




The climate benefit of seagrass blue carbon is reduced by methane fluxes and enhanced by nitrous oxide fluxes

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Blue carbon is carbon stored long-term in vegetated coastal ecosystems, which constitutes an important sink for atmospheric carbon dioxide (CO₂). However, because methane (CH₄) and nitrous oxide (N₂O) have higher global warming potentials (GWP) than CO₂, their production and release during organic matter diagenesis can affect the climate benefit of blue carbon. Here, we present a meta-analysis synthesizing seagrass CH₄ and N₂O fluxes and long-term organic carbon burial rates, and use these data to estimate the reduced climate benefit (offsets) of seagrass blue carbon using three upscaling approaches. Mean offsets for individual seagrass species (34.7% GWP₂₀; 1.0% GWP₁₀₀) and globally (33.4% GWP₂₀; 7.0% GWP₁₀₀) were similar, but GWP₂₀ offsets were higher, and GWP₁₀₀ offsets were lower than globally, for the Australian region (41.3% GWP₂₀; 1.1% GWP₁₀₀). This study highlights the importance of using long-term organic carbon burial rates and accounting for both CH₄ and N₂O fluxes in future seagrass blue carbon assessments.

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Improving the capacity of natural ecosystems to assimilate carbon dioxide (CO₂) and store organic carbon (C_{org}) long-term is an important strategy for mitigating climate change¹. As such, restoring the carbon sequestration capacity of terrestrial ecosystems, such as tropical rainforests and farmland, has been the focus of many conservation efforts². Vegetated coastal ecosystems, particularly mangroves, salt marshes, and seagrasses also store large amounts of organic matter^{3–5}. Seagrass communities account for up to half the global carbon accumulated in vegetated coastal habitats⁶. However, resolving the climatic benefit of marine ecosystems requires knowing the CO₂ sequestration potential through long-term (>100 years) C_{org} burial^{7,8}, as well as quantification of the methane (CH₄) and nitrous oxide (N₂O) flux during early diagenetic processes^{9–11}.

Methanogens produce CH₄ via hydrogenotrophic (CO₂ reduced to CH₄ using H₂), acetoclastic (acetate disproportionation used to form CH₄), and methylotrophic (methyl groups of methylated compounds used to form CH₄) pathways¹². N₂O can be produced during a variety of processes but mostly nitrification and denitrification, e.g. ¹³. CH₄ and N₂O have a global warming potential (GWP) that is, depending on the 20-year or 100-year time-horizon, 79.7 to 27.0 for CH₄ or 273 for N₂O times respectively more powerful than CO₂¹⁴. As such, the production and release of CH₄ and N₂O from marine sediments has the potential to reduce (offset) the climatic benefit of C_{org} sequestered through long-term (>100 years) C_{org} burial (i.e., blue carbon)^{9,11}. Similarly, an uptake of CH₄ and N₂O has the potential to enhance the climate benefit of vegetated coastal communities^{15–17}. Although CH₄ and N₂O are released during the short-term decomposition of organic matter that is not buried, their long-term influence on the atmosphere supports a comparison to long-term C_{org} burial.

Three studies have used either CH₄ fluxes¹⁸ or CH₄ and N₂O fluxes^{11,19} in seagrass communities to estimate offsets for individual sites that range from zero to 10% (GWP₁₀₀), but none used

measured long-term (>100 year) C_{org} burial rates. Two studies used seagrass CH₄ fluxes to estimate global offsets that range from 0.5 to 4.5% (GWP₁₀₀), but both these studies used global seagrass organic carbon accumulation estimates^{20,21}, which do not represent long-term C_{org} burial rates. Considering the implications for policies and practice incorporating blue carbon habitat conservation and restoration as a natural strategy for CO₂ removal, there is a clear need to re-assess the climate benefit of seagrass blue carbon based on a synthesis of seagrass CH₄ and N₂O fluxes and long-term C_{org} burial rates.

In this study we present a meta-analysis synthesizing seagrass long-term C_{org} burial rates (and C_{org} accumulation rates for comparison) and CH₄ and N₂O fluxes (Fig. 1 and Supplementary Tables 1–4), and use the combined CO₂-equivalent CH₄ and N₂O fluxes to estimate the reduced climate benefit (offsets) to seagrass blue carbon (1) for individual seagrass species (2) for the Australian region, and (3) globally using the mean and median of all rates. We further present new water-air CH₄ and N₂O fluxes for one study site in Australia (Wallagoot Lake), which increased the limited number of seagrass N₂O fluxes, added N₂O fluxes for a new seagrass species, doubled the number of seagrass water-air N₂O fluxes, and also added an additional seagrass CH₄ flux. We found CH₄ and N₂O fluxes offset on average around 7% to 35% of the global climate benefits of seagrass blue carbon.

Results

Methane and nitrous oxide water-air fluxes in a *Ruppia megacarpa* community. Over the diel cycle (20 h), water overlying the *R. megacarpa* community in Wallagoot Lake had an average temperature and salinity of 25.8 ± 2.2 °C and 29.5 ± 0.2, respectively. The CH₄ concentration varied between 50.4 and 86.2 nmol l⁻¹ without following a diel pattern. In parallel, the N₂O concentration slightly increased from 4.5 to 5.6 nmol l⁻¹ in

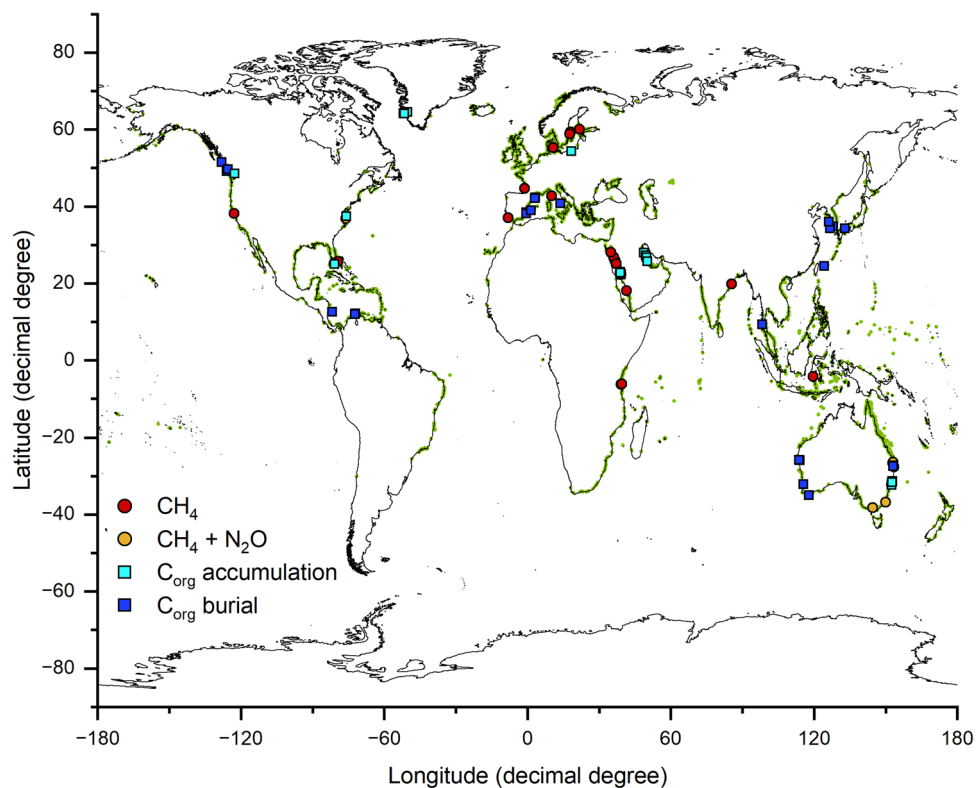


Fig. 1 Global distribution of CH₄ and N₂O fluxes, C_{org} accumulation and long-term C_{org} burial rates measured in seagrass communities. Seagrass areas (green areas) adapted from UNEP-WCMC, 2021 (<https://data.unep-wcmc.org/datasets/7>; data from Supplementary Tables 1–4). Long-term (>100 years).

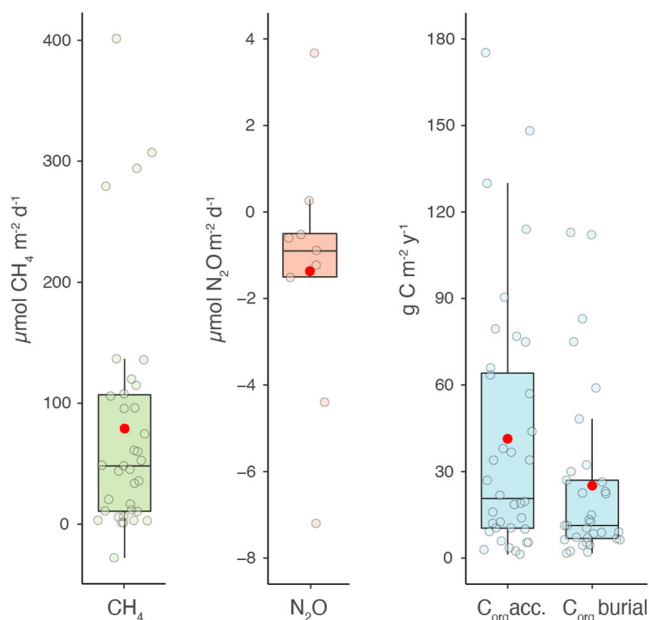


Fig. 2 Boxplots CH₄ and N₂O fluxes, C_{org} accumulation and long-term C_{org} burial rates. Boxplots showing median, mean (red circle), 25th and 75 percentiles (boxes), 10th and 90th percentiles (bars) and data points (circles) of CH₄ ($n = 35$; green) and N₂O fluxes ($n = 9$; pink) and C_{org} accumulation (acc.) ($n = 36$; blue) and long-term (>100 years) C_{org} burial rates ($n = 33$; blue) in seagrass communities (Supplementary Tables 1–4).

the first 4 h of the survey, thereafter gradually decreasing back to the initial concentration. The *R. megacarpa* community was a source of CH₄ and a sink of N₂O to the atmosphere. Water-air CH₄ fluxes ranged from 16.8 to 57.3 $\mu\text{mol CH}_4 \text{ m}^{-2} \text{ day}^{-1}$ with a mean of $32.5 \pm 0.4 \mu\text{mol CH}_4 \text{ m}^{-2} \text{ day}^{-1}$ (\pm standard error (SE), $n = 1202$) (Supplementary Fig. 1). Water-air N₂O fluxes ranged from -2.0 to $-0.4 \mu\text{mol N}_2\text{O m}^{-2} \text{ day}^{-1}$ with a mean of $-0.9 \pm 0.01 \mu\text{mol N}_2\text{O m}^{-2} \text{ day}^{-1}$ (\pm SE, $n = 1202$) (Supplementary Figure 1).

Seagrass organic carbon accumulation and burial rates. Global seagrass community C_{org} accumulation rates ranged from 1.3 to 175.3 $\text{g C m}^{-2} \text{ year}^{-1}$ with a mean (\pm SE) of $41.4 \pm 7.4 \text{ g C m}^{-2} \text{ year}^{-1}$ and a median (IQR) of 20.7 (53.8) $\text{g C m}^{-2} \text{ year}^{-1}$ (Fig. 2 and Supplementary Table 1). Global seagrass community long-term C_{org} burial rates (>100 years) ranged from 1.7 to 112.9 $\text{g C m}^{-2} \text{ year}^{-1}$ with a mean (\pm SE) of $25.1 \pm 5.3 \text{ g C m}^{-2} \text{ year}^{-1}$ and a median (IQR) of 11.3 (20.2) $\text{g C m}^{-2} \text{ year}^{-1}$ (Fig. 2 and Supplementary Table 2). Although the mean and median C_{org} accumulation rates were higher than mean and median C_{org} burial rates they were not significantly different ($p = 0.78$). ¹⁴C measured long-term burial rates (mean \pm SE $24.5 \pm 6.7 \text{ g C m}^{-2} \text{ year}^{-1}$; median (IQR) 9.0 (16.8) $\text{g C m}^{-2} \text{ year}^{-1}$) were also not significantly different ($p = 0.94$) than ²¹⁰Pb measured rates (mean \pm SE $27.1 \pm 6.6 \text{ g C m}^{-2} \text{ year}^{-1}$; median (IQR) 24.4 (25.3) $\text{g C m}^{-2} \text{ year}^{-1}$).

Global seagrass methane and nitrous oxide fluxes. Global seagrass community CH₄ fluxes ranged from -27.8 to 401.3 $\mu\text{mol CH}_4 \text{ m}^{-2} \text{ day}^{-1}$ with a mean (\pm SE) of $79.0 \pm 16.8 \mu\text{mol CH}_4 \text{ m}^{-2} \text{ day}^{-1}$ and a median (IQR) of 48.2 (96.3) $\mu\text{mol CH}_4 \text{ m}^{-2} \text{ day}^{-1}$ (Fig. 2 and Supplementary Table 3). Mean (\pm SE) ($103.6 \pm 39.0 \mu\text{mol CH}_4 \text{ m}^{-2} \text{ day}^{-1}$) and median (IQR) (67.4 (135.2) $\mu\text{mol CH}_4 \text{ m}^{-2} \text{ day}^{-1}$) water-air CH₄ fluxes were higher than mean ($70.5 \pm 19.5 \mu\text{mol CH}_4 \text{ m}^{-2} \text{ day}^{-1}$) and

median (IQR) (46.8 (97.6) $\mu\text{mol CH}_4 \text{ m}^{-2} \text{ day}^{-1}$) sediment-water CH₄ fluxes, but they were not significantly different ($p = 0.34$). Seagrass community N₂O fluxes ranged from -7.2 to 3.7 $\mu\text{mol N}_2\text{O m}^{-2} \text{ day}^{-1}$ with a mean (\pm SE) of $-1.4 \pm 1.0 \mu\text{mol N}_2\text{O m}^{-2} \text{ day}^{-1}$ and a median (IQR) of -0.9 (1.0) $\mu\text{mol N}_2\text{O m}^{-2} \text{ day}^{-1}$ (Fig. 2 and Supplementary Table 4). Mean (\pm SE) water-air N₂O fluxes ($-1.2 \pm 0.3 \mu\text{mol N}_2\text{O m}^{-2} \text{ day}^{-1}$) were similar to mean sediment-water N₂O fluxes ($-1.4 \pm 1.3 \mu\text{mol N}_2\text{O m}^{-2} \text{ day}^{-1}$). In contrast, median (IQR) N₂O water-air uptakes (-1.2 (0.3) $\mu\text{mol N}_2\text{O m}^{-2} \text{ day}^{-1}$) were higher than median N₂O sediment-water uptakes (-0.6 (2.7) $\mu\text{mol N}_2\text{O m}^{-2} \text{ day}^{-1}$).

Reduced climate benefit of seagrass communities. Measurements of CH₄ and N₂O fluxes and long-term C_{org} burial rates were available for only three seagrass species (Supplementary Tables 2–4). All three species were a source of CH₄ and a sink for N₂O. *Zostera sp.* and *Halophila sp.* were a CH₄ + N₂O-CO₂e equivalent (CO₂e) source when using 20-year global warming potential (GWP₂₀) and a CH₄ + N₂O-CO₂e sink when using the 100-year global warming potential (GWP₁₀₀), and *Posidonia sp.* was a CH₄ + N₂O-CO₂e equivalent (CO₂e) source (GWP_{20,100}). All three species were net CO₂e sinks when long-term C_{org} burial was included. The mean seagrass community CH₄ + N₂O-CO₂e sources reduces the climate benefit of C_{org} long-term burial 15.8 to 58.3% (GWP₂₀) (average of means 34.7%) across the three seagrass species (median 25.8 to 89.9% (average of medians 54.0%)) (Table 1). CO₂e offsets were much lower using GWP₁₀₀ reducing the climate benefit of C_{org} long-term burial from -16.9 to 18.5% (average of means 1.0%) across the four seagrass species (median -6.5 to 28.6% (average of medians 7.1%)).

All seagrass communities in Australia were a source of CH₄, except for one site (Supplementary Table 3), and a sink for N₂O, except for one site (Supplementary Table 4), and an overall CH₄ + N₂O-CO₂e source. Seagrasses in the Australian region were a net CO₂e sink when long-term C_{org} burial was included. Using the GWP₂₀, the mean Australian seagrass community CO₂e source reduces the climate benefit of C_{org} long-term burial by 41.3% (median 33.9%) (Table 1). Seagrass CH₄ + N₂O-CO₂e offsets in Australia were much lower using the GWP₁₀₀ with a mean reduction of the climate benefit of C_{org} long-term burial of 1.1% (median 2.1%).

Globally, seagrass communities were a source of CH₄, except for one site (Supplementary Table 3), and seven of the nine seagrass communities were a sink for N₂O (Supplementary Table 4), and an overall CH₄ + N₂O-CO₂e source. Seagrasses globally were a net CO₂e sink when long-term C_{org} burial was included. Using the GWP₂₀, the mean global seagrass CH₄ + N₂O-CO₂e source reduces the climate benefit of C_{org} long-term burial by 44.6% (median 33.9%). Seagrass CH₄ + N₂O-CO₂e offsets were lower using the GWP₁₀₀ with a mean reduction of the climate benefit of C_{org} long-term burial of 8.8% (median 7.0%).

Discussion

Burial, methane and nitrous oxide processes in seagrass communities. The range of seagrass long-term C_{org} burial rates (1.7 to 112.9 $\text{g C}_{\text{org}} \text{ m}^{-2} \text{ year}^{-1}$) in this synthesis (Supplementary Table 2) is similar to previous global ranges of long-term burial rates (e.g., 9 to 122 $\text{g C}_{\text{org}} \text{ m}^{-2} \text{ year}^{-1}$)⁵; However, our mean \pm SE global long-term C_{org} burial rate ($25.1 \pm 5.3 \text{ g C}_{\text{org}} \text{ m}^{-2} \text{ year}^{-1}$; $n = 33$) is much lower than a previous estimate of the mean long-term burial rate based on only *P. oceanica* from the Mediterranean ($58 \text{ g C}_{\text{org}} \text{ m}^{-2} \text{ year}^{-1}$)⁵; Similarly, our mean seagrass accumulation rate ($41.4 \pm 7.4 \text{ g C}_{\text{org}} \text{ m}^{-2} \text{ year}^{-1}$; $n = 36$) is lower than previous estimates that have also included C_{org} mass balances ($53 \text{ g C}_{\text{org}} \text{ m}^{-2} \text{ year}^{-1}$)⁵; Using the most recent global

Table 1 Seagrass long-term burial rates, CH₄ and N₂O fluxes, net climate benefit and offsets.

Community	Burial g C _{org} m ⁻² year ⁻¹	Burial g CO ₂ m ⁻² year ⁻¹	CH ₄ flux μmol CH ₄ m ⁻² day ⁻¹	CH ₄ flux GWP ₂₀ g CO ₂ e m ⁻² year ⁻¹	CH ₄ flux GWP ₁₀₀ g CO ₂ e m ⁻² year ⁻¹	N ₂ O flux μmol N ₂ O m ⁻² day ⁻¹	N ₂ O flux GWP ₂₀ g CO ₂ e m ⁻² year ⁻¹	N ₂ O flux GWP ₁₀₀ g CO ₂ e m ⁻² year ⁻¹	Net climate benefit GWP ₂₀ g CO ₂ e m ⁻² year ⁻¹	Net climate benefit GWP ₁₀₀ g CO ₂ e m ⁻² year ⁻¹	Offset GWP ₂₀ %	Offset GWP ₁₀₀ %
Global Median (IQR)	11.3 (20.2)	41.4 (74.1)	48.2 (96.3)	22.4 (44.8)	7.6 (15.2)	-0.9 (1.0)	-3.9 (4.4)	-3.9 (4.4)	23.0	37.8	44.6	8.8
Mean ± SE	25.1 ± 5.3	92.1 ± 20.9	79.0 ± 18.8	36.8 ± 8.7	12.5 ± 3.0	-1.4 ± 0.6	-6.0 ± 2.5	-6.0 ± 2.5	61.3	85.6	33.4	7.0
Seagrass species Median (IQR)	11.3 (23.5)	41.4 (86.2)	35.8 (97.4)	16.6 (45.3)	5.6 (15.4)	-1.4 (1.9)	-6.0 (8.3)	-6.0 (8.3)	30.8	41.8	25.8	-0.8
Mean ± SE	22.9 ± 6.5	84.1 ± 9.0	79.1 ± 26.9	36.8 ± 13.8	12.5 ± 4.7	-2.6 ± 1.6	-11.4 ± 6.8	-11.4 ± 6.8	58.7	83.1	30.2	1.2
Median (IQR)	7.2 (0.0)	26.4 (0.0)	45.4 (58.6)	21.1 (27.8)	7.2 (9.2)	-2.0 (2.4)	-8.9 (10.3)	-8.9 (10.3)	14.1	28.1	46.5	-6.5
Mean ± SE	26.4 ± 0.0	26.4 ± 0.0	28.0 ± 17.7	13.0 ± 8.2	4.4 ± 2.8	-2.0 ± 3.3	-8.9 ± 10.3	-8.9 ± 10.3	22.2	30.9	15.8	-16.9
Median (IQR)	62.4 (62.4)	96.8 (228.8)	192.7 (86.7)	89.7 (40.3)	30.4 (13.7)	-0.6 (0.0)	-2.7 (0.0)	-2.7 (0.0)	9.8	69.1	89.9	28.6
Mean ± SE	40.7 ± 11.1	149.2 ± 40.8	192.7 ± 86.7	89.7 ± 40.3	30.4 ± 13.7	-0.6 ± 0.0	-2.7 ± 0.0	-2.7 ± 0.0	62.2	121.5	58.3	18.5
Australian region Median (IQR)	8.9 (8.6)	32.6 (31.5)	33.8 (41.7)	15.7 (19.4)	5.3 (6.6)	-1.1 (1.6)	-4.6 (7.2)	-4.6 (7.2)	21.6	32.0	33.9	2.1
Mean ± SE	12.3 ± 2.3	45.1 ± 8.5	58.8 ± 40.6	27.4 ± 18.9	9.3 ± 6.4	-2.0 ± 1.1	-8.8 ± 5.0	-8.8 ± 5.0	26.5	44.6	41.3	1.1

Table 2 Published reduction in the net climate benefit of seagrass communities due to methane and nitrous oxide fluxes (% offsets).

Community	Accumulation g C _{org} m ⁻² year ⁻¹	CH ₄ flux μmol CH ₄ m ⁻² day ⁻¹	N ₂ O flux μmol N ₂ O m ⁻² day ⁻¹	Recalculated GWP ₂₀ Offset %	Recalculated GWP ₁₀₀ Offset %	Published GWP ₂₀ Offset %	Published GWP ₁₀₀ Offset %	Reference
Lower	69.0	105.8	-	19.5	6.6	-	-	Garcias-Bonet and Duarte ²⁰
Upper	169.0	105.8	-	7.9	2.7	-	-	
Median	138.0	108.2	-	10.0	4.0	-	4.8	Al-Haj and Fulweller ²¹
Mean	42.0	119.0	2.3	31.8	16.0	-	0.3	Oreska et al. ¹¹
Bare sediment removed	337.3	106.0	-	4.0	1.4	0	4-5	Schorn et al. ¹⁸
	-	10.5	-1.46	-	0	0	-	Ollivier et al. ¹⁹

Offsets have also been recalculated using Eqs. (1)-(6) and the CH₄ and N₂O fluxes and organic carbon accumulation rates from the publication.

seagrass area of 160,387 km²²² gives mean and median global seagrass long-term C_{org} burial of 4.0 and 1.8 Tg C_{org} year⁻¹ respectively, which represents a minor coastal sink compared to the 250 Tg C year⁻¹ uptake of CO₂ on the continental shelf²³. Most importantly, our mean ± SE global seagrass C_{org} burial rate of 25.1 ± 5.3 g C_{org} m⁻² year⁻¹ is also much lower than mean global accumulation estimates that have been used in previous global offset estimates (e.g., 119 g C_{org} m⁻² year⁻¹²⁰; 138 ± 38 g C_{org} m⁻² year⁻¹²¹). Global seagrass C_{org} accumulation estimates of refs. ^{20,21} do not reflect long-term C_{org} burial because many of the estimates are based on carbon mass balances, not long-term (<100 year) ¹⁴C and ²¹⁰Pb C_{org} burial rates, and are biased toward the “matte”-forming *P. oceanica*^{7,8}. Therefore, we argue that the long-term C_{org} burial rates we used here are a better estimate of blue carbon⁷ to compare to Green House Gas-CO₂e fluxes and to estimate offsets.

Our revised global mean ± SE seagrass community CH₄ flux of 79.0 ± 16.8 μmol CH₄ m⁻² day⁻¹ (median(IQR) 48.2 (96.3) μmol CH₄ m⁻² day⁻¹; *n* = 35; Supplementary Table 3) in this study is lower than the most recent seagrass compilation (mean 112.5 ± 62.5 μmol CH₄ m⁻² day⁻¹; median 81.2 (87.5) μmol CH₄ m⁻² day⁻¹; *n* = 18²⁴); and based upon almost twice as many measurements. Although seagrass CH₄ emissions are lower than from mangroves and salt marshes²⁴, seagrasses cover a larger surface area, globally. Using the most recent global seagrass area of 160,387 km²²² gives mean and median global seagrass CH₄ fluxes of 0.074 and 0.045 Tg CH₄ year⁻¹, respectively. Our revised global CH₄ emission estimates are about 40% of the most recent estimate²⁴, due to a lower mean and median CH₄ flux rate and a smaller surface area of seagrass, and as such, represents a small contribution to global estuarine CH₄ emissions (mean 0.9 Tg CH₄ year⁻¹²⁴).

Our compilation demonstrates that CH₄ production in seagrass communities is widespread, with rates up to 401.3 μmol CH₄ m⁻² day⁻¹ (Supplementary Table 3), despite seagrasses being found in marine waters where sediments are considered to have negligible CH₄ emissions²⁵. The release of methylated compounds from plants may fuel CH₄ production; a recent study showed that seagrass CH₄ production was sustained exclusively via methylated compounds produced and released by the plant¹⁸. The more common pathways of hydrogenotrophic and acetoclastic CH₄ production in anoxic sediment were undetected in seagrasses and were most likely outcompeted by sulfate-reducing bacteria¹⁸.

This is the first compilation of measured N₂O fluxes for seagrass communities (Supplementary Table 4). Although²⁶ included seagrass N₂O fluxes in the estimation of coastal and inland water N₂O emissions, a separate seagrass N₂O flux was not presented. A recent synthesis of N₂O rates for seagrasses²⁷ were based on denitrification rates in seagrasses and N₂O:N₂ ratios and not on direct N₂O flux measurements. Using the most recent global seagrass area²² gives mean and median global seagrass N₂O uptakes of -0.004 and -0.002 Tg N₂O year⁻¹ respectively, which represents a minor sink in marine N₂O emissions^{26,27}. Previous global estimates have suggested that seagrasses are a source of N₂O²⁷, which highlights the problem with using N₂O:N₂ ratios and denitrification rates to estimate seagrass N₂O fluxes.

Seven of the nine seagrass sites showed an uptake of N₂O, with uptakes as high as -7.2 μmol N₂O m⁻² day⁻¹ in the Noosa Estuary, Australia (Supplementary Table 4). This is similar to mangrove and estuarine systems that show an uptake of N₂O when NO₃⁻ concentrations are below 5 μmol l⁻¹^{28,29}. However, some of the N₂O uptakes in the seagrasses were greater than N₂O uptakes in mangroves^{15,29}. This may reflect even lower water column NO₃⁻ concentrations at some seagrass sites. For example, NO₃⁻ concentrations in Wallis Lake and the Noosa and

Maroochy estuaries were all below 1.0 μmol l⁻¹^{16,17}. This combination of low NO₃⁻ concentrations and high rates of denitrification in seagrasses^{30–32} may result in N₂O consumption via denitrification. Conversely, nutrient enrichment would increase N₂O fluxes and reduce the climate benefit of seagrass communities.

Implications for the climate benefit of seagrass blue carbon.

We present three approaches for estimating the mean and median reduction of the climate benefit of seagrass C_{org} long-term burial (offsets). Mean and median offsets were similar for the individual seagrass species and globally (Table 1). Although this might be expected since the individual seagrass species were calculated from a subset of the data used in the global offsets. The reduced climate benefit of the Australian region was also calculated from a subset of the global data, but the mean and median GWP₂₀ offsets were much higher mostly due to lower long-term burial rates, but the GWP₁₀₀ offsets were lower due to the N₂O-CO₂e sink reducing the CH₄-CO₂e source. As such, the resolved geographic variability in long-term burial rates and greenhouse gas fluxes has important implications for evaluating the climate benefit of seagrass across different regions. Offsets calculated using the GWP₁₀₀ were much lower than those calculated using GWP₂₀ because the CH₄ GWP₁₀₀ multiplier (27.0) is much lower than the CH₄ GWP₂₀ multiplier (79.7), while the N₂O multiplier is the same for GWP₂₀ and GWP₁₀₀. By reducing the GWP₁₀₀ CH₄-CO₂e source it allows the GWP₁₀₀ N₂O-CO₂e sink to greatly reduce the combined GWP₁₀₀ CO₂e CH₄ and N₂O reduction of the climate benefit of long-term seagrass C_{org} burial.

Despite accounting for N₂O uptakes in seagrass (i.e., increasing the climate benefit seagrass C_{org} long-term burial) the mean global seagrass CH₄ and N₂O offset (33.4% GWP₂₀) is still higher than the global CH₄ offset estimated for mangroves (20.5% GWP₂₀⁹). Although CH₄ fluxes are higher in mangroves (0 to 2127.2 μmol CH₄ m⁻² day⁻¹), the lower mangrove offset reflects the much higher C_{org} burial rates in mangroves (56.6 to 651.0 g C m⁻² year⁻¹⁹), compared to seagrass communities (Supplementary Table 2). The mangrove CH₄ offset would also be further reduced, particularly for GWP₁₀₀, if N₂O uptake, which is common in mangrove waterways¹⁵, were included.

Mean offsets for the individual seagrass species from our synthesis are much higher than previous offset estimates (Table 2). The higher offsets in this study were mostly due to the use of long-term C_{org} burial rates, compared to short-term C_{org} accumulation rates being used in previous studies. Our mean global offsets (GWP₁₀₀) in seagrasses are only a little higher than two previous global offset estimates^{20,21}; Table 2). However, this similarity is a coincidence, and not an agreement, due to the high C_{org} accumulation rates used in the previous offset estimates and the N₂O fluxes used in our estimates, which cancel each other out when using GWP₁₀₀. The difference between previously published offsets and our offsets due to different combinations of C_{org} long-term burial rates, and CH₄ and N₂O fluxes, highlights importance of measuring all three parameters when assessing the net climate benefit (Blue Carbon) of seagrass communities (Table 1), and when deciding which seagrass communities to include in restoration projects. We argue that our global seagrass Green House Gas offsets are more realistic because we include a larger number of CH₄ fluxes, we include N₂O fluxes and we only include long-term C_{org} burial rates. In addition, we also provide the first estimates of seagrass global offsets using GWP₂₀.

Uncertainties in offsets and future research. Our three offset estimates show that CH₄ can reduce the climate benefit of seagrass communities for GWP₂₀ and with a reduced effect for

Table 3 Uncertainties in the reduction of the net climate benefit of seagrass communities due to methane and nitrous oxide fluxes.

<p>Uncertainty likely to result in offsets being under-estimated</p> <ul style="list-style-type: none"> - Emission of other greenhouse gases (e.g., isoprene) - CaCO₃ burial - Choice of global warming potential <p>Uncertainty likely to result in offsets being over-estimated</p> <ul style="list-style-type: none"> - Sediment-water fluxes higher than water-air fluxes - Differences in timescales of long-term burial and greenhouse gas production - Low 100 year burial rates from ¹⁴C measurements <p>Unknown which way offsets may be affected</p> <ul style="list-style-type: none"> - Limited spatial and temporal measurements of seagrass CH₄ and N₂O fluxes and long-term organic carbon burial rates - Allochthonous organic carbon (net heterotrophic seagrass communities) - Export and burial of seagrass organic carbon off site - Bias due to measurements used in synthesis not being undertaken at the same location

GWP₁₀₀ and N₂O fluxes can enhance the climate benefit of seagrass communities (GWP_{20,100}). However, there are a number of uncertainties in our synthesis that should be considered, as they may result in either over- or under-estimations of seagrass offsets (Table 3). These uncertainties also highlight areas for further research.

The seagrass species approach for estimating offsets shows a large range in the possible seagrass blue carbon offset by CH₄ and N₂O fluxes. *Posidonia* had the highest offsets (GWP₂₀ and GWP₁₀₀) due to high CH₄ fluxes. However, this high offset estimate may be due to the limited data availability, with *Posidonia* estimate based on only two measurements of CH₄ fluxes and one N₂O flux (Supplementary Tables 3 and 4). *Halophila sp.* showed a net CH₄ + N₂O-CO₂e uptake (GWP₁₀₀) due to low CH₄ fluxes and high N₂O fluxes, but this was based on only two measurements of N₂O fluxes and one long-term burial rate. Globally, there was limited N₂O flux data (9 sites globally). In particular, there were few, or no, measurements from Africa, South America and Southeast Asia (Fig. 1). There were also no simultaneous measurements of CH₄ and N₂O fluxes and C_{org} long-term burial from the one location which may result in a bias in our offsets³³. Clearly, more measurements of CH₄ and N₂O fluxes and C_{org} long-term burial in the same seagrass communities, and across a range of seagrass species and locations, is required for accurate blue carbon assessments.

CH₄ offsets were mostly based on seagrass sediment-water CH₄ fluxes (26 sites) with less water-air CH₄ fluxes (9 sites; Supplementary Table 3). Although it is unknown if sediment-water CH₄ fluxes from seagrass communities reach the atmosphere, water column CH₄ oxidation rates at salinities >6 are typically low³⁴. This is consistent with negligible water column oxidation at the Wallis Lake site¹⁶. Mean and median seagrass water-air CH₄ fluxes were also higher, but not significantly different ($p = 0.34$), than seagrass sediment-water CH₄ fluxes suggesting sediment-water fluxes do not systematically over-estimate seagrass CH₄ fluxes to the atmosphere. Similarly, some of the CH₄ and N₂O flux studies were only undertaken in one season, and some were undertaken multiple seasons. However, there was no significant difference between single season and multiple season CH₄ fluxes ($p = 0.64$). As such, differences in the temporal scale of collection, does not appear to have added any bias into our analysis.

This study has only considered two (long-term burial, CH₄ and N₂O fluxes) of the many processes that determine the net climate benefit of seagrass communities. For example, we have not considered CaCO₃ burial which greatly reduces, and in some cases completely removes, the climate benefit of seagrasses (e.g. refs. ^{16,35,36}). Seagrasses also emit other climate warming

greenhouse gases like isoprene³⁷, which we have not considered. In addition, we have not compared the net climate benefit of seagrass communities to the net climate benefit of adjacent unvegetated sediments. Without comparing CH₄ and N₂O fluxes to adjacent bare sediments the CH₄ and N₂O fluxes in this synthesis are a maximum attributable to the seagrass community (see refs. ^{11,38}). Similarly, without comparing long-term burial rates to adjacent bare sediments the long-term burial rates in this synthesis are a maximum attributable to the seagrass community.

An input of allochthonous C_{org} is major process not considered by this study. Although we only used ²¹⁰Pb and ¹⁴C measured rates of seagrass C_{org} long-term burial across a broad range of seagrass species and locations, these estimates may still be too high because of an input allochthonous C_{org}, both recalcitrant and labile^{8,39}. For example, up to 50% of the C_{org} in seagrass communities may be derived from non-seagrass sources, including macroalgae (e.g. refs. ^{40–42}). In some seagrass communities that are net heterotrophic there can even be a net flux of CO₂ due to an input of allochthonous organic carbon⁴³. If we assume 50% of the seagrass C_{org} long-term burial is from non-seagrass sources, this would increase our global mean offsets from 33.4% GWP₂₀ and 7.0% GWP₁₀₀ to 66.8% GWP₂₀ and 14.0% GWP₁₀₀. As such, our seagrass offsets should be considered a lower estimate as an input of any allochthonous C_{org} would result in higher offsets. However, this assumes that the allochthonous C_{org} is not included as seagrass “Blue Carbon” but the CH₄ and N₂O produced during its decomposition are included. It could be argued that the CH₄ and N₂O fluxes associated with the allochthonous C_{org} should also not be included, and therefore the allochthonous component would not affect the offsets, unless it produces CH₄ and N₂O differently to the autochthonous C_{org} (Table 3). Similarly, C_{org} produced by the seagrass community, but transported offsite and buried is unaccounted for by the long-term burial rates measured in the seagrass community. However, when this material is buried offsite it will still result in the production or consumption of CH₄ and N₂O, which would also contribute to an offset. The local conditions of long-term burial and associated production or consumption of CH₄ and N₂O would determine if this results in an over- or under-estimate of the offset (Table 3).

The long-term burial rates may also be too low. Although there was no significant difference between the ¹⁴C and ²¹⁰Pb measured long-term burial rates in this synthesis, ¹⁴C long-term burial rates are up to 1000's of years old, and may be lower than seagrass long-term burial rates over 100's of years (e.g. ref. ⁴⁴), resulting in an over-estimate of offsets (Table 3). There are also timescale differences between the long-term burial rates and CH₄ and N₂O fluxes. Long-term burial is C_{org} that has been sequestered for

>100 years compared to CH₄ and N₂O fluxes which are a recent measurement, typically only undertaken once or over one annual cycle (Supplementary Tables 3 and 4). It is unknown if the recently measured CH₄ and N₂O fluxes are representative of the seagrass community for the longer period over which C_{org} has been buried. In particular, recent disturbance of the seagrass community may change the CH₄ and N₂O fluxes. For example, warming and shading could result in higher seagrass CH₄ fluxes^{20,45} and nitrogen enrichment may reduce the uptake of N₂O in seagrasses¹⁷, both of which would result in an overestimate of offsets (Table 1).

Our choice of global warming potential (i.e., IPCC 2021) also influences the net climate benefit offset estimates. For example had we chosen to use the sustained global warming potential (SGWP⁴⁶) our global mean offset would have increased from 33.4% GWP₂₀ and 7.0% GWP₁₀₀ to 41.8% GWP₂₀ and 14.8% GWP₁₀₀. Despite a higher SGWP₁₀₀ value of 349 for N₂O uptakes, which would reduce the offset, the offset is still higher due to the higher SGWP₁₀₀ value for CH₄ (45⁴).

In summary, this study shows that CH₄ fluxes can reduce, and N₂O fluxes can enhance, the climate benefit of seagrass blue carbon. We also highlight the importance of using long-term C_{org} burial rates when assessing the climate benefit of seagrass blue carbon. These findings will contribute to policies and practice incorporating blue carbon habitat conservation and restoration as a natural strategy for CO₂ removal.

Materials and methods

Wallagoot Lake study area, experimental procedure, and calculations. Wallagoot Lake is a small slightly degraded temperate Intermittently Closed and Open Lake and Lagoon (ICOLL) on the southern New South Wales coast. *R. megacarpa* occurs in the shallow water (<2 m) around the edge of the whole lake. A 20-h time-series measuring continuous water CH₄ and N₂O concentrations over a *R. megacarpa* seagrass community (S36°47'39"; E 149°56'19") was undertaken in summer 2016. Water was pumped from 30 cm water depth and passed through a showerhead equilibrator connected to a cavity-ring-down spectroscopy (Picarro, G2308) analyzer. CH₄ and N₂O concentrations were measured at ~1 Hz (precision at 1 min <7 ppb ± 0.05% of reading). Wind speed was measured hourly with a digital anemometer (Q1411, Dick Smith Electronics), as well as water temperature and salinity at 15 min intervals (Hydrolab HL4 Sonde, Aqualab).

The CH₄ and N₂O water-air flux (*F*) was estimated as $F = k K_0 (C_{\text{water}} - C_{\text{air}})$, where *k* is the gas transfer velocity (m day⁻¹), *K*₀ is the solubility coefficient (mol kg⁻¹ atm⁻¹) at the measured water temperature and salinity^{47,48}, and *C*_{water} and *C*_{air} are the partial pressures (µatm) of CH₄ or N₂O in the water and air, respectively⁴⁹. Due to variability in *k* obtained by different empirical models⁵⁰, three models were selected as adequate for the investigated area to determine the gas transfer velocity^{51–53}, and the resulting fluxes were averaged.

Blue carbon offset calculations. Scopus and google scholar were searched for “seagrass AND methane”, “seagrass AND nitrous oxide” and “seagrass AND burial”. Additional papers were identified from reading the papers found in the searches. Sediment-water (cores, benthic chambers) and water-air (open water, floating chambers) seagrass CH₄ and N₂O fluxes were included in the synthesis. Because we were interested in the seagrass CO₂e offset to long-term (>100 years) seagrass C_{org} burial, only seagrass accumulation rates obtained using ²¹⁰Pb and ¹⁴C dating were included⁷. Studies that used sediment accumulation rates from the literature were excluded (i.e. refs. ^{54,55}). Multiple CH₄ and N₂O fluxes and long-term C_{org} burial rates for a given seagrass species at a given site were averaged (site mean). Temporal CH₄ and N₂O flux measurements (e.g., diel, seasonal) were also averaged.

Each of the seagrass C_{org} accumulation studies identified were further assessed to determine if they could be considered long-term (>100 years) seagrass C_{org} burial following the best practice outlined in ref. ⁸. To be considered long-term (>100 years) seagrass C_{org} burial for cores dated using ²¹⁰Pb the study had to show ²¹⁰Pb concentrations profiles so we could determine that there was no sediment mixing and C_{org} concentration profiles to determine if C_{org} was buried below the zone of rapid carbon remineralisation (i.e., where concentrations no longer decrease and become constant⁸); If an average of the C_{org} concentration profile was used, but the C_{org} concentration profile increased or was constant with depth this was considered acceptable. To be considered long-term (<100 years) seagrass C_{org} burial for cores dated using ¹⁴C C_{org} concentration profiles were required. All studies that did not meet the long-term burial criteria were assigned to C_{org} accumulation.

CH₄ and N₂O fluxes were converted to CO₂ equivalents using the 20-year and 100-year GWP of each gas. The GWP₂₀ and GWP₁₀₀ for CH₄ are 79.7 and 27 respectively, and the GWP₂₀ and GWP₁₀₀ for N₂O is 273¹⁴. The reduced climate benefit of seagrass blue carbon was calculated three ways. Firstly, seagrass species offsets were calculated using the mean and median of long-term C_{org} burial rates and CH₄ and N₂O fluxes rates for all individual seagrass species for which all three parameters were available (Supplementary Tables 2–4 and Fig. 1). Secondly, the Australian seagrass offset was calculated using the mean and median of all seagrass long-term C_{org} burial rates and CH₄ and N₂O fluxes for the Australian region (Supplementary Tables 2–4 and Fig. 1). This was done because Australia is the only region where there was sufficient data for this calculation. Thirdly, the global offset was calculated using the mean and median of all seagrass long-term C_{org} burial rates and CH₄ and N₂O fluxes (Supplementary Tables 2–4 and Fig. 1). Although we use the term “global” this doesn’t reflect the mean or median long-term C_{org} burial rates, CH₄ and N₂O fluxes and %offsets at any given location, as this will depend on site specific factors. Both the mean and median as the central statistic is presented as per²⁴ to allow comparisons with past and future studies. The following six equations were used to calculate offsets from the mean and median of long-term C_{org} burial rates and CH₄ and N₂O fluxes:

$$\text{Offset(\%)} = (\text{Total CO}_2\text{e source} / \text{CO}_2\text{e long term C}_{\text{org}} \text{ burial}) \times 100\% \quad (1)$$

$$\text{Net climate benefit} = \text{C}_{\text{org}} \text{ CO}_2\text{e long term burial} - \text{CH}_4 \text{ CO}_2\text{e flux} - \text{N}_2\text{OCO}_2\text{e flux} \quad (2)$$

$$\text{Total CO}_2\text{e source} = \text{CH}_4 \text{ CO}_2\text{e flux} + \text{N}_2\text{OCO}_2\text{e flux} \quad (3)$$

$$\text{CH}_4 \text{ CO}_2\text{e flux} (\text{g CO}_2 \text{ m}^{-2} \text{ year}^{-1}) = \text{CH}_4 \text{ flux} (\mu\text{mol CH}_4 \text{ m}^{-2} \text{ day}^{-1}) \times 10^6 \times 365 \times 16 \times 79.7 (\text{GWP}_{20}) \text{ or } \times 27.0 (\text{GWP}_{100}) \quad (4)$$

$$\text{N}_2\text{OCO}_2\text{e flux} (\text{g CO}_2 \text{ m}^{-2} \text{ year}^{-1}) = \text{N}_2\text{O flux} (\mu\text{mol N}_2\text{O m}^{-2} \text{ day}^{-1}) \times 10^6 \times 365 \times 44 \times 273 (\text{GWP}_{20,100}) \quad (5)$$

$$\text{C}_{\text{org}} \text{ CO}_2\text{e long term burial} (\text{g CO}_2 \text{ m}^{-2} \text{ year}^{-1}) = \text{g C}_{\text{org}} \text{ m}^{-2} \text{ year}^{-1} \times 12/44 \quad (6)$$

Statistical analysis. The Welch two sample *t*-test was used to test whether the means of two sample populations are different, assuming independent samples for unequal variances and sample sizes under normality. The *t*-tests were performed in R (R version 4.0.3 (2020-10-10))⁵⁶.

Data availability

The dataset is published in the repository Figshare 10.6084/m9.figshare.24070998.

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Author contributions

B.D.E., N.C., J.A.R. and R.N.G. contributed to the conceptual development of the manuscript, and reviewed and edited the manuscript. B.D.E. compiled the datasets, did the data analysis and wrote the manuscript with input from the other authors. N.C. helped with compiling the datasets. J.A.R. helped with the data analysis.

Competing interests

The authors declare no competing interests.

Additional information

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