaboration Statement

Thank you to the Traditional Owners and knowledge holders of the Laynhapuy IPA and all peoples of the Dhaḻwaŋu Clan and the Gurrumuru *ninydjiya* community for allowing outside researchers access and accommodation on their lands. Access to the Gurrumuru *ninydjiya* community for this research was granted through the Northern Land Council Work (Research) Permit ID: 127934 and verbally agreed to by the Gurrumuru Ranger and *djuŋgayi* (manager) Lanydjana Munuŋgurr, as well as the Yirralka Rangers. A memorandum of understanding between the Yirralka Rangers and Macquarie University outlining the roles and responsibilities of both parties regarding research and collaboration within the Laynhapuy IPA has been in place since 2021.

Data Availability Statement

The raw data and code to reproduce all results and figures were made available to the reviewers and editors during the peer review process. All R script used in the data analysis are available in the following Zenodo data repository: https://doi.org/10.5281/zenodo.15310284 (Crameri, 2025a). As this research was conducted on Aboriginal-owned land, specifically the Gurrumuru homeland in the Laynhapuy IPA, appropriate data stewardship and cultural protocols must be observed. The raw data are managed and stored jointly between the Yirralka Rangers and Macquarie University. It has been placed into a restricted-access repository with Zenodo as follows: https://doi.org/10.5281/zenodo.15314213 (Crameri, 2025b). Data will be made available following CARE Principles with detailed instructions for access available in the above Zenodo repository. Multiple contacts are provided with the restricted-access repository to ensure long-term access is possible.

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