Original Research Article

Impacts of feral grazers and unseasonal summer flooding on floodplain carbon dynamics: A case study

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ABSTRACT

Wetlands are amongst the world's most effective natural carbon sinks, and also have the potential to emit large quantities of stored carbon back into the atmosphere if disturbed. In the Murray-Darling Basin, high consumptive demand for water has led to widespread wetland loss and degradation. Remaining wetlands are commonly under additional pressure from grazing and trampling by feral herbivores or livestock and unseasonal flooding in summer to meet peak irrigation demand. Here, during a summer flood in Barmah National Park, we compared soil carbon and nitrogen and carbon emissions within, and outside of, a feral herbivore exclusion plot. The sustained global warming potential from the whole wetland (i.e., both within- and outside of the exclusion plot), totalled from both carbon dioxide (CO_2) and methane (CH_4) emissions, averaged 132.27 ± 9.88 g CO_2-e m^{-2} d^{-1}, an estimated 28- to 89-fold higher than the global average for natural wetlands. The high warming potential of the wetland was driven strongly by CH_4 emissions, which made up over 90% of total CO_2-equivalents, with CO_2 contributing <10%. We expect these values represent peak CH_4 emissions from the site due to high water and soil temperatures, and low water levels, at the time of sampling. Soil carbon and nitrogen did not differ significantly within and outside of the exclusion plot, but surface soil samples indicated recent condition improvement in the absence of feral herbivores. We suggest that an emissions avoidance incentive could be developed around unseasonal, summer watering of forested floodplains where flood timing can be controlled.

1. Introduction

Wetlands play a significant role in global carbon cycling, storing up to 70% of terrestrial carbon in their soils and emitting up to 20–30% of the world's methane (CH_4) (Adhikari et al., 2009; Mitra et al., 2005; Morrissey et al., 2014). Rates of carbon sequestration are higher in wetlands than any other ecosystem, due to high plant productivity and low decomposition rates under anaerobic conditions that occur during inundation (Kayranli et al., 2010;

Morrissey et al., 2014). Disturbances to wetland hydrology and soils influence carbon cycling by altering the balance between carbon sequestration and mineralization to carbon dioxide (CO_2) (Adhikari et al., 2009). Large carbon stores in wetland soils can be released when disturbed, potentially shifting the ecosystem from a net carbon sink to a carbon source (Bridgham et al., 2013; Fenstermacher et al., 2016). Understanding the extent to which different disturbances trigger carbon release from wetlands is a key component of climate-focused ecosystem management.

Hydrology is a fundamental driver of wetland carbon cycling e.g. (Bernal and Mitsch, 2012). In seasonal wetlands, the presence or absence of water is a strong de-

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terminant of both carbon dioxide and methane emissions (Boon and Mitchell, 1995; Limpert et al., 2020; Treby et al., 2020), and rates of decomposition and carbon sequestration (Carnell et al., 2018). In riverine wetlands such as floodplains, river regulation substantially alters wetland hydrology by reducing flow volumes, increasing the duration of the dry phase, and in turn, reducing the duration and amount of water in the wet phase (Chesterfield, 1986; Lytle and Poff, 2004; Orthia, 2002; Vivian et al., 2014; Walker et al., 1995).

River regulation can also change wetland hydrology by shifting the timing of inundation from natural winter-spring flooding seasons to the drier summer months, when irrigation demand increases (Bren, 1988). This alters the ecology of the system and can impact both plant and animal communities (Chong and Ladson, 2003; Lytle and Poff, 2004; Thoms et al., 2000). As water and soil temperatures are known to influence greenhouse gas emissions from wetlands (e.g. Moore and Dalva, 1993; Ollivier et al., 2019b; Updegraff et al., 2001; Song et al., 2003; Wang et al., 2017), unseasonal flooding in warmer months has the potential to substantially increase wetland global warming potential.

The Murray-Darling is Australia's largest and economically most important river basin. Its location on the eastern, most populous part of the continent, puts heavy demand on the system for consumptive use, providing an estimated 50 per cent of Australia's irrigated produce each year (Murray Darling Basin Authority, 2016). River regulation since the 1920s has resulted in the reduction of up to 60% of the Murray's flows, with up to 95% of diversions allocated to irrigation (Kingsford et al., 2011). Consequently, the past two decades have seen increasing pressure on governments to manage the Basin's competing agricultural and environmental demands (Pittock and Finlayson, 2011; Saintilan et al., 2013). Of particular interest are the Murray River's most iconic wetlands, prioritised for conservation. Barmah Forest and National Park, one of 'The Living Murray' icon sites, is one of 16 Ramsar-listed wetland sites across the Murray-Darling Basin (Ramsar, 2019). Together with the adjacent Millewa Forest in New South Wales, Barmah-Millewa Forest is the largest remaining river red gum (*Eucalyptus camaldulensis*) stand in the world, (Robinson, 1998).

Barmah Forest is subjected to two distinct interventional flooding regimes: the first is 'environmental water' (rewetting) – a managed intervention that supplements water in streams and wetlands which have been drained or hydrologically modified as a result of river regulation, implemented in Barmah-Millewa in the 1990s (Stewart and Harper, 2002). In Barmah-Millewa Forest, environmental water allocations aim to reinstate natural hydrology, i.e. winter-spring flooding cycles, to support unique vegetation communities such as moira grass (*Pseudoraphis spinescens*), a key character of the Barmah Forest Ramsar listing (Kingsford, 2000; Vivian et al., 2015, 2014). The second flooding method involves the delivery of water through Barmah Forest to meet irrigation demand downstream (Orthia, 2002). This typically occurs in low-rainfall periods from summer to autumn, and its diversion from natural flooding cycles is a key threat to Barmah

Forest's ecological values (Chesterfield, 1986; Chong and Ladson, 2003). For example, summer flooding reduces the cover of moira grass and encourages river red gum encroachment on to marsh floodplains, threatening the sites' Ramsar listing and associated protection (Bren, 1988; Parks Victoria, 2018).

Barmah Forest is home to a number of feral species – as well as pigs and several species of deer, approximately 700 feral horses occur in Barmah National Park, with a rapidly increasing population (Parks Victoria, 2018). Feral herbivores are a key threat to the ecological character of Barmah Forest, causing significant damage to wetland soils and vegetation through grazing and trampling (Parks Victoria, 2018). While pest management programs for deer and pigs are widely accepted by the general public, the control of horse populations is contentious (Knight, 2019; Nimmo and Miller, 2007). Heavy, hooved ungulates do not occur naturally in Australia, and reduce soil quality through erosion, compaction, and reduction of native vegetation (Nimmo and Miller, 2007; Nuñez et al., 2010; Waqar Ahmed Khan et al., 2019). In agricultural areas, livestock grazing negatively influences wetland carbon processes through biomass removal, changes to plant species composition and reduced plant regeneration from soil compaction (Lal, 2014; Oduor et al., 2018; Pachauri, 2004). Similar effects are likely to result from the grazing and trampling activity of feral herbivores where they occur in wetland environments. However, the influence of feral herbivores on carbon cycling in Australian wetlands is currently unknown, highlighting a gap in our understanding of the link between key ecological threats and climate change mitigation.

This study aimed to compare wetland carbon responses to these two important management issues: the impact of feral herbivores, and unseasonal flooding through Barmah Forest National Park. We used Little Rushy Swamp (LRS), a marsh floodplain within Barmah Forest and the site of a feral herbivore exclusion plot, as a case study. We sampled soil carbon and soil nitrogen and monitored carbon emissions from within- and outside of the exclusion plot in January 2019, following an unseasonal summer flood. We hypothesised that: 1) carbon emissions would be higher than similar wetlands flooded in winter-spring, due to higher water temperatures at the time of sampling; 2) carbon emissions would be lower in the fenced half of the wetland due to improved soil condition in the absence of feral herbivores; and 3) soil carbon and nitrogen content would be higher, and soil bulk density would be lower, in the fenced half of the wetland, due to increased vegetative cover and reduced compaction in the absence of feral herbivores.

2. Materials and methods

2.1. Site history & description

Little Rushy Swamp (−35.9°, 145.1°; 95 m ASL) is a 12-ha marsh floodplain within Barmah Forest, characterised by the presence of moira grass (*Pseudoraphis spiniscens*) and giant rush (*Juncus ingens*), surrounded by river red gum (*Eucalyptus camaldulensis*) forest. Soils in Barmah
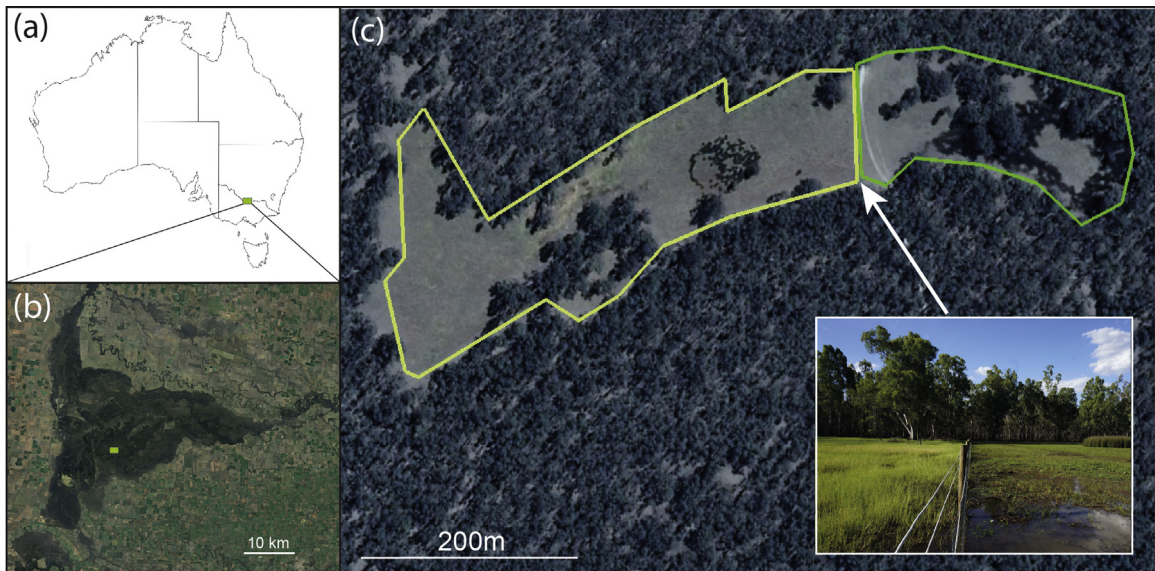
Figure 1. Site location & experimental design. (a) Map of Australia showing state borders and site location; (b) Barmah-Millewa Forest with Little Rushy Swamp highlighted in light green; and (c) Little Rushy Swamp showing the fence perimeter in yellow (feral herbivores excluded; left), and unfenced wetland area (feral species present; right) in green. Inset: fence line in January 2019 showing vegetation differences between the fenced and unfenced zones.

Forest are predominately vertosols, and the surrounding land is used for grazing, dryland cropping, and irrigated cropping (Australian Government, 2021; Agriculture Victoria, 2021; ASRIS, 2021). Historically, Little Rushy Swamp was the site of a mustering flat when cattle were grazed through Barmah Forest, from the 1880s until 2007 (Victorian Heritage Register, 2009). After cattle were removed, wetland grazing and trampling have continued due to feral horses (*Equus callabus*), sambar deer (*Rusa unicolor*), fallow deer (*Dama dama*), and pigs (*Sus scrofa*). In April 2017, exclusion fencing was installed over the western 7ha of Little Rushy Swamp, leaving the remaining 5 ha subject to continued grazing and trampling (Parks Victoria, 2018; Fig. 1). The fencing is penetrable by native herbivores such as eastern grey kangaroos (*Macropus giganteus*). As such, differences in condition between the fenced and unfenced wetland zones can be attributed specifically to feral species (Parks Victoria, 2018; Fig. 2). Little Rushy Swamp falls within a semi-arid region of south-eastern Australia, and has mean annual temperatures of 4–31°C and mean annual precipitation of 426 mm (Echuca Aerodrome; Bureau of Meteorology, 2019).

Sampling was carried out in January 2019 (Austral summer), at the drawdown phase of an unseasonal summer flood in Barmah National Park. The sampling window was restricted to a period of only several days prior to the wetland drying, and as such, intensive sampling was carried out over two days and nights. The experimental design divided the wetlands into two zones – the first within the exclusion plot; 'fenced', where feral herbivores were excluded, and the second outside of the exclusion plot; 'unfenced', where feral herbivores were present (Fig. 1).

2.2. Carbon emissions

Carbon dioxide (CO_2) and methane (CH_4) diffusive emissions were recorded in replicates of 10 per wetland zone (fenced and unfenced) per diel period (day and night) over two days ($n = 80$). GHG recordings were made for a minimum of 300 seconds at each station, using opaque PVC chambers attached to an ultraportable greenhouse gas analyzer (UGGA; Los Gatos Research, San Jose, California, USA). Sampling was carried out between 14:00 and 20:00 (day), and 21:00 and 02:00 (night). GHG emissions, represented as mmol m^{-2} d^{-1}, were calculated using a standard diffusive flux equation based on the best fit linear regression of emissions over time (Lambert and Fréchette, 2005). Carbon dioxide equivalents (CO_2e) for CH_4 were calculated using the 20-year sustained global warming potential (SGWP) figures described in Neubauer and Megonigal (2015).

2.3. Soil sampling & processing

Eight soil cores were taken per zone (fenced and unfenced), ($n = 16$). Soil cores were sampled manually using 50 mm diameter polyvinyl chloride (PVC) pipe to a maximum depth of 10 cm from the soil surface. This depth was based on Carnell et al. (2018), showing accretion rates in wetlands of south-east Australia range from 0.14–0.9 mm per year, and our aim to capture differences since exclusion fencing was installed two years prior to sampling (2017). A correction factor was used to adjust depth and volume calculations affected by soil compaction during sample collection, wherein the difference between the soil depth within and outside of the PVC soil core was added to the depth of the sample collected. This correction fac-

Figure 2. Vegetative cover at Little Rushy Swamp. (a) Within the exclusion plot (fenced zone), moira grass (*Pseudoraphis spinescens*) dominates and has greater cover and biomass than (b) outside of the exclusion plot (unfenced zone), where emerging *P. spinescens* and other aquatic vegetation has reduced cover and biomass. Quadrat is 50×50 cm.

tor assumes any compaction is equivalent at all depths of the core, although greater compaction likely occurs closer the soil surface. Samples were sectioned into segments as follows: 0–1 cm, 1–2 cm, 2–3 cm, 3–4 cm, 4–6 cm and 6–8 cm, then oven-dried until a stable mass was reached, and weighed to calculate dry bulk density (DBD; g cm^{-3}). The samples were homogenized and ground using a RM-200 electric mortar grinder (Retsch, Haan, Germany). Soil organic carbon (SOC) and nitrogen concentrations were obtained using a MicroElemental CN analyzer with Callidus v5.1 software (EuroVector, Pavia, Italy). Molar C:N ratio was calculated by converting carbon and nitrogen concentration values to an arbitrary mass of 1 kg each, dividing each by the atomic mass of the element (12 mmol C per kg; 14 mmol N per kg), then dividing mmol C kg^{-1} by mmol N kg^{-1} (Lawless, 2012).

2.4. Analysis

2.4.1. Carbon emissions

Three separate two-way analysis of variance (ANOVA) models were run for: (1) methane (CH$_4$), (2) carbon dioxide (CO$_2$), and (3) carbon dioxide equivalents (CO$_2$e), in R (R core team, 2017; https://www.R-project.org/) using the lm() function within "stats" package (Wilkinson and Rogers, 1973). Each model included zone (fenced or unfenced) and diel period (day or night) as fixed factors. All models met the assumptions of normality (tested visually using Q-Q plots and using the Shapiro-Wilk test (shapiro.test() in the "stats" package (Wilkinson and Rogers, 1973)) and homoscedasticity, confirmed using Levene's test (LeveneTest() in the "car" package (Fox and Weisberg, 2019)).

2.4.2. Soil carbon and nitrogen

Five separate two-way analysis of variance (ANOVA) models were run in R (as above) for: (1) soil dry bulk density (DBD), (2) soil nitrogen concentration (N %); (3) soil organic carbon concentration (SOC %), (4) soil organic carbon density (g SOC cm^{-3}), and (5) C:N (carbon to nitrogen ratio). Each model included zone (fenced or unfenced) and soil depth as fixed factors. SOC and N concentration both underwent a natural log transformation prior to analysis. All models met the assumptions of normality and homoscedasticity (tested as above).

3. Results

3.1. Carbon emissions

3.1.1. Methane (CH$_4$)

CH$_4$ emissions ranged from 8.26 to 381.64 mmol m^{-2} d^{-1} and averaged 78.64 ± 6.31 mmol m^{-2} d^{-1} across all samples (i.e. day and night, fenced and unfenced zones). We found no significant effect of either fencing treatment (F = 0.59, p = 0.45) or diel period (F = 0.001, p = 0.99) on CH$_4$, and no significant interactive effect of these two variables (F = 0.97, p = 0.33) (Fig. 3).

3.1.2. Carbon Dioxide (CO$_2$)

CO$_2$ emissions ranged from 13.63 to 633.21 mmol m^{-2} d^{-1} and averaged 251.1 ± 14.22 mmol m^{-2} d^{-1} across all samples. We found a significant interactive effect of diel period and zone (F = 6.45, p = 0.01, Fig. 3). This effect was driven by higher mean CO$_2$ emissions at night in the unfenced zone compared to daytime, but no difference in emissions from the fenced zone between day and night. Zone alone was a highly significant driver of CO$_2$, with emissions higher in the fenced zone than the unfenced zone (F = 56.05, p <0.001). Diel period as a main effect did not significantly influence CO$_2$ emissions (F = 0.12, p = 0.73) (Fig 3).
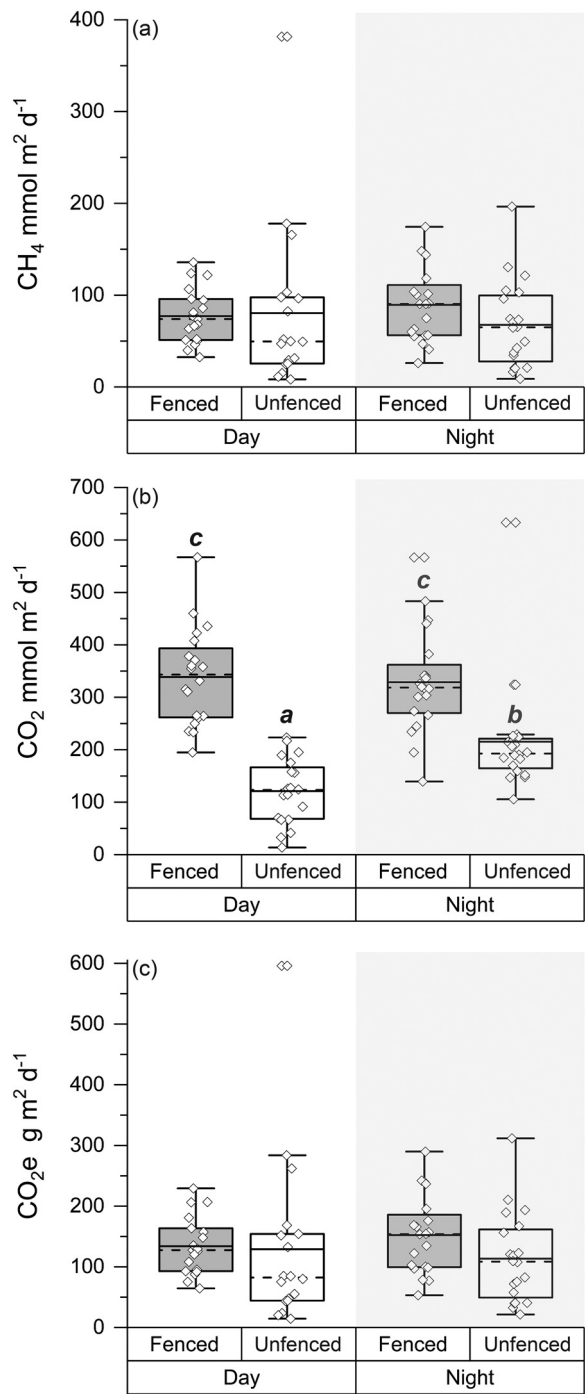
Figure 3. Carbon emissions of (a) methane (CH_4); (b) carbon dioxide (CO_2); and (c) 20-year sustained global warming potential (SGWP; see Neubauer and Megonigal, 2015) of both gases in carbon dioxide equivalents (CO_2e); at day and night in the fenced (feral herbivores excluded) and unfenced (feral herbivores present) zones of Little Rushy Swamp. Horizontal lines within boxes show group mean (solid) and median (dashed). Letters above bars show the significance of differences between means (Tukey's HSD, p <0.05).

Table 1
Relative contributions of CH_4 and CO_2, represented as percentages of the total sustained global warming potential (SGWP, CO_2-equivalents) of Little Rushy Swamp in January 2019.

Diel Period	Zone	Percentage of total measured emissions	
		CH_4	CO_2
Day	Fenced	87.7%	12.3%
	Unfenced	95.6%	4.4%
Night	Fenced	89.6%	10.4%
	Unfenced	90.9%	9.1%
Average	(All)	90.95%	9.05%

3.1.3. Sustained Global Warming Potential (CO_2-equivalents)

The 20-year sustained global warming potential (SGWP) of the site for combined CH_4 and CO_2 emissions ranged from 14.56 to 596.11 g CO_2e m^{-2} d^{-1} and averaged 132.27 ± 9.88 g CO_2e m^{-2} d^{-1} across all samples (i.e. day and night, fenced and unfenced zones). We found no significant main effect of either zone (F = 1.272, p = 0.26) or diel period (F = 0.006, p = 0.94) on SGWP (CO_2e), and no significant interactive effect of these two variables (F = 0.719, p = 0.4) (Fig 3). Methane emissions contributed, on average, 90.9% of CO_2-equivalents to the SGWP of the wetland, with carbon dioxide contributing the remaining 9.1% (Table 1). Within the fenced zone, relative contributions of CO_2 to SGWP were higher (12.3% in the day and 10.4% in the night) than in the unfenced zone (4.4% in the day and 9.1% in the night) (Table 1).

3.2. Soils

3.2.1. Soil Dry Bulk Density

Mean dry bulk density (DBD) was 0.97 ± 0.36 g cm^{-3} and ranged from 0.34–1.83 g cm^{-3} across all samples. Zone did not significantly influence dry bulk density (Fig. 4, Table 1). Soil depth significantly influenced dry bulk density, which increased down-profile in samples from both the fenced and unfenced zones (Fig. 4; Table 2).

3.2.2. Soil Nitrogen

Mean N concentration was 0.39 ± 0.19% and ranged from 0.14–0.94% across all samples. Zone and soil depth each significantly influenced N concentration, which was higher at the unfenced zone, and decreased down-profile in samples from both the fenced and unfenced zones (Fig. 4; Table 2). There was no significant interactive effect of soil depth and zone on N concentration (Table 2).

3.2.3. Soil Carbon (concentration)

Mean SOC concentration was 4.79 ± 2.97% and ranged from 1.28–12.71% across all samples. Zone did not significantly influence SOC concentration (Fig. 4; Table 2). Soil depth significantly influenced SOC concentration, which decreased down profile in samples from both the fenced and unfenced zones (Fig. 4; Table 2). There was no significant interactive effect of soil depth and zone on SOC concentration (Table 2).

3.2.4. Soil Carbon (density)

Mean SOC density was 37.81 ± 13.93 mg cm^{-3} and ranged from 17.28–80.58 mg cm^{-3} across all samples. Zone
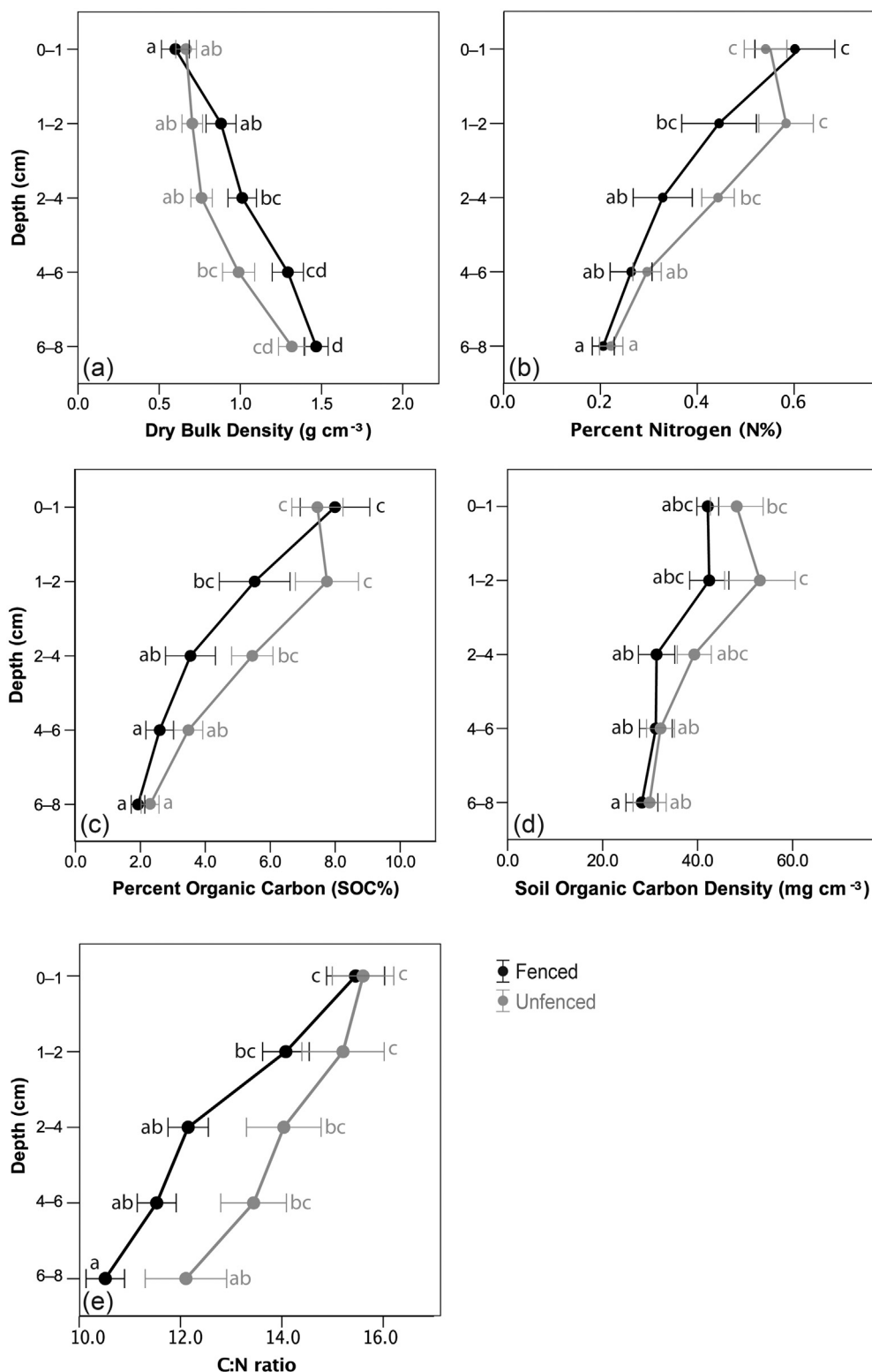
Figure 4. Soil characteristics compared by depth between the fenced (feral herbivores excluded) and unfenced (feral herbivores present) zones of Little Rushy Swamp, Barmah Forest. (a) Mean dry bulk density (DBD); (b) Mean soil nitrogen concentration (N %); (c) Mean soil organic carbon concentration (SOC %); (d) Mean SOC density (mg cm^{-3}); and (e) C:N ratio. Error bars show standard error. Letters beside markers show significance of differences between means within each variable (points that share a letter do not differ significantly from one another) and are not comparable between panels (Tukey's HSD, $p < 0.05$).

Table 2

Analysis of Variance (ANOVA) summary statistics (*F*-values) of dry bulk density (DBD), nitrogen concentration (N), soil organic carbon (SOC) concentration and density, and C:N ratio in soil samples (10 cm depth) from Little Rushy Swamp.

	DBD (g cm^{-3})	N (%)	SOC (%)	SOC (g cm^{-3})	C:N
Depth	17.33***	19.28***	14.03***	7.60***	15.16***
Zone	0.33	5.21*	0.03	4.14*	11.98***
Depth * Zone	1.49	0.97	1.08	0.48	0.74

p $\leq$ 0.05; ** p $\leq$ 0.01; *** p $\leq$ 0.001; no asterisk indicates p > 0.05
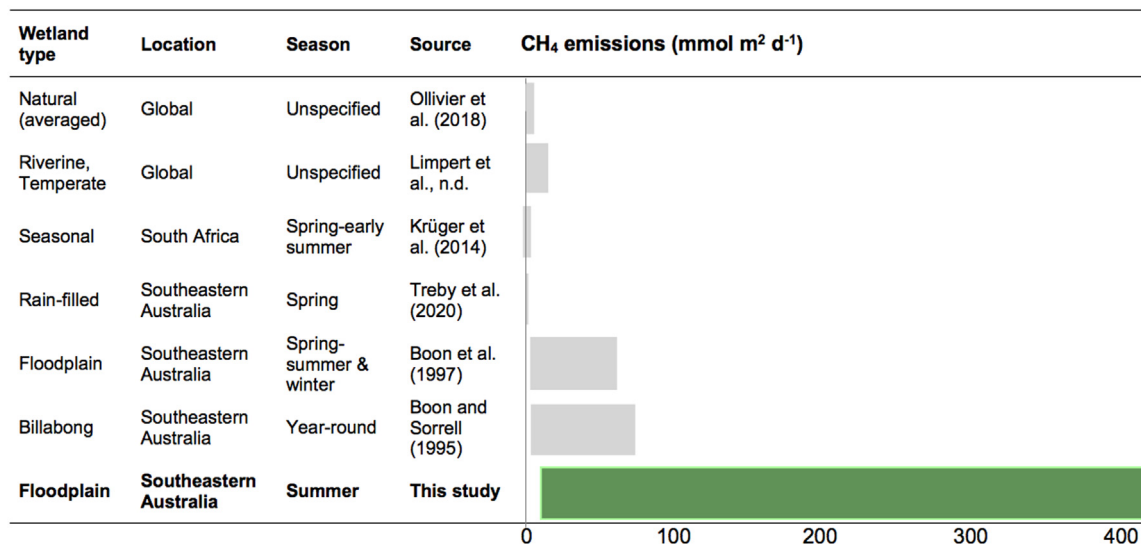
Figure 5. CH$_4$ emissions from comparable natural wetlands described in previous studies. Emissions data have been converted to mmol m^{-2} d^{-1} for comparison with the present study.

and soil depth both significantly influenced SOC density (Fig. 4; Table 2). SOC density decreased down profile in samples from both the fenced and unfenced zones, except at 1–2 cm depth in the unfenced zone (Fig. 4). There was no significant interactive effect of soil depth and zone on SOC density (Table 2).

3.2.5. Soil Carbon to Nitrogen ratio

Mean C:N was 13.45 $\pm$ 2.32 and ranged from 9.11–19.05 across all samples. Zone and soil depth both significantly influenced C:N (Fig. 4; Table 2). C:N was consistently higher in the unfenced zone and decreased down profile in samples from both the fenced and unfenced zones, except the top 0-1 cm when C:N was effectively equivalent between zones (Fig. 4). There was no significant interactive effect of soil depth and zone on C:N (Table 2).

4. Discussion

4.1. Unseasonal flooding and carbon emissions

This study reports extremely high carbon emissions from Little Rushy Swamp, recorded during an unseasonal summer flood in 2019. The sustained global warming potential (SGWP; represented as CO$_2$ equivalents; CO$_2$e) of the site was between 28–89-fold higher than other natural wetlands, and even 11–40-fold higher than average for constructed wetlands (Maltais-Landry et al., 2009; Ollivier et al., 2019a) (Fig. 5). This key finding presents a new argument in the case for managed flows following natural hydrological regimes, where flood timing is critical not only for floodplain ecohydrology, but also for avoiding significant methane emission to the atmosphere.

Methane emissions made up over 90% of the sustained global warming potential (SGWP) of the wetland at the time of sampling (Table 1), which is supported by previous research showing that, across a range of different wetland types, CH$_4$ contributes a greater proportion of total global warming potential than both CO$_2$ and N$_2$O (Page and Dalal, 2011; Tian et al., 2011; Wang et al., 2021).

Temperature alone is a strong driver of CH$_4$ production e.g. (Brix et al., 2001;Chen et al., 2021;Mitsch et al., 2012), with optimum growth of methanogenic microbes at 30–40°C (Whalen, 2005), which corresponds to water temperatures at Little Rushy Swamp at the time of this research (estimated at >30°C). This is consistent with a number of studies showing that wetland CH$_4$ emissions peak in summer (e.g. Jeffrey et al., 2019; Kandel et al., 2019; Ollivier et al., 2019b), however, even compared with a wetland in the same region in spring-summer, emissions from Little Rushy Swamp were around 7-fold higher (Boon et al., 1997; Boon and Sorrell, 1995; Krüger et al., 2014; Fig. 5). This is likely owing to complex interactions between soil and water temperatures, soil water content, and surface water levels, which together control wetland carbon emissions (Song et al., 2003). At the time of sampling, Little

Rushy Swamp was in the draw-down phase of the wet-dry cycle, with an average water depth of only 7.9 cm. A lower water table facilitates heating of the water column, which increases gas release rates (Shelley et al., 2015; Yvon-Durocher et al., 2014), in addition to transferring both heat and moisture into soils, creating conditions that enhance microbial activity, promoting rates of methanogenesis and heterotrophic respiration (e.g. Moyano et al., 2013; Gondwe et al., 2021). Further, it reduces the amount of time available for methanotrophic processes to occur in the water column, resulting in higher net CH_4 emissions (Bastviken et al., 2003). Song et al. (2003) demonstrate that surface water level is the key controlling factor over wetland CH_4 emission (above temperature), and that while both soil and water temperatures influence carbon emissions from wetlands, soil temperature is the stronger driver of the two. CO_2 emissions are also highly correlated with soil temperature, increasing linearly with incremental rises in temperature (e.g. Kayranli et al., 2010; McKenzie et al., 1998; Moore and Dalva, 1993). By sampling over a short, mid-summer period at end of the wet phase, our results likely represent peak CH_4 emissions for the site, owing to the suitability of a high-temperature, low-oxygen environment for promoting methanogenesis (Wilson et al., 2011; Boon et al., 1997). We would expect that (a) watering during the cooler months would reduce wet-phase emissions of both CH_4 and CO_2; and (b) during the dry phase, total emissions would be higher than during a winter-spring flood but lower than a summer flood, with CO_2 contributing more to overall carbon emissions (due to the availability of oxygen for methane oxidation) (Treby, 2021).

Ephemeral wetlands, such as floodplains, typically produce greater volumes of CH_4 than permanent wetlands due to higher biogeochemical activity (Altor and Mitsch, 2008; Evans and Wallenstein, 2012). This may be driven by higher respiration rates in methanogenic microbes in these systems, which are well adapted to dynamic changes in redox conditions (Boon et al., 1997; Kannenberg et al., 2015), and/or increased availability of labile carbon, driven by high primary productivity, i.e., autochthonous carbon sources such as course woody debris, litter, and aquatic macrophytes (Robertson et al., 1999). In floodplain wetlands, high loads of allochthonous carbon, sourced from upstream erosion and riverine transport, may also provide a labile substrate for methanogenesis in sediments (Robertson et al., 1999). Where surface and groundwater interact during wetland recharge, the biogeochemical mixing zone between them can become an important conduit for diffusive CH_4 emissions from groundwater to the atmosphere (Wu et al., 2020), in addition to providing a source of carbon to riverine food webs (Feris et al., 2003). Thus, here, contributions of groundwater CH_4 and CO_2 may have contributed to the net emissions recorded. In ephemeral wetlands, during periods when the water table is below the soil surface (i.e. there is no surface water present), wetland sediments have the potential to become net CH_4 sinks, as rates of organic matter decomposition in the system increase (Song et al., 2003). We suggest that quantification of dry-phase carbon emissions/uptake at the site e.g. (Treby, 2021) in addition to winter/spring

wet phase sampling, would provide context to the fundings of the present study, and would enable estimates of annual carbon emissions from the site to be generated.

4.2. Carbon emissions and feral herbivore exclusion

Higher CO_2 emissions corresponding to feral herbivore exclusion at Little Rushy Swamp are most likely the result of increased plant respiration where *Pseudoraphis spinescens* biomass has increased following the reduction of grazing and trampling. Net ecosystem exchange (NEE) reflects the carbon balance of the system, where NEE is the balance of CO_2 uptake through photosynthesis (gross primary productivity; GPP) and CO_2 emitted via ecosystem respiration (e.g. Waring and Running, 2007; Yakir, 2003). The dark chamber method, used in this study, captures only CO_2 respiration, as blocking light penetration during measurement prevents plant photosynthetic activity (Lankreijer et al., 2009; Larsen et al., 2022). Therefore, while measured CO_2 respiration was higher within the exclusion plot, photosynthetic activity from increased plant biomass was also almost certainly higher (e.g. Reichstein and Carvalhais, 2019), which would reduce net CO_2 emissions from this part of the wetland. Furthermore, the additional carbon accrued in plant biomass in the continued absence of feral herbivores will likely contribute to future increases in soil carbon, and potentially to long-term sequestration (Craft and Richardson, 1993; Hossler and Bouchard, 2010; Bernal and Mitsch, 2013). In future research, the use of transparent flux chambers and/or eddy covariance methods may help elucidate relationships between plant biomass, hydrological cycles, and CO_2 emission and uptake, as a consequence of grazing disturbance and recovery.

CH_4 emissions did not differ significantly between zones, showing no influence of grazing and trampling on methanogenic or methanotrophic microbial activity in the wetland. This is in contrast with what we hypothesized. Trampling can reduce CH_4 oxidation through disturbance to the oxic-anoxic interface between soils and plant roots, and change soil compaction levels and nutrient movement (Frenzel and Rudolph, 1998; Sitaula et al., 2000; Yamulki and Jarvis, 2002). No detectible change in CH_4 emissions following grazing removal corresponds to our finding that soil compaction (measured as dry bulk density) did not differ significantly between wetland zones, discussed further below. However, we did observe more variability in CH_4 fluxes in the unfenced wetland zone, which could be attributable to trampling effects on soils that increase heterogeneity and microspatial variation across the wetland (Oates et al., 2008). Overall, the similar rates of CH_4 emission between the two areas of the wetland suggest that here, hydrological factors – including flood timing, duration, and water level (and consequent soil and water temperatures) – are stronger drivers of wetland carbon emissions than grazing disturbance.

4.3. Soil condition and feral herbivore exclusion

Feral herbivore exclusion did not result in any significant changes in soil bulk density, nitrogen concentration or

carbon concentration, however, there was a reversal trend in the top 1 cm (Fig. 4), indicating a shift in soil condition in recent history. In the surface horizon, soil nitrogen and carbon concentrations were slightly higher in the fenced zone than in the unfenced zone, while bulk density was slightly lower. Based on shallow freshwater marsh sediment accretion rates in southeastern Australia, this surface layer may reflect the past 7–25 years (Carnell et al., 2018). We therefore expect that the top 1 cm captures differences attributable, at least in part, to the exclusion of feral herbivores at Little Rushy Swamp. It is likely that subsequent increases in above- and belowground biomass, predominantly that of *P. spinescens*, are driving this shift in soil condition (e.g. Fontaine et al., 2004; Maucieri et al., 2014). Across the site, soil characteristics appeared similar to averages for other wetlands across Victoria (Carnell et al., 2018). Soil carbon concentrations were slightly lower than the state-wide wetland average (7.7%), but higher than the global wetland average of 2.13% (Dong et al., 2022). Soil carbon density and bulk density were almost identical to the state-wide averages of 31 mg cm^{-3} and 1 g cm^{-3}, respectively (Carnell et al., 2018). Below the surface, soil carbon concentrations were consistently lower, and bulk density was consistently higher, in the fenced zone. We speculate that this relates to the former mustering station having more concentrated cattle activity in the now-fenced zone of Little Rushy Swamp, and consequent land use legacy impacts ;(e.g. Holl and Aide, 2011; Peralta et al., 2018; Treby et al., 2020; Victorian Heritage Register 2009) ; ;), although we were unable to find historical records to substantiate this.

4.4. Management implications

Our findings have important implications for land managers and/or policy advisors seeking to achieve carbon emission reductions through natural resource management. We suggest that floodplain carbon emissions could be substantially reduced by changing the timing of water delivery to actively prevent summer floods through forested floodplains, both within the Murray-Darling Basin and more widely. Chong and Ladson (2003) discuss approaches for better managing unseasonal flows to reduce summer flooding through Barmah-Millewa Forest. Maintaining a natural flow regime in riverine systems is critical for floodplain ecology and biogeochemical cycling, and interactions between these two critical aspects of a healthy wetland ecosystem (Robertson et al., 199). Hydrology controls the growth, productivity, and survival of floodplain vegetation, which determines the quantity of carbon available for downstream transport, underpins riverine food webs, and provides habitat for wetland fauna, including many threatened species (Beesley et al., 2011; Chong and Ladson, 2003; Robertson et al., 1999). An additional benefit of avoiding summer flood events is the reduced risk of hypoxic blackwater events. (e.g. McCarthy et al., 2014; Small et al., 2014; Watts et al., 2017). Blackwater is created through the contribution of dissolved organic carbon (DOC) leaches from leaf litter and detritus on floodplains (e.g., Howitt et al., 2007; Kerr et al., 2013). High carbon loads in blackwater are consumed by aquatic microorganisms,

which depletes dissolved oxygen levels, creating hypoxic or anoxic conditions that can lead to mass fish and crustacean deaths in the river network (e.g. McCarthy et al., 2014; Small et al., 2014; Watts et al., 2017). The risk of hypoxic blackwater events is heightened in summer, as higher temperatures lead to: decreased O_2 solubility in water, increases microbial metabolic rates, enhances enzyme reaction rates, and alters DOC solubility (Whitworth et al., 2012). Forested floodplains typically have large amounts of labile carbon on the forest floor, owing to large volumes of leaf litter and other debris (Robertson et al., 1999). When flooded, this carbon is readily leached from litter into the water column (e.g. Watts et al., 2017; Whitworth et al., 2012), and here, was likely a significant contributor to the carbon used in methanogenesis, leading to high net CH_4 emission from Little Rushy Swamp. Summer flooding has triggered a number of hypoxic blackwater events of varying sizes and impacts in the Murray-Darling Basin (Robertson et al., 2001; Howitt et al., 2007; Whitworth et al., 2012), and blackwater risk mitigation is a current management priority (Joehnk et al., 2020). Thus, we would expect that by delivering flows in winter-spring rather than spring-summer, several beneficial ecohydrological and biogeochemical outcomes could be achieved through this single management strategy.

Australia's Emissions Reduction Fund provides incentives for shifting the timing of savanna burns from late season to early season, to reduce fire intensity, resulting in emissions avoidance (Department of the Environment and Energy, 2018; Department of the Environment and Energy, 2016). We recommend continued research into seasonal flooding and greenhouse gas emissions for a similar emissions avoidance scheme to be developed for regulated, riverine wetland ecosystems. However, as climate change continues to be realised, natural flooding cycles are following decreasing cool season rainfall, independent of managed watering (Murray Darling Basin Authority, 2019). Therefore, some consideration needs to be made for the impact this will have on floodplain wetland carbon emissions, where a positive feedback loop for climate change may further exacerbate these environmental shifts.

4.5. Limitations and further research

Dry conditions in 2019 and 2020 presented a limitation to this study, where insufficient inflows prevented follow-up monitoring during a winter-spring watering event at Little Rushy Swamp. As such, our inferences about the seasonal influence on wetland emissions, while well documented elsewhere, are speculative. Further research should aim to repeat sampling at Little Rushy Swamp in a winter/spring watering event, to more definitively attribute the high emissions documented here to flooding seasonality. We expect that monitoring over a longer period would show continued soil and vegetation recovery in the absence of feral herbivores, and recommend continued monitoring of carbon responses to more conclusively inform wetland management. A further limitation of our study method may have been the relatively shallow depth of soil cores taken (10 cm). We based this depth on known soil accretion rates in the area, but the impacts of trampling

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