



Non-native mangroves support carbon storage, sediment carbon burial, and accretion of coastal ecosystems

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Abstract

Mangrove forests play an important role in climate change adaptation and mitigation by maintaining coastline elevations relative to sea level rise, protecting coastal infrastructure from storm damage, and storing substantial quantities of carbon (C) in live and detrital pools. Determining the efficacy of mangroves in achieving climate goals can be complicated by difficulty in quantifying C inputs (i.e., differentiating newer inputs from younger trees from older residual C pools), and mitigation assessments rarely consider potential offsets to CO₂ storage by methane (CH₄) production in mangrove sediments. The establishment of non-native *Rhizophora mangle* along Hawaiian coastlines over the last century offers an opportunity to examine the role mangroves play in climate mitigation and adaptation both globally and locally as novel ecosystems. We quantified total ecosystem C storage, sedimentation, accretion, sediment organic C burial and CH₄ emissions from ~70 year old *R. mangle* stands and adjacent uninvaded mudflats. Ecosystem C stocks of mangrove stands exceeded mudflats by 434 ± 33 Mg C/ha, and mangrove establishment increased average coastal accretion by 460%. Sediment organic C burial increased 10-fold (to 4.5 Mg C ha⁻¹ year⁻¹), double the global mean for old growth mangrove forests, suggesting that C accumulation from younger trees may occur faster than previously thought, with implications for mangrove restoration. Simulations indicate that increased CH₄ emissions from sediments offset ecosystem CO₂ storage by only 2%–4%, equivalent to 30–60 Mg CO₂-eq/ha over mangrove lifetime (100 year sustained global warming potential). Results highlight the importance of mangroves as novel systems that can rapidly accumulate C, have a net positive atmospheric greenhouse gas removal effect, and support shoreline accretion rates that outpace current sea level rise. Sequestration potential of novel mangrove forests should be taken into account when considering their removal or management, especially in the context of climate mitigation goals.

KEYWORDS

²¹⁰Pb, methane, Moloka'i, non-native species, restoration, *Rhizophora mangle*, sediment

1 | INTRODUCTION

Mangrove ecosystems sequester and store large amounts of carbon dioxide (CO₂) from the atmosphere in the form of live tree and detrital biomass (Alongi, 2012). Large amounts of detrital C are also stored in sediments through the daily deposition of suspended organic C from oceanic and riverine water inundation (Alongi, 2014; Santos, Maher, Larkin, Webb, & Sanders, 2019). Thus, the conservation or restoration of mangrove forests has received attention as a potential sink for atmospheric CO₂ and an important tool for climate change mitigation (Alongi, 2014; Crooks, Herr, Tamelander, Laffoley, & Vandever, 2011; Davidson, Cott, Devaney, & Simkanin, 2018). This has also led to large-scale mangrove restoration projects as countries seek to generate income through various C finance mechanisms (e.g., REDD+) or to lower greenhouse gas (GHG) emissions for United Nations reporting (Ahmed & Glaser, 2016; Románach et al., 2018).

High C burial rates in anoxic and water-saturated sediments are the major driver of large C stocks in mangroves compared to other forested ecosystems. The global C sediment burial rate for mangroves is 1.74 Mg C ha⁻¹ year⁻¹, but ranges from 1.0 to 9.2 Mg C ha⁻¹ year⁻¹ due to intersite differences in primary production, variability in C content of suspended sediments, and to an extent tree (and thus root) diversity of mangrove forests (Alongi, 2012, 2014). Forest age can also influence sediment C burial rates, with higher rates often observed in younger mangrove plantations than older ones. Adame et al. (2018), for example, found that sediment C burial rates in 5 year old mangrove plantations were three to six times greater than in intact forests. A recent global meta-analysis found that mangrove expansion into mudflats, on average, doubled sediment C pools (Davidson et al., 2018), and previous surveys have shown that sediment organic C concentrations are two- to threefold greater for non-native mature *Rhizophora mangle* stands on the Hawaiian islands than for adjacent sandflats (Demopoulos & Smith, 2010). In subtropical China, planted mangrove stands have also been shown to achieve two- to threefold gains in sediment organic matter content within the first 10 years after planting (Ren et al., 2009).

While intact mangrove ecosystems typically function as net sinks of atmospheric CO₂ (often referred to as “blue carbon”), some proportion of this fixed C may be exported from mangrove sediments in the form of the GHG, methane (CH₄; Rosentreter, Maher, Erler, Murray, & Eyre, 2018), and this effect is often ignored in mitigation projects. Because a single molecule of CH₄ has a 20 year sustained global warming potential (SGWP) that is 96 times greater than that of CO₂ (Neubauer & Megonigal, 2015), CH₄ emission has the potential to offset positive C storage benefits. Thus, determining the net climate impact of mangroves (with regard to their conservation, deforestation, or restoration) is dependent on the ability to quantify the magnitude of this offset. However, because the majority of mangrove stands have been in existence for hundreds of years and stand ages are unknown, in part due to difficulty of aging mangrove trees (Alongi, Sasekumar, Tirendi, & Dixon, 1998), it is challenging to directly calculate a net CO₂-equivalent balance. A small number of studies have attempted to quantify GHG offsets by contrasting rates

of sediment C burial or ecosystem C stocks with CH₄ or nitrous oxide (N₂O) emission. Maher, Call, Santos, and Sanders (2018) calculate that CH₄ and N₂O offset sediment C burial by 6% and 0.5%, respectively, for subtropical mangroves in Australia. Globally, Rosentreter et al. (2018) calculate that this offset ranges from 18% to 22%, using a 20 year carbon-CH₄ GWP equivalency value. Emissions rates of CH₄ from exposed mangrove sediments are highly variable, and range globally from zero to 2,000+ μg m⁻² day⁻¹. Although typically lower in magnitude, CH₄ emissions continue from the surface of the water column overlaying sediments during tidal inundation (Rosentreter et al., 2018). This variability has been attributed to seasonality and magnitude of rainfall, porewater salinities, the quantity of sulfate in marine water, and processes that influence rate of evasion or consumption of methane by methanotrophs such as tidal height, presence of pneumatophores or crab burrows, and rates of ebullition (Rosentreter et al., 2018; Sea, Garcias-Bonet, Saderne, & Duarte, 2018). Generally, however, the absence of large datasets has precluded testing many hypotheses regarding broad controls on CH₄ emissions in mangrove ecosystems (Rosentreter et al., 2018).

Another complication for climate change mitigation projects, particularly when deforested or degraded sites are restored, is the challenge in discerning new C inputs to sediments from mangrove regrowth from the high levels of sediment C stocks that can still remain following deforestation (Kauffman et al., 2017). Mangroves converted to shrimp ponds or pasture in Latin American and Indonesia, for example, contained nearly 50% of their original sediment C stocks (Kauffman et al., 2017), while in Cambodia, deforested and degraded mangrove forests have nearly 70% and 90%, respectively, of their original sediment C stocks (Sharma, unpublished data). Thus, estimating sediment C burial rates in “novel” mangrove forests (areas which have not previously supported woody mangrove vegetation) provides an opportunity to more effectively quantify new C inputs because background C levels in mudflats are likely to be much lower than mangrove forests.

The well-documented establishment of non-native *R. mangle* (red mangrove) along Hawaii's coastlines provides an excellent model system to examine how GHG fluxes can offset C stocks in mangroves, as well as to determine how novel mangrove growth contributes to C stocks in mangrove sediments. Mangroves are not native to the volcanic oceanic islands of Hawai'i, presumably having never colonized the remote archipelago despite the presence of suitable climate and geomorphic settings (Allen, 1998). However, in the early 1900s, *R. mangle* was introduced to the island of Moloka'i to protect coral reefs and nearshore waters from upland soil erosion due to increased deforestation and the presence of non-native ungulates (e.g., feral goats, pigs, and Axis deer). Since then, *R. mangle* has spread unassisted to colonize mudflats, riverbanks, lagoons, canals, and even rocky intertidal zones across most of the archipelago (Allen, 1998; Chimner, Fry, Kaneshiro, & Cormier, 2006; MacKenzie & Kryss, 2013). On the islands of Moloka'i and Oah'u, for example, mangroves now occupy 150 and 240 ha of coastal land area, respectively (Chimner et al., 2006; D'Iorio, 2003). Because of the relatively recent timing of

introduction, the rate of *R. mangle* spread and thus the age of novel stands can be easily determined using historical aerial photography. Furthermore, because the age of the mangrove stands are known, comparison of C stocks between invaded mangrove areas and adjacent mudflats can be used to calculate annual inputs of C to mangrove sediments.

Another benefit of quantifying C stocks and GHG gases from novel mangroves is to determine the potential that non-native mangroves have to provide similar climate change mitigation benefits as they do in their native ranges. Worldwide, mangrove expansion and invasion is occurring in many areas, including Pacific and Indian Ocean islands and the east coast of Asia, and is predicted to increase both by poleward movement and colonization of new habitats (e.g., unvegetated salt flats; Davidson et al., 2018). Currently, the management of these non-native mangroves can be a subject of ongoing contention (Allen, 1998; Fronza, Lane-Kamahele, & Harry, 2008; Lewis, 2000). In Hawai'i, for example, large areas of mangroves have been removed as they are thought to degrade threatened and endangered native bird habitat, destroy native Hawaiian cultural sites (Allen, 1998; Chimner et al., 2006), and alter nearshore invertebrate community composition and food web structure (Demopoulos, Fry, & Smith, 2007; Demopoulos & Smith, 2010). However, non-native mangroves have also been shown to protect coral reefs by trapping large amounts of upland-derived sediments (D'Iorio, 2003), as well as provide habitat to native fish assemblages (Goecke & Carstenn, 2017; MacKenzie & Kryss, 2013). Given that mangroves have been shown to be very large reservoirs of C that can mitigate climate change impacts, non-native mangrove stands may also act as large C sinks in Hawai'i where they replace low C ecosystems such as tidal mudflats. Existing data suggest that the seedling density, biomass, and productivity of these non-native mangroves are greater than in their native range, comparable to other highly productive systems in the Indo-Pacific (Cox & Allen, 1999). Overall, assessment of the net climate impacts of non-native mangrove establishment must account for both net C storage and any offsets from increased CH₄ emissions to the atmosphere. Balancing these fluxes over the lifetime of a non-native mangrove stand requires knowledge of both time of establishment and baseline conditions. Generally, however, invasion effects of mangroves, especially with regard to C cycling, are understudied in comparison to invasion dynamics of salt marshes (Davidson et al., 2018). To our knowledge, no estimates exist that characterize total gains in ecosystem C (above- and belowground biomass and sediment) of non-native mangroves, or their potential offsets by enhanced CH₄ emission.

In this study, we quantified the net effect of non-native *R. mangle* mangrove invasions on ecosystem C sequestration over the ~70 years since their establishment on the island of Moloka'i, Hawai'i. To compare established mangrove stands of known age with adjacent uninvaded mudflats, we estimated standing ecosystem C stocks, measured fluxes of CH₄ from sediments to the atmosphere, and used ²¹⁰Pb to estimate sedimentation, accretion, and sediment C burial rates. We then use several scaling scenarios to calculate CO₂-CH₄ offsets, and compare accretion rates to current estimates of sea

level rise in order to assess the potential of non-native mangrove stands to provide climate adaptation and mitigation services.

2 | MATERIALS AND METHODS

2.1 | Study site

Field sampling for this project was conducted on the south coastal Pala'au land division of the volcanic island of Moloka'i, Hawai'i, United States (21°6'7"N, 157°4'34"W). The red mangrove (*R. mangle*) was first introduced at the beginning of the 20th century, and aerial imagery indicates that sites for this study were invaded in the 1940s. Since then, they have reached high densities and are interspersed with areas of uninvaded tidal mudflats characterized by an absence of woody vegetation and algal mats. Informal surveys of local land and business owners indicate that interspersed mudflat areas have been maintained by active removal of mangrove seedlings to preserve aesthetic characteristics and coastal access over the course of several decades (Litton, personal communication). The coastline has a maximum tidal range of 0.9 m, mean annual temperature of 24°C, and mean annual precipitation of 630 mm, with a wet season extending from November to April.

Sample plots were situated in three different mangrove forest sites along a 3 km stretch of open, non-embayed coastline (Figure S1). Three uninvaded mudflat sites were also sampled, two of which were situated directly adjacent to sampled mangrove sites (>90 m), and a third located ~2.5 km away.

2.2 | Determination of stand age

Mangrove stand ages were determined with repeat aerial photography. Aerial photographs taken by the USDA Farm Bureau from 1940 to 1950 were uploaded and georectified in Google Earth and compared to the most recent LANDSAT 8 images (2012), also in Google Earth. The age of sample plots was then determined by estimating the linear spread of the edge of the mangrove forests between 1940, 1950, and 2012 (Table S1).

2.3 | Ecosystem carbon stocks

In February 2016, ecosystem C stocks were quantified using a modified version of established sampling protocols (Kauffman & Donato, 2012). Within each of the three mangrove plots, three circular subplots of 7 m radius were established in monotypic stands of *R. mangle* in a linear fashion and approximately 25 m apart. At each subplot, standing trees, forest floor litter, and seedlings were measured and four 12 m long woody debris transects were established at cardinal directions from the center (Figure S2) to survey downed wood (dead wood debris on the forest floor). A full description of biomass sampling and conversion to C stocks is described in the Supplementary Methods.

Sediment samples were collected to point of refusal using a 5 cm diameter open-face peat gouge auger, with three cores taken per

plot. Core depths were never >1 m due to underlying coral/bedrock. Sediment cores were divided into depth intervals of 0–15, 15–30, 30–50, and 50–100 cm where applicable. A relatively uniform and representative 5 cm section of sediment was collected from each of the four depth intervals, avoiding sections with large roots. Sediment samples were dried to a constant mass at 60°C, and weighed to the nearest 0.1 g, ground to a fine powder using a Wiley mill, and sieved through a 2 mm mesh sieve to remove pieces of wood or rocks. Bulk density was determined for each interval by dividing the total dry weight by the total sample volume (96 cm³). A subsample from each sediment interval was acidified by three sequential additions of 0.5 M HCl and analyzed for organic C using a continuous flow isotope ratio mass spectrometer (Model Delta V Advantage; Thermo-Environmental) at the Cornell University Stable Isotope Laboratory. Sediment C stock (Mg C/ha) was calculated as the sum of the product of bulk density (g/cm³), C content expressed as a whole number (%), and total depth interval (cm, Table S2).

2.4 | ²¹⁰Pb dating and sedimentation rate calculations

A second sediment core was collected from the first subplot of each plot and analyzed for the naturally occurring radionuclide ²¹⁰Pb. Cores were collected as described above, but were sectioned into 2 cm intervals from 0 to 20 cm and then 4 cm intervals from 20 to 60 cm. The radionuclide ²¹⁰Po was then measured from each sediment interval as a proxy for its grandfather, ²¹⁰Pb, assuming the two radionuclides were in secular equilibrium. Sediments were extracted and analyzed as described in MacKenzie et al. (2016) at the School of Freshwater Sciences at the University of Wisconsin at Milwaukee.

Sedimentation, accretion, and sediment C burial rates were calculated using the Constant Rate of Supply Method for systems where belowground production or sediment inputs without excess ²¹⁰Pb can periodically dilute the initial concentration of unsupported ²¹⁰Pb activity (Appleby & Oldfield, 1978). ²¹⁰Pb activity was first plotted against cumulative mass to estimate depth and activity of supported ²¹⁰Pb for each core. Total unsupported ²¹⁰Pb activity was summed for the entire core, and also summed below each interval. The age (years) of each interval was determined by using the radioactive decay law and these two activities. Sedimentation (g cm⁻² year⁻¹) and sediment accretion rates (mm/year) were then determined for each interval by dividing the interval mass (g/cm²) and interval depth, respectively, by the age (years) of the interval. Sediment organic C burial rate was calculated by multiplying each interval's sedimentation rate by its C concentration. Sediment organic C burial was also determined from the sediment cores collected to estimate sediment C stocks described above. For each core, total C stocks were summed across intervals that were identified as post-invasion intervals based on the ²¹⁰Pb core from the same core. The total C stock to that interval was then divided by the number of years that mangrove forest had colonized that area. Sediment C burial in mudflats was similarly determined by dividing the total C stock of the sediment core by the age of the mangrove forest. This is likely

a conservative estimate as mudflats were almost certainly present before mangroves invaded.

Sediment cores for ²¹⁰Pb analysis were only collected from mangrove forests (invaded mudflats). To determine the impact of mangrove invasion on sedimentation, sediment C burial, and accretion rates, sediment core intervals were sorted into post-invasion and pre-invasion by comparing the range of dates for each interval (as determined from ²¹⁰Pb) to the dates the sites were invaded. Sediment C burial and accretion rates across post- and pre-invasion intervals were averaged within each core. Post-invasion intervals were intervals whose date range was older than the year mangroves had established at that site (Table S2), while pre-invasion intervals were younger than establishment.

2.5 | Sediment CH₄ fluxes

Sampling of CH₄ fluxes from mangrove and mudflat sediments was conducted in February 2016. At each of the six sites (three non-native mangrove stands and three uninvaded mudflats), seven circular PVC collars (bases for flow through chambers) were deployed and sampled over the course of 1 day per site. Sampling was conducted when sediments were exposed by the tide between 9 a.m. and 4 p.m. To account for temporal variability from sediment drying after tidal inundation, CH₄ measurements were repeated three to five times for each collar over a period of 4–5 hr and averaged, for a total of 90 flux measurements for mangroves and 50 for mudflats.

Instantaneous CH₄ emissions from sediments were measured using an ultraportable GHG analyzer (Los Gatos Research) that employs a flow-through chamber design in which ambient air is pulled into the chamber and across the sediment surface before being directed to the measurement instrument. Chambers consisted of PVC collars (25.5 cm in diameter, 15 cm height), inserted 4 cm into the sediment and topped with flat, transparent plexiglass lids with an intake and outtake port. CH₄ concentrations were monitored until they stabilized, and chamber samples were alternated with concentration samples of ambient air, which were subtracted to generate net flux values for the sediment.

2.6 | GWP offsets

To constrain lifetime CH₄ emissions from mangrove stands, measured instantaneous sediment–air CH₄ flux values were extrapolated using stand age and functions describing the rate of increase in CH₄ emissions over time since stand establishment. Two separate functions were applied, intended to represent upper and lower bounds on potential emissions, because the actual function describing the rate of increase of emissions is unknown. The “linear” scaling function assumes that CH₄ emissions began at the same magnitude as the present-day mudflat emissions and increased linearly to reach current observed values over the lifetime of the stand. The “constant” scaling function implies that CH₄ emissions reached their current magnitude instantaneously after mangrove establishment and remained constant over stand lifetime (Figure S4). Measured average non-inundated CH₄ sediment–air fluxes were corrected using a global

average ratio for sediment–air to water–air flux presented in Rosentreter et al. (2018) of 1.35, on the basis of 50% inundation. Sampling was conducted during the Hawaiian wet season when CH₄ fluxes are likely to be greatest due to lower surface salinity (e.g., Rosentreter et al., 2018) and insufficient data existed to correct for the effect of seasonality on annual emissions. Thus, point fluxes are likely to overestimate, rather than underestimate annual emissions.

Where “net” values are presented, they refer to the value for mangrove stands minus the value for paired uninvaded mudflats, that is, net CH₄ emissions are equal to emissions from mangroves minus mudflats over mangrove lifetime. Because one mangrove site was located ~2 km from the nearest mudflat, this site was contrasted with the average for all mudflat sites.

CH₄ emissions were converted to equivalent CO₂ emissions using the SGWP values, which better account for ecosystem fluxes that tend to be maintained over time, as compared to GWP conversion factors that are more appropriate for pulsed emissions (Neubauer & Megonigal, 2015). We present values for both 20 year (SGWP₂₀) and 100 year time horizons (SGWP₁₀₀).

2.7 | Statistical analyses

Statistical analyses were conducted in JMP Pro 13.2 (SAS Institute). Mixed models were used to test the effect cover type on gas fluxes, including site and collar ID (blocked within site) as random effects. Data were transformed using a Johnson SI transformation to meet model assumptions and residuals assessed for normality of distribution. For each sediment core, sedimentation, sediment organic C burial, and accretion rates were first averaged over pre- and post-sediment intervals. Average sedimentation, sediment organic C burial, and accretion rates were then compared between pre- and post-sediment intervals from ²¹⁰Pb cores using a one-way analysis of variance (ANOVA). Ecosystem C and sediment organic C burial rates determined from C stock cores were similarly compared between mangroves and mudflats using a one-way ANOVA. Core analyses were conducted in SYSTAT 12.02 (SYSTAT Incorporated). Significance values were set at $\alpha = .05$.

3 | RESULTS

3.1 | Ecosystem carbon stocks

Mangrove sediments were relatively shallow, ranging from 48 to 89 cm maximum depth, but accounted for 32%–44% of ecosystem C across the three mangrove sites, equivalent to 184 ± 15 Mg C/ha. By contrast, mudflat sites without mangroves had substantially shallower sediment layers (27–43 cm) and lower sediment C stocks of 30 ± 5.6 Mg C/ha (Table 1). Of the biomass carbon present in forested sites, 93%–95% occurred as live biomass dominated by the above-ground fraction, with the remainder composed largely of small and medium woody debris and leaf litter (Table 1).

Total ecosystem C stocks (including aboveground and belowground biomass, detritus, and sediments) for non-native mangrove stands ranged from 398 ± 5 to 501 ± 42 Mg C/ha, indicating a net C

TABLE 1 Carbon stocks (Mg C/ha) in ecosystem components (biomass, litter, woody debris, and sediment) for non-native mangrove ecosystems and adjacent uninvaded mudflats (n = 3 per site)

	Mg C/ha													
	Trees—above-ground	Trees—belowground	Seedlings	Litter	Debris—large sound	Debris—large rotten	Debris—medium	Debris—small	Debris—fine	Sediment (0–15 cm)	Sediment (15–30 cm)	Sediment (30–50 cm)	Sediment (50–100 cm)	Ecosystem C stock
Mangrove 1														
Average	143.3	57.8	7.1	7.5	—	3.7	1.6	0.1	70.1	50.5	40.2	16.3	398.2	
SE	2.5	1.4	0.6	0.5	—	1.7	0.3	—	4.2	4.1	3.4	4.1	5.6	
Mangrove 2														
Average	216.3	99.3	4.6	9.2	0.2	7.3	1.8	—	56.8	40.8	34.0	46.2	501.2	
SE	31.1	13.1	0.9	0.6	0.2	0.7	0.8	—	11.1	4.8	2.1	44.4	41.9	
Mangrove 3														
Average	178.3	77.8	2.0	8.2	0.5	9.3	1.4	—	73.7	56.1	34.3	50.4	492.5	
SE	7.5	5.0	0.2	0.3	0.5	1.0	0.4	—	7.0	14.5	14.1	5.3	27.6	
Mudflats														
Average	—	—	—	—	—	—	—	—	8.8	16.9	13.3	—	30.1	
SE	—	—	—	—	—	—	—	—	2.4	6.4	—	—	5.6	

Note: Bold values under ecosystem C stock represent the sum of all other C pools.

gain since establishment (a period of 69–75 years) between 368 and 471 Mg C/ha (Figure 1, Table 1) and an average range of net ecosystem productivity of 5.7–6.7 Mg C ha⁻¹ year⁻¹.

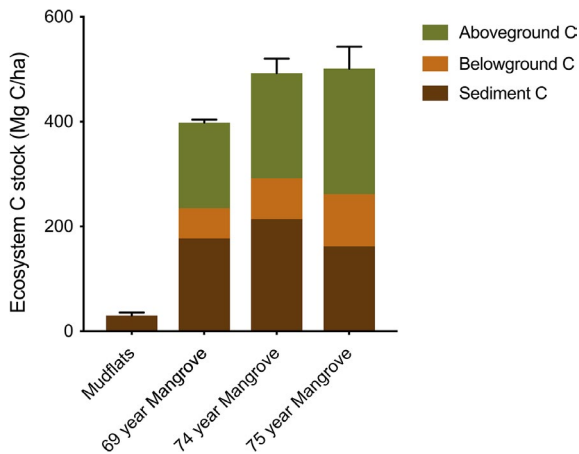


FIGURE 1 Carbon storage in major ecosystem components for uninvaded mudflats or non-native mangrove stands (aged 69–75 years). Errors bars indicate +1 SE for total ecosystem C storage at each site ($n = 3$ each)

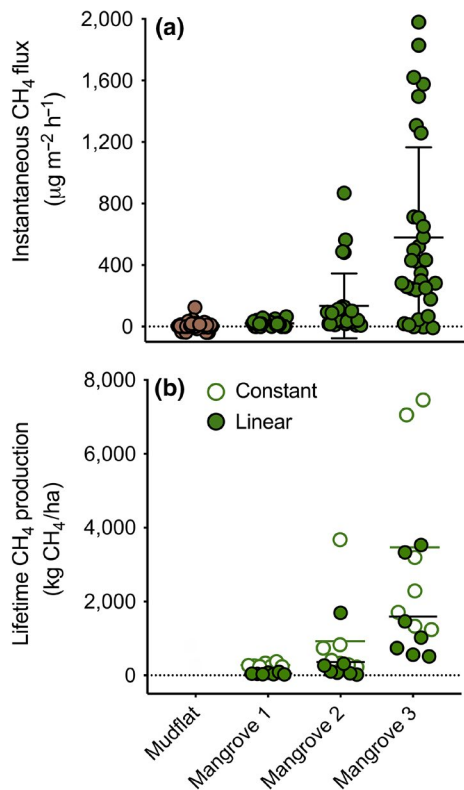


FIGURE 2 (a) Instantaneous CH₄ fluxes and (b) range of estimated net lifetime CH₄ emissions from three *Rhizophora mangle* mangrove stands on southern Moloka'i, HI. Bars represent mean ± 1 SD. Lifetime emissions are modeled on two functions intended to predict the range of potential emissions—"linear" (closed circles) assumes a linear rate of increase in sediment CH₄ fluxes between mangrove establishment and present day, and "constant" (open circles) assumes that fluxes increased immediately to contemporary values upon mangrove establishment and did not fluctuate thereafter

3.2 | Sediment CH₄ fluxes

Both production (positive atmospheric flux values) and consumption (negative flux values) of CH₄ were observed in uninvaded mudflat sediments, and emission values across all three mudflat sites averaged $2.5 \pm 13 \mu\text{g C m}^{-2} \text{s}^{-1}$ (mean ± 1 SD, Figure 2a). CH₄ fluxes were highly variable both between and within mangrove stands, ranging from $21 \pm 10 \mu\text{g C m}^{-2} \text{s}^{-1}$ (69 year old site) to $577 \pm 461 \mu\text{g C m}^{-2} \text{s}^{-1}$ (75 year old site; Figure 2a). CH₄ fluxes from the 75 year old stand were significantly higher than the other two mangrove sites ($p < .05$).

3.3 | GWP offsets

Extrapolating CH₄ fluxes over the lifetime of non-native mangrove stands generated net positive emissions estimates in the range of $670 \pm 200 \text{ kg CH}_4/\text{ha}$ (linear scaling function) to $1,340 \pm 450 \text{ kg CH}_4/\text{ha}$ (assuming constant flux magnitude, Figure 2b). Using a SGWP₂₀, these values are equivalent to 17 ± 27 to $35 \pm 54 \text{ Mg CO}_2\text{-eq/ha}$ (linear or constant scenario, respectively). Over this range, CH₄ production offset total ecosystem CO₂ storage in sediments and biomass by between 3.8% and 7.6% (Figure 3). The offset was reduced to 1.8%–3.6% when considering the impact of CH₄ emissions over a 100 year period (Figure 3).

3.4 | Sedimentation, accretion, and sediment carbon burial

All three ²¹⁰Pb sediment cores exhibited typical decreases in excess ²¹⁰Pb activity with depth and were deep enough to estimate supported ²¹⁰Pb activity (0.2–0.5 dpm/g). All three cores, with the

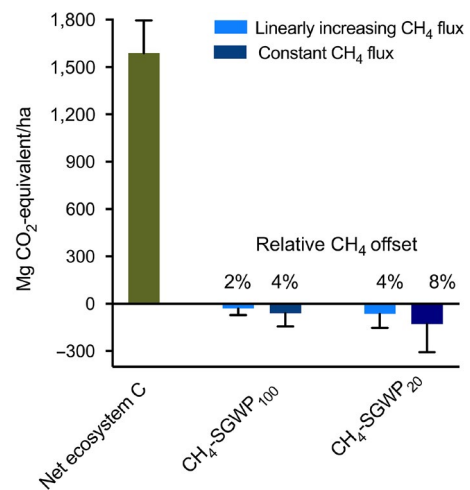


FIGURE 3 Net ecosystem carbon storage by non-native *Rhizophora mangle* mangroves, and sensitivity of methane offset to estimation parameters. Ecosystem C (Mg CO_{2e}/ha) refers to the total mangrove ecosystem C stock minus adjacent mudflat C stock. Net CH₄ fluxes are converted to CO₂-equivalents using a CH₄ 20 or 100 year sustained global warming potential value (SGWP₂₀ or ₁₀₀) of 45 and 96, respectively (Neubauer & Megonigal, 2015). Sensitivity scenarios assumed either linear increase or constant emission of CH₄ with mangrove stand age (Figure 2)

exception of one mangrove site, exhibited a bimodal distribution in sedimentation, sediment C burial, and accretion rates (Figure 4). Rates were greater in the topmost recent post-invasion intervals (2014–2016), before decreasing but then again increasing in deeper post-invasion sediment intervals. M1 exhibited sedimentation, sediment C burial, and accretion rate peaks from 1976 to 1980, M2 from 1973 to 1975, and M3 in 1972. Rates then decreased to pre-invasion levels. In M1, additional sedimentation, sediment C burial, and accretion rate peaks were observed in post-invasion intervals from 1994 to 1995. Patterns in sedimentation, sediment C burial, and accretion rates generally corresponded to patterns in sediment organic C content (Figure 4).

Post-mangrove invasion sediment C burial and accretion rates were both greater than pre-mangrove invasion (Table 2, Figure 4). Average post-invasion sediment organic C burial rates ($4.5 \pm 1.5 \text{ Mg C ha}^{-1} \text{ year}^{-1}$) were $15\times$ greater than pre-invasion rates ($0.3 \pm 0.1 \text{ Mg C ha}^{-1} \text{ year}^{-1}$; $p < .05$, $F_{1,4} = 8.0$, $df = 1$). Sediment C burial rates calculated from C stock cores were lower than those calculated from ^{210}Pb cores. However, they were still $5\times$ greater in mangrove C stock cores ($2.1 \pm 0.2 \text{ Mg C ha}^{-1} \text{ year}^{-1}$) compared to mudflat C stock cores ($0.4 \pm 0.1 \text{ Mg C ha}^{-1} \text{ year}^{-1}$; $p < .001$, $F_{1,4} = 71.8$, $df = 1$; Table 1). Average post-invasion accretion rates increased by more than 1.0 cm/year ($p < .05$, $F_{1,4} = 11.6$, $df = 1$). Although average sedimentation rates were higher in post-invasion intervals ($0.24 \pm 0.07 \text{ g cm}^{-2} \text{ year}^{-1}$; mean $\pm 1 \text{ SD}$), these values were not

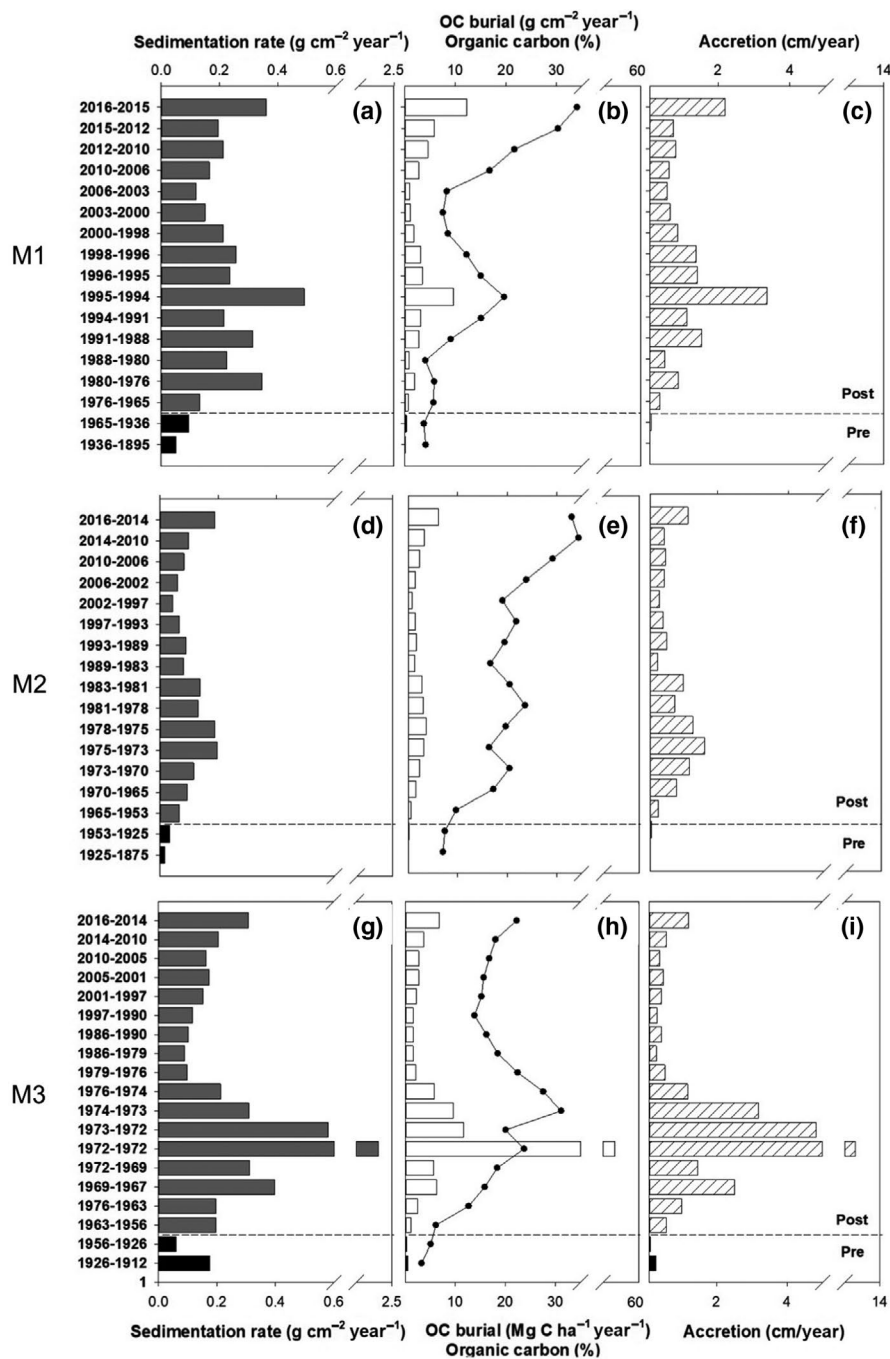


FIGURE 4 Average sedimentation rate (a, d, g), sediment organic carbon (OC) burial rate (b, e, h), and accretion rate (c, f, i) for three non-native *Rhizophora mangle* stands (M1, M2, M3 = mangrove site 1, 2 and 3, respectively) at intervals before and after mangrove colonization of coastal mudflats

Site	Sedimentation (g cm ⁻² year ⁻¹)	Sediment OC burial (Mg C ha ⁻¹ year ⁻¹)	Accretion (cm/year)
Post-invasion mangrove 1	0.24 ± 0.03	3.7 ± 0.9	1.15 ± 0.20
Post-invasion mangrove 2	0.11 ± 0.01	2.4 ± 0.4	0.78 ± 0.11
Post-invasion mangrove 3	0.35 ± 0.14	7.4 ± 3.2	1.58 ± 0.61
Average post-invasion	0.24 ± 0.07	4.5 ± 1.5	1.27 ± 0.34
Pre-invasion mangrove 1	0.07 ± 0.02	0.3 ± 0.1	0.12 ± 0.02
Pre-invasion mangrove 2	0.03 ± 0.01	0.2 ± 0.1	0.11 ± 0.03
Pre-invasion mangrove 3	0.12 ± 0.06	0.4 ± 0.1	0.21 ± 0.08
Average pre-invasion	0.07 ± 0.03	0.3 ± 0.1*	0.15 ± 0.03*

* $p < .05$ for pre/post contrasts.

statistically different to pre-invasion intervals (0.07 ± 0.03 g cm⁻² year⁻¹; $p = .09$, $F_{1,4} = 4.6$, $df = 1$) at an α level of .05.

4 | DISCUSSION

The invasion of Hawaiian mudflats by non-native *R. mangle* provides a unique opportunity to assess for the first time the role that novel mangrove forests may play in climate change mitigation and adaptation at the local and global level. We found that C stocks of adjacent mudflats were similar to those from sediment intervals that predated mangrove invasion, allowing us to quantify how mangrove production affects stocks in invaded coastal ecosystems. Furthermore, knowing the age of the invaded mangrove forests allowed us to predict the range of potential CH₄ offsets over the forest lifetime and thus estimate a net CO₂-equivalent uptake balance. Overall, our data suggest that young, non-native mangrove ecosystems have the potential to establish large C sinks with sediment accretion rates that will maintain coastal elevations relative to current regional rates of sea level rise. Extending these C sequestration rates to young restored, planted, or non-native mangrove systems elsewhere may help assess their C uptake rates independent of shifting baseline C stocks.

4.1 | Net carbon uptake

Despite being significantly younger than most mangrove stands, which can persist for hundreds to thousands of years but are challenging to age (Alongi et al., 1998), ~70 year old Moloka'i mangrove forests have accumulated above- and belowground ecosystem C stocks on the order of 464 ± 33 Mg C/ha. However, they have not yet reached the C storage potential reported for other mangrove systems, either globally (average 885 Mg C/ha; Kauffman & Bhomia, 2017), or for oceanic mangroves in the Indo-Pacific region (990 Mg C/ha; Donato et al., 2011). Although forecasting future C storage potential of these systems is challenging (given their novel combination of climate and species origin), it is likely that overall C stocks will continue to increase. In established oceanic tropical mangrove forests, the vast majority of C storage (~80%) occurs in belowground (sediment and root) pools down to 3 m depth (Donato

TABLE 2 Average sedimentation rate, sediment organic carbon (OC) burial rate, and accretion rate for three non-native *Rhizophora mangle* stands, prior to and after date of establishment on tidal mudflats

et al., 2011). In the Moloka'i mangrove stands, this value is substantially lower (in the range of 52%–59%), but sediments have not yet reached depths of greater than 1 m, likely due to their young age. Given that ongoing sedimentation is a common feature of even mature mangrove forests (Alongi & Mukhopadhyay, 2015), it is likely that non-native *R. mangle* forests will continue to accrue and store C in sediments if they are left intact, though the magnitude will depend in part on future terrestrial sediment transfer rates. Accrual of coarse woody debris is also relatively low in this system (constituting only 3%–6% of aboveground biomass) compared with tropical mangrove sites elsewhere (~12% is common, Kauffman, Heider, Cole, Dwine, & Donato, 2011; Kauffman, Heider, Norfolk, & Payton, 2014), again likely reflecting the young stand age. High C stores may also be a function of high tissue C:N ratio, lignin and tannin content of mangrove leaves (Robertson et al., 2008) that deter grazing by native detritivores not adapted to non-native mangroves as a food source and slow organic matter decomposition (Demopoulos & Smith, 2010). One challenge to this and other studies of C storage in mangrove forests is a limited ability to assess C laterally exported from mangrove stands in the form of dissolved inorganic, dissolved organic, or particulate organic C (Alongi, 2014). Although comprehensive estimates of the magnitude of these fluxes are still relatively rare, export in several systems has been estimated to be equivalent to or greater than the rate of sediment C burial (Maher et al., 2018; Santos et al., 2019). Total carbon storage may actually be larger given potential lateral fluxes. Furthermore, because of the long residence time of DIC in the ocean, DIC exported from mangrove systems may also act as a long-term C sink, substantially increasing the overall net C storage potential (Alongi, 2014; Santos et al., 2019).

While mangrove establishment does serve to increase sediment emissions of CH₄ to the atmosphere compared with the mudflats they have replaced, the estimated GWP offset of these emissions is minor relative to net CO₂ uptake by non-native mangrove forests. CH₄ emissions were variable across the three forests we surveyed, but even assuming the “upper bound” (constant) scaling scenario (that CH₄ fluxes increased to present rates immediately upon mangrove establishment, rather than increasing more gradually) generates total emissions of 1.34 ± 0.45 Mg CH₄/ha. Given that rates were extrapolated from wet season sampling (a period of higher emissions in other tropical mangrove systems; Rosentreter et al., 2018), this

value may also tend to overestimate annual fluxes. Considering the sustained GWP of this quantity of emitted CH_4 over a 20 year timescale, this flux only offsets net mangrove CO_2 removal from the atmosphere by $\sim 7.6\%$ (or 3.6% when considering a longer 100 year SGWP). These estimates are broadly in agreement with the few other studies of native mangrove systems, which conclude that CH_4 emissions offset sediment C burial by between 6% and 24% , with a global estimated mean of 18% – 22% using GWP_{20} (Maher et al., 2018; Rosentreter et al., 2018). This global estimate is based on relatively few sites, varies strongly with latitude (with highest emission rates predicted for mid-latitudes), and also considers only offsets to contemporary C burial in sediment. The range of CH_4 GWP offset values for Moloka'i is lower partly because the offset is able to account for ecosystem C accrual in biomass since establishment. Although estimates do not include all potential CH_4 emission sources (such as ebullition, emissions from mangrove creek or estuarine waters, or conduit of sediment-generated methane through trees stems; Dutta, Bianchi, & Mukhopadhyay, 2017; Rosentreter et al., 2018), overall atmospheric warming offsets would likely be further decreased if also considering the persistence of DIC and other lateral exports from mangrove forests.

4.2 | Potential value of non-native mangroves in climate change mitigation and adaptation

In addition to coastline C stocks, non-native *R. mangle* invasion also increased average sediment C burial and accretion rates by an order of magnitude or more compared to non-invaded mudflats. Although sedimentation rates were substantially greater at all sites during most time intervals following mangrove invasion, this effect was not consist across all years. The presence of *R. mangle* trunks and above-ground prop roots increased the tertiary structure of invaded mudflats, likely resulting in slower water velocity such that suspended sediments are more readily deposited on the mangrove forest floor (Furukawa & Wolanski, 1996; Furukawa, Wolanski, & Mueller, 1997). Roots can then trap and incorporate these particles into mangrove sediments (Krauss et al., 2014). Increased sediment trapping efficiency of *R. mangle*-invaded mudflats is also evidenced by the peaks in sedimentation, sediment C burial, and accretion rates observed in the deeper, post-colonization intervals from cores M1 (1976–1980), M2 (1973–1975), and M3 (1972). These dates correlate with the 1975 tsunamis, as well as Hurricane Kate in 1976 and Fico in 1978 that would have increased sediment deposition to coastal areas through wave action as well as inland flooding (Fletcher, Grossman, Richmond & Gibbs, 2002). Sedimentation, sediment C burial, and accretion rate peaks observed in sediment cores collected from Florida mangroves were also attributed to hurricane activity in that region (Breithaupt, Smoak, Smith, & Sanders, 2014). However, these peaks were correlated with lower organic C content in sediments, likely due to the deposition of CaCO_3 sands from adjacent coastal areas. Organic C content was typically highest during peak sedimentation, sediment C burial, and accretion rates at the Molok'i sites, potentially reflecting deposition of upland-derived terrestrial matter high in C content.

The correlation between organic carbon content and peak sedimentation, sediment C burial, and accretion rates may also reflect root growth. Sedimentation, sediment C burial, and accretion rates are typically greatest in the root zone near the top of wetland cores and decrease with depth as roots become less abundant and C leaches out of the system. The peak rates observed in the deeper post-invasion intervals of M1 (1976–1980), M2 (1973–1975), and M3 (1972) may also be due to higher root growth and sediment expansion from newly established mangrove stands, as these intervals correspond to an age of 25–30 years after mangroves had become established at those sites. Sediment C stocks in restored mangroves can be equivalent to intact reference sites after 10–25 years (Adame et al., 2018; DelVecchia et al., 2014; Krauss et al., 2017; Osland et al., 2012). This has been attributed to higher root growth of younger trees coupled with initial higher rates of sedimentation that occur from the presence of roots and trunks that trap sediments out of the water column (Krauss et al., 2017). This would also explain peak sedimentation, sediment C burial, and accretion rates occurring during peaks in percent organic C content of sediments.

Increased C stocks and sediment C burial rates provide a potentially important climate change mitigation mechanism, while increased accretion rates provide an important adaptation mechanism by increasing coastline stability and resilience. Although mangroves occupy only 0.35% of the area of Moloka'i ($\sim 2.4 \text{ km}^2$; D'Iorio, 2003), our measurements show that they account for $>1\%$ of Molokai's total ecosystem C stocks (Selmants et al., 2017). After only 70 years of growth, mangroves store 40% – 50% more C (per unit area) than tropical wet forests across the Hawaiian islands, and are rivaled only by non-native tree plantations (Selmants et al., 2017). Current rates of sea level rise (SLR) throughout the Hawaiian Islands range from 1.41 ± 0.22 to $2.95 \pm 0.31 \text{ mm/year}$ (NOAA, 2017). Sea water damage to communities and infrastructure, both during baseline tidal cycles and during storm surges, has been recognized as a critical social and economic challenge in the state (Anderson et al., 2018; HCCMAC, 2017). Vertical sediment accretion by mangroves has been identified as a key function in protecting coastlines by matching or exceeding coastal water level increases (Hoque et al., 2015; van Maanen, Coco, & Bryan, 2015) and in Vietnam, surface accretion in mangrove plantations exceeds local SLR (MacKenzie et al., 2016). Accretion rates measured from pre-invasion sediment core intervals ranged from 0.1 to 0.2 cm/year and in post-invasion intervals from 0.7 to 1.8 cm/year . Assuming that pre-invasion sediment core rates are equivalent to current rates, the invasion of mudflats by mangroves has significantly increased accretion rates relative to current rates of SLR, likely increasing coastline stability and resilience. Taking a more conservative approach and determining accretion rates by dividing the total depth of the mudflat and mangrove C stock cores by the age of the adjacent mangrove forest results accretion rates of mangrove sites (0.9 cm/year) that are still three times greater than mudflats (0.3 cm/year). Comparing these more conservative rates to SLR still supports the idea that non-native mangroves are increasing the coastal resilience of these oceanic island coastlines.

4.3 | Implications for management

Mangrove expansion and invasion is not unique to Hawaii, but is occurring on other oceanic islands and landmass margins globally. The management of non-native mangroves in the Hawaiian islands has balanced the desire to reverse perceived ecological (e.g., losses of habitat for native water bird species; Allen, 1998) and socioeconomic impacts (e.g., damage to culturally significant fishing pools; Fronda et al., 2008), with the reality that effective management is very expensive, labor-intensive, and often must be maintained indefinitely (Rauzon & Drigot, 2002). The state of Hawaii, like many governmental bodies worldwide, has enacted legislation aimed at implementing the goals of the Paris Accord (Act 32, SLH, 2017). Within this framework, specific aims include reducing production of GHG, implementing sea level rise adaptation strategies, and increasing GHG sequestration in natural environments (Act 15, SLH, 2018). In accordance with these goals, we propose that the climate mitigation and coastal resiliency potential of non-native *R. mangle* should be considered alongside socioeconomic and ecological factors in weighing whether to remove non-native mangrove forests. The conclusion that younger forests can have particularly high rates of C accrual could be extrapolated to decision-making regarding intentionally outplanting or restoring existing mangroves elsewhere in the tropics. Resources to support decision-making frameworks that emphasize balancing multiple ecosystem management goals in “novel” ecosystems, versus more traditional “pristine state” conservation practices, are now increasingly available (Hobbs et al., 2014; Hobbs, Higgs, & Harris, 2009).

In addition to the clear potential for intact non-native mangroves to continue to sequester C, any removal of current mangrove stands is likely to result in increased C emissions to the atmosphere that may continue for several years, if not decades. Globally, C emissions associated with the removal of mangroves or conversion to other land use types (e.g., shrimp ponds) are variable, but generally very large. Reported ranges span from a conservative ~410 Mg CO_{2e} (CO₂-equivalent)/ha up to as much as 3,600 Mg CO_{2e}/ha, depending on assumptions and the magnitude of underlying C stocks (Donato et al., 2011; Kauffman et al., 2014; Pendleton et al., 2012). Mangrove removal reduces productive aboveground biomass and can expose previously suboxic sediment C to microbial degradation and destabilization, resulting in sediment erosion (some of which may be redeposited on reefs or the nearshore environment) and ultimately returning sequestered C to the atmosphere as CO₂ or CH₄ (Crooks et al., 2011; Kauffman et al., 2014; Lang'at et al., 2014; Pendleton et al., 2012). Where aboveground mangrove biomass was manually removed as part of management efforts on O'ahu, sediments continued to show elevated decomposition of belowground biomass for at least 6 years after removal (Sweetman et al., 2010). This suggests that any CO₂ emissions associated with mangrove removal would likely persist for some time, and would thus be carried forward to future emissions budgets. In addition, root collapse and sediment compaction after mangrove removal leads

to rapid subsidence, counteracting any gains in surface elevation (Lang'at et al., 2014).

5 | CONCLUSIONS

By exploring a novel mangrove system in which contemporary C inputs can be readily distinguished, we find that young mangrove stands have especially high potential for C accrual early after establishment. Non-native *R. mangle* mangrove stands established on mudflats within the last ~70 years show stand-lifetime C accrual in the range of 434 ± 33 Mg C/ha, with annual sediment organic C burial rates of 4.5 ± 0.3 Mg C ha⁻¹ year⁻¹ expected if contemporary sedimentation rates continue. Large net gains are only minimally offset by variable but increased emission of CH₄ from mangrove sediments, regardless of choice of scaling scenario. In addition, sediment accretion by mangrove forests could play a role in protecting parts of the coastal zone from inundation as a result of sea level rise. Given the prevalence of mangrove expansion and invasion worldwide, this potential for adaptation and mitigation should be weighed in decision-making frameworks that inform management actions such as mangrove removal.

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CONFLICT OF INTEREST

No conflict of interest is reported.

AUTHOR CONTRIBUTIONS

J.P.S., R.A.M., S.S., and C.M.L. conceived and designed the study. J.P.S., R.A.M., C.M.L., S.S., and T.G.C. performed the research. F.M.S., S.S., and R.A.M. analyzed the data and performed statistical analyses. All authors interpreted results and contributed to the M.S., with writing led by F.S. and R.A.M.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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