



# Sediment properties and CO<sub>2</sub> efflux from intact and cleared temperate mangrove forests

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**Abstract.** Temperate mangrove forests in New Zealand have increased in area over recent decades. Expansion of temperate mangroves in New Zealand is associated with perceived loss of other estuarine habitats, and decreased recreational and amenity values, resulting in clearing of mangrove forests. In the tropics, changes in sediment characteristics and carbon efflux have been reported following mangrove clearance. This is the first study in temperate mangrove (*Avicennia marina*) forests investigating the impact of clearing on sediment CO<sub>2</sub> efflux and associated biotic and abiotic factors.

Sediment CO<sub>2</sub> efflux rates from intact ( $168.5 \pm 45.8$  mmol m<sup>-2</sup> d<sup>-1</sup>) and cleared ( $133.9 \pm 37.2$  mmol m<sup>-2</sup> d<sup>-1</sup>) mangrove forests in New Zealand are comparable to rates measured in tropical mangrove forests. We did not find a significant difference in sediment CO<sub>2</sub> efflux rates between intact and cleared temperate mangrove forests. Pre-shading the sediment for more than 30 min prior to dark chamber measurements was found to have no significant effect on sediment CO<sub>2</sub> efflux. This suggests that the continuation of photosynthetic CO<sub>2</sub> uptake by biofilm communities was not occurring after placement of dark chambers. Rather, above-ground mangrove biomass, sediment temperature and chlorophyll *a* concentration were the main factors explaining the variability in sediment CO<sub>2</sub> efflux in intact mangrove forests. The main factors influencing sediment CO<sub>2</sub> efflux in cleared mangrove forest sites were sediment organic carbon concentration, nitrogen concentration and sediment grain size. Our results show that greater consideration should be given regarding the rate of carbon released from mangrove forest following clearance and the relative contribution to global carbon emissions.

## 1 Introduction

Mangroves are generally confined to the tropics, between latitudes 30° N and 30° S. However, approximately 1.4 % of the global mangrove forests are located outside this latitudinal range, growing in conditions which may be broadly characterised as temperate (Morrisey et al., 2010). Temperate mangrove forests mainly occur in Australia, New Zealand, the USA and South Africa (Morrisey et al., 2010; Giri et al., 2011). These forests are subject to colder and generally more variable climatic conditions, and are typically associated with lower diversity of tree species and lower faunal abundance and diversity than in the tropics (Alfaro, 2006; Morrisey et al., 2010). However, little is known about sediment properties and the factors driving the storage and exchange of carbon (C) in temperate mangrove sediments (Livesley and Andrusiak, 2012).

Temperate mangrove forest cover has increased significantly over the last 50–60 years (Morrisey et al., 2010; Saintilan et al., 2014). A landward expansion of mangroves into salt marsh has been observed in Australia and the USA (Cavanaugh et al., 2014; Saintilan et al., 2014), while mangrove expansion into tidal flats is typically observed in New Zealand (Stokes et al., 2009; Lundquist et al., 2014a). The expansion of mangroves in New Zealand has been linked to increased sedimentation leading to vertical accretion of tidal flats (Swales et al., 2007; Stokes, 2010), increased nutrient inputs (Lovelock et al., 2007), and climatic factors (Burns and Ogden, 1985).

The recent expansion of temperate mangrove forests has led to a push towards mangrove removal in New Zealand,

largely from local communities concerned about the loss of diversity of estuarine habitats caused by mangrove expansion, or for human amenities such as recreational access and water views (Harty, 2009). Numerous legal and illegal mangrove clearings have occurred in recent decades, ranging in scale from < 0.1 to > 100 ha (Morrisey et al., 2010; Lundquist et al., 2014a).

Carbon cycling and storage are important ecosystem services provided by mangrove forests (Twilley et al., 1992; Bouillon et al., 2008; Kristensen et al., 2008; Alongi, 2014). The global net primary productivity in mangrove forests has been estimated at  $218 \pm 72 \text{ Tg C a}^{-1}$ , which includes the rate of litterfall and above- and below-ground biomass production (Bouillon et al., 2008). An important component of the C cycle is the efflux of carbon dioxide (CO<sub>2</sub>) from the sediment into the atmosphere (Raich and Schlesinger, 1992). Sediment CO<sub>2</sub> efflux is the total of CO<sub>2</sub> released through root/mycorrhizae respiration (autotrophic respiration) and microbial respiration (heterotrophic respiration) associated with the decomposition of organic matter (Bouillon et al., 2008). Quantifying C emissions and understanding the factors influencing C storage and exchange has become increasingly important due to the rapid rise in atmospheric CO<sub>2</sub> concentrations and associated impact on global climate (IPCC, 2013).

Clearing of mangrove forests has an impact on tree and sediment C storage and fluxes (Lovelock et al., 2011; Sidik and Lovelock, 2013; Lang'at et al., 2014). Following mangrove clearing, the accumulation of mangrove-derived C into the sediment is halted, yet the release of CO<sub>2</sub> from the sediment continues (Lovelock et al., 2011; Sidik and Lovelock, 2013). The rates of sediment CO<sub>2</sub> efflux from cleared tropical mangrove peat forests in Belize, Central America, have been shown to be significantly higher compared to intact mangrove forests (Lovelock et al., 2011). However, the impact of clearing on sediment CO<sub>2</sub> efflux and C content has not been investigated in temperate mangrove ecosystems.

Studies from tropical mangrove forests have shown that sediment CO<sub>2</sub> efflux is influenced by abiotic and biotic sediment characteristics including sediment C and nutrient quantity and quality (Kristensen, 2000), sediment grain size (Chen et al., 2010), redox potential (Chen et al., 2010; Chen et al., 2012; Leopold et al., 2013), sediment water content (Alongi, 2009) and sediment temperature (Chen et al., 2012). A study by Lovelock (2008) on temperate and tropical mangrove forests reported a positive correlation between leaf area index and sediment CO<sub>2</sub> efflux. Further, biofilm communities, which are present on the sediment surface, may play an important role in mediating CO<sub>2</sub> flux from the sediment (Alongi et al., 2012; Leopold et al., 2013; Leopold et al., 2015). Biofilm communities include a wide variety of diatoms, bacteria, fungi, and microfauna (Decho, 2000). The autotrophic biofilm communities contribute significantly to the primary productivity in estuarine ecosystems and supply energy to biofilm and other primary and secondary con-

sumers, whereas the heterotrophic biofilm communities mineralise organic matter (Van Colen et al., 2014).

The aim of this study was to assess the effect of temperate mangrove forest clearing on sediment CO<sub>2</sub> efflux and sediment characteristics. The specific objectives were to (1) quantify the sediment CO<sub>2</sub> efflux from intact and cleared mangrove forest, (2) investigate the relative contribution of abiotic and biotic factors on sediment CO<sub>2</sub> efflux and (3) measure the effect of pre-shading on sediment CO<sub>2</sub> efflux. This was to test whether CO<sub>2</sub> uptake during dark chamber measurements can be attributed to the continuation of photosynthetic activity by surface biofilm communities at the onset of dark measurements (Leopold et al., 2015).

## 2 Materials and methods

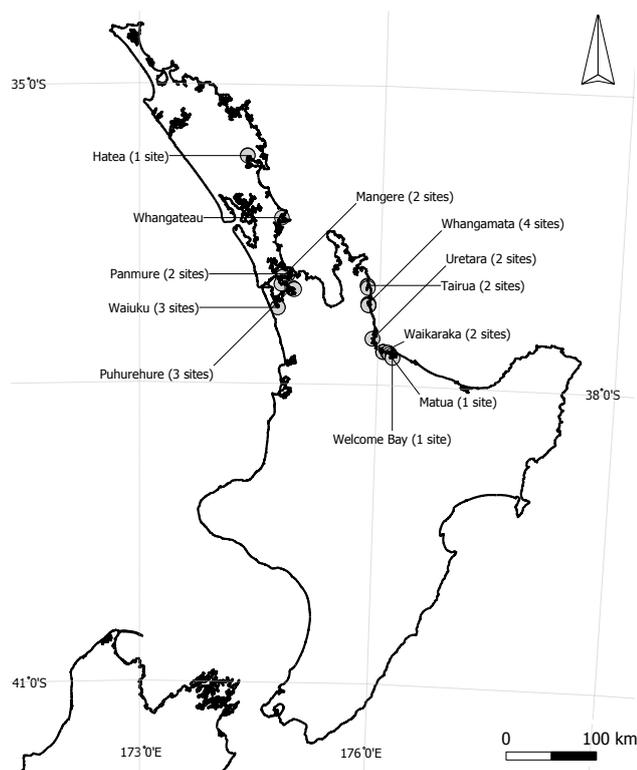
### 2.1 Study species

The only mangrove species in New Zealand, *Avicennia marina* subsp. *australasica*, occurs from the top to the central North Island (Morrisey et al., 2010). The southernmost limit (38°) is most likely due to low temperatures (Duke, 1990), lack of suitable conditions for propagule dispersal, and lack of suitable habitat (Lange and Lange, 1994). The height of mature mangrove trees in New Zealand ranges from less than 1 to over 6 m, with smaller trees often occurring towards the southern range limit (Morrisey et al., 2010).

### 2.2 Study area and selection of study sites

This study was conducted at 23 sites covering a large proportion of the geographic range of mangroves (35 to 37°41' S) in New Zealand (Fig. 1). We investigated cleared ( $n = 23$ ) and, where possible, adjacent intact mangrove forest sites ( $n = 13$ ). The time since mangrove removal ranged from 1 month to over 8 years. Cleared mangrove sites ranged in size from < 0.1 to > 13 ha. Besides the difference in size and time since clearing, the sites differed in shape of cleared area, hydrodynamic conditions (sheltered: protected from direct wind and wave action, generally located in the upper reaches of the estuary; exposed: exposed to wind and wave action, generally located in the lower reaches of the estuary), and method of mangrove removal (Table S1 in the Supplement). Mean air temperature ranges from 19° C during summer to 11° C during winter. Mean monthly rainfall varies from 77 to 152 mm, respectively (NIWA, 2014). Tides for the sites are semi-diurnal with a range of 1.3–4.1 m (LINZ, 2014).

Field measurements and sampling were undertaken during late spring and summer (November 2013–January 2014). Weather conditions during sampling were sunny or overcast, with no rainfall. Additional measurements were undertaken during winter (May–June 2015) within intact mangrove forest at one site (Hatea 1; Fig. 1).



**Figure 1.** Location of the cleared mangrove sites (●) and estuary locations throughout the North Island, New Zealand.

## 2.3 Sediment CO<sub>2</sub> efflux measurements

### 2.3.1 Pre-shading the sediment

The effect of pre-shading the sediment prior to dark chamber measurements was investigated at site Hatea 1. Three frames (0.5 m<sup>2</sup>) were deployed throughout the mangrove forest, at least 10 m from each other and the mangrove edge. Frames were located approximately 20 cm above the sediment surface. The frame was completely covered by layered cloth to exclude light penetration. After 30 min of shading, two CO<sub>2</sub> efflux measurements using a dark respiration chamber were conducted at different locations within the 0.5 m<sup>2</sup> area, before and after the removal of the surface biofilm. The biofilm (top ~ 2 mm of surface sediment) was scraped off using a spatula. Biofilm removal measurements were collected immediately following biofilm intact measurements in the identical location. Corresponding dark CO<sub>2</sub> efflux measurements were also conducted at locations that had not been pre-shaded (control) adjacent to each shaded measurement, as well as corresponding biofilm removal measurements to account for heterogeneity in sediment conditions.

### 2.3.2 Sediment CO<sub>2</sub> efflux from intact and cleared temperate mangrove

Sediment CO<sub>2</sub> efflux was measured in the centre of the cleared sites at three randomly selected locations. Locations in the intact mangrove forest were > 10 m from the cleared areas. No pre-shading of the sediment was undertaken prior to measurements.

The sediment CO<sub>2</sub> efflux was measured at low tide, between 08:00 and 18:00 local time, using an infrared CO<sub>2</sub> analyser (environmental gas monitor (EGM-4) with a dark sediment respiration chamber (SRC-1, PP Systems Ltd., Amesbury, MA, USA)). Using a dark chamber prevents the photosynthetic activity of biofilm communities which results in the uptake of CO<sub>2</sub>. A PVC collar (10 cm height) was attached to the base of the respiration chamber to protect the chamber from potential flooding. The collar was inserted approximately 5 mm into the sediment, avoiding damage to surface roots. Sediment within the chamber included crab burrows and pneumatophores < 7 cm which fit within the respiration chamber. The sediment area covered by each chamber was 0.00785 m<sup>2</sup>. Chamber height was measured during each measurement as collar insertion varied based on sediment characteristics. Total chamber volume varied between 1.72 and 1.98 L depending on the depth of collar insertion. The CO<sub>2</sub> concentration in the chamber was measured at 5 s intervals over a 90 s period. Air and sediment temperature (Novel Ways temperature probe) and moisture (CS620, Campbell Scientific, Logan, UT, USA) at a depth of 12 cm were measured with each CO<sub>2</sub> efflux measurement.

In addition to measuring CO<sub>2</sub> efflux in intact (undisturbed) sediment, sediment CO<sub>2</sub> efflux was re-measured at the same location after the removal of the surface biofilm. Measurements were made within 30 s following the removal of the surface biofilm.

Sediment CO<sub>2</sub> efflux was calculated from linear regression of the CO<sub>2</sub> concentration within the chamber over time. Only regressions with *r*<sup>2</sup> values ≥ 0.8 were used for flux calculations.

The sediment CO<sub>2</sub> efflux rate (μmol m<sup>-2</sup> s<sup>-1</sup>) was calculated as follows:

$$\text{Sediment CO}_2 \text{ efflux} = (\Delta\text{CO}_2/\Delta t) \cdot ((P \cdot V)/(R \cdot T)/A), \quad (1)$$

where  $\Delta\text{CO}_2/\Delta t$  is the change in CO<sub>2</sub> concentration over time, based on the slope of the linear regression (μmol mol<sup>-1</sup> s<sup>-1</sup> = ppm s<sup>-1</sup>); *t* is time (s); *P* is the atmospheric pressure (mbar); *V* is the volume of the chamber including collar (L); *A* is the surface area covered by each chamber (m<sup>2</sup>); *T* is the temperature (K); and *R* is the ideal gas constant (83.144621 L mbar K<sup>-1</sup> mol<sup>-1</sup>). Daily sediment CO<sub>2</sub> efflux (mmol CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>) was estimated by extrapolating the measured efflux rates, assuming constant efflux rates.

## 2.4 Sediment characteristics

At each site, three sediment samples, next to the location of the sediment CO<sub>2</sub> efflux measurements, were collected using two small sediment cores (2 cm deep, 2 cm in diameter). After collection the samples were immediately frozen and stored in the dark before analysis.

### Sediment carbon and nitrogen concentration

Samples were dried (60 °C for 48 h) and then pulverised using mortar and pestle. Total carbon (C) and nitrogen (N) concentration was determined using an elemental analyser (TruSpec LECO CNS, Leco Corporation, St. Joseph, MI). A subset of samples (14% of samples, ranging from 0.17 to 12.63% total C) were acidified to remove the inorganic C (Brodie et al., 2011). Briefly, 300 mg of sediment was mixed with 0.5 mL of distilled water and 1.5 mL of 20% HCl and then dried on a hot plate at 60 °C. Organic C concentration was then determined using the elemental analyser. A linear regression function between total C and organic C ( $r^2 = 0.98$ ,  $p < 0.001$ ) was used to calculate organic C concentrations of non-treated samples.

### Grain size

One sediment sample per site was analysed for grain size. The samples were homogenised and a subsample of approximately 5 g of sediment was taken and digested in ~9% hydrogen peroxide until bubbling ceased (Day, 1965). The sediment sample was then wet-sieved through 2000 and 63 µm mesh sieves. Pipette analysis was used to separate the <63 µm fraction into >3.9 and ≤3.9 µm. All fractions were then dried at 60 °C until a constant weight was achieved (fractions were weighed at ~40 h and then again at 48 h). Grain size fractions were calculated as percentage weight of gravel/shell hash (>2000 µm), sand (63–2000 µm), silt (3.9–62.9 µm) and clay (≤3.9 µm).

### Chlorophyll *a*

One sediment sample per site was analysed for chlorophyll *a*. The samples were freeze-dried within a month of sampling, weighed, and homogenised and then a subsample (~5 g) was taken for extraction. Chlorophyll *a* was extracted by boiling the sediment in 90% ethanol. The absorption of the extract was measured at 665 and 750 nm using a spectrophotometer (UV-1800, Shimadzu, Kyoto, Japan). Immediately after the absorbance reading, 0.05 mL of 1 mol HCl was added to separate degradation products from chlorophyll *a*. The absorption of the acidified extract was re-measured after 30 s (Hanson, 1988; Moed and Hallegraef, 1978). Chlorophyll *a* con-

centration was calculated based on the following equation:

$$\text{Chlorophyll } a (\mu\text{g g}^{-1} \text{ sediment}) = (750a - 665a) - (750 - 665) \cdot \text{Abs} \cdot (\text{ethanol in extraction (l)}/\text{sediment analysed (g)}), \quad (2)$$

where 750 and 665 are the absorptions at wavelengths 750 and 665 nm, 750*a* and 665*a* are the absorptions at wavelengths 750 and 665 nm after acidification, and Abs is the absorbance correction factor for chlorophyll *a* in ethanol (28.66).

## 2.5 Tree and root biomass

Within intact mangrove forests the tree height of the closest five mangrove trees to each measurement/sampling point and the density (number of mangroves within a 2 m × 2 m area) was recorded. Above-ground biomass was estimated using the allometric equations developed for *Avicennia marina* in New Zealand (Woodroffe, 1985):

$$\text{Total above-ground biomass}^{-1/3} (\text{g dry weight}) = -4.215 + 0.121 \cdot \text{height (cm)}. \quad (3)$$

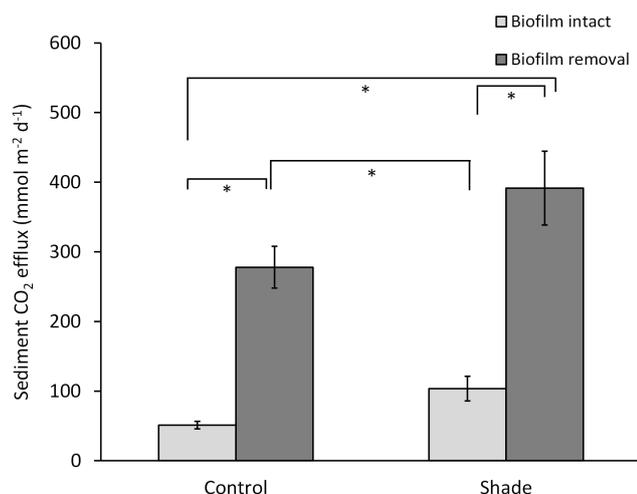
At two sites, Mangere 1 (Auckland) and Hatea 1 (Northland) mangrove height exceeded the range the allometric equation was designed for (determined from trees ranging in height from 40 to 248 cm). Here, trunk diameter (at 30 cm height) of the closest five mangrove trees to each sampling point was used to estimate biomass for all trees at Mangere 1 and Hatea 1:

$$\text{Total above-ground biomass}^{-1/3} (\text{g dry weight}) = 0.264 + 2.597 \cdot \text{diameter (cm)}. \quad (4)$$

At each cleared site a quadrat (0.5 m × 0.5 m) was sampled at three randomly selected locations (within a 10 m radius). The following characteristics were recorded within each quadrat: the proportion of surface covered by mangrove leaf litter, proportion of surface covered by macroalgae, number of mangrove seeds and seedlings, and number of pneumatophores. Further, three randomly located root biomass cores (13 cm diameter, 15 cm depth) were collected at each clearing site. After sorting, all vegetative material was air-dried for 1 week on aluminium trays, and then oven-dried at 70 °C for approximately 4 days until dry weight stabilised. Surface characteristics and root biomass were not measured at intact mangrove forest sites.

## 2.6 Data analysis

Replicates per site were averaged to provide mean site values. Mean site values were used in subsequent data analysis. Coefficient of variation (CV) values were determined (standard deviation/mean) to compare variation within and among sites.



**Figure 2.** Mean sediment ( $\pm$ SE) CO<sub>2</sub> efflux ( $\text{mmol m}^{-2} \text{d}^{-1}$ ) before and after surface biofilm removal, from control ( $n = 6$ ), and pre-shaded sediment ( $n = 6$ ) at intact mangrove site Hatea 1. \*Significant difference ( $p < 0.01$ ).

Data were tested for normality using the Shapiro–Wilk test. The Mann–Whitney rank-sum test was used to determine differences in sediment CO<sub>2</sub> efflux and other site characteristics between shaded and control measurements and between intact and cleared mangrove sites as data did not conform to normality.

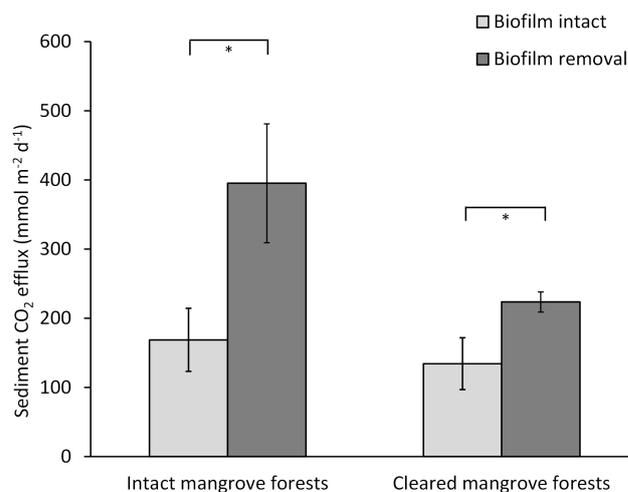
Backward multiple linear regression analysis was used to identify the sediment and ecosystem characteristics that predicted CO<sub>2</sub> efflux. Levene’s test was used to verify the homogeneity of variance. Sediment CO<sub>2</sub> efflux values from intact mangrove forest site Matua and cleared mangrove forest site Waiuku 2 were considered outliers (mean values were  $>3$ -fold the overall mean and  $>2$ -fold the next highest value) and not included in the regression analysis. A significance level of  $p < 0.05$  was used for the linear models and the individual coefficients.

A significance level of  $p < 0.05$  was used for the linear models and the individual coefficients, unless otherwise stated.

### 3 Results

#### 3.1 Shading experiment

No significant difference was detected in mean CO<sub>2</sub> efflux between shaded ( $103.6 \pm 17.8 \text{ mmol m}^{-2} \text{d}^{-1}$ ) and control ( $51.1 \pm 5.5 \text{ mmol m}^{-2} \text{d}^{-1}$ ) treatments ( $p = 0.08$ ; Fig. 2). Removing the surface biofilm resulted in significantly higher CO<sub>2</sub> efflux for both shaded ( $391.5 \pm 53.1 \text{ mmol m}^{-2} \text{d}^{-1}$ ) and control ( $278.0 \pm 29.9 \text{ mmol m}^{-2} \text{d}^{-1}$ ) treatments ( $p < 0.01$ ; Fig. 2).



**Figure 3.** Mean sediment ( $\pm$ SE) CO<sub>2</sub> efflux ( $\text{mmol m}^{-2} \text{d}^{-1}$ ) before and after surface biofilm removal, from intact mangrove forest (13 sites), and cleared mangrove forest (23 sites). \*Significant difference ( $p < 0.01$ ).

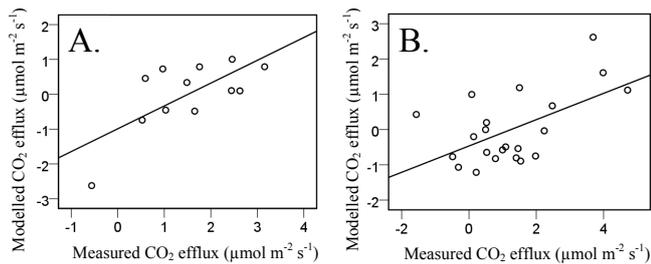
#### 3.2 Sediment CO<sub>2</sub> efflux and sediment characteristics from intact and cleared mangrove forest sites

No significant difference in sediment CO<sub>2</sub> efflux was found between intact ( $168.5 \pm 45.8 \text{ mmol m}^{-2} \text{d}^{-1}$ ,  $n = 13$ ) and cleared ( $133.9 \pm 37.2 \text{ mmol m}^{-2} \text{d}^{-1}$ ,  $n = 23$ ) mangrove sites ( $p > 0.05$ ; Fig. 3). Removing the surface biofilm resulted in significantly higher CO<sub>2</sub> efflux at intact (2.34-fold increase) and cleared (1.66-fold increase) mangrove forest sites ( $p < 0.01$ ; Fig. 3).

Mangrove above-ground biomass ranged from 0.5 to  $13.5 \text{ kg dry weight m}^{-2}$  with an average value of  $4.5 \text{ kg dry weight m}^{-2}$  (Table 1). Sediment characteristics varied considerably among sites, and no significant differences ( $p > 0.05$ ) were detected in sediment characteristics between intact and cleared mangrove forest sites (Table 1).

Sediment CO<sub>2</sub> efflux varied considerably within and among sites. However, the mean variability within individual sites (CV = 0.55 for intact mangrove and CV = 1.1 for cleared mangroves) was lower than mean variability among sites (CV = 0.99 for intact mangroves and CV = 1.34 for cleared mangroves).

Individual sites were grouped based on whether CO<sub>2</sub> efflux exceeded (“high-efflux group”) or was below (“low-efflux group”) the mean CO<sub>2</sub> efflux rate for intact mangrove forests ( $168.5 \pm 45.8 \text{ mmol m}^{-2} \text{d}^{-1}$ ) in order to determine whether site characteristics were significantly different between high- and low-efflux groups. Mean sediment CO<sub>2</sub> efflux of the high-efflux group (Matua, Tairua 2, Uretara 1, Waikareao, and Welcome Bay 1) was  $310.8 \pm 80.7 \text{ mmol m}^{-2} \text{d}^{-1}$ , significantly higher ( $p < 0.05$ ) than the  $80.1 \pm 23.4 \text{ mmol m}^{-2} \text{d}^{-1}$  measured in the low efflux group. Chlorophyll *a* concentration was significantly



**Figure 4.** (a) Modelled values of mangrove forest CO<sub>2</sub> efflux compared to measured CO<sub>2</sub> efflux (modelled CO<sub>2</sub> efflux ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) =  $2.454 - 0.215 \times$  mangrove biomass,  $r^2 = 0.49$ ,  $p < 0.05$ ). (b) Modelled values of cleared mangrove forest CO<sub>2</sub> efflux compared to measured CO<sub>2</sub> efflux (modelled CO<sub>2</sub> efflux ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) =  $0.0713 + 0.430 \times$  sediment organic carbon concentration,  $r^2 = 0.32$ ,  $p < 0.05$ ).

higher in the high-efflux group ( $53.3 \pm 7.0 \mu\text{g}^{-1} \text{g}^{-1}$  sediment) than in the low-efflux group ( $26.6 \pm 7.0 \mu\text{g}^{-1} \text{g}^{-1}$  sediment;  $p < 0.05$ ). In addition, sediment temperature ( $^{\circ}\text{C}$ ) was significantly higher in the high-efflux group ( $21.3 \pm 1.0$ ) than in the low-efflux group ( $17.9 \pm 0.8$ ;  $p < 0.05$ ; Table S2).

Similarly, cleared mangrove sites were grouped based on whether CO<sub>2</sub> efflux exceeded (high-efflux group) or was below (low-efflux group) the mean CO<sub>2</sub> efflux rate for cleared mangrove ( $133.9 \pm 37.2 \text{ mmol m}^{-2} \text{d}^{-1}$ ). Mean sediment CO<sub>2</sub> efflux of the high-efflux group (Mangere 1; Pahurehure 4; Waiuku 1, 2 and 3; Welcome Bay 1; Whangamata E) was  $338.0 \pm 71.3 \text{ mmol m}^{-2} \text{d}^{-1}$ , significantly higher ( $p < 0.05$ ) than  $45.2 \pm 18.3 \text{ mmol m}^{-2} \text{d}^{-1}$  measured in the low-efflux group. Sediment organic C concentration ( $4.2 \pm 0.8\%$  vs.  $2.1 \pm 0.4\%$ ), N concentration ( $0.5 \pm 0.1\%$  vs.  $0.3 \pm 0.1\%$ ), and sediment clay content ( $28.2 \pm 4.3\%$  vs.  $15.1 \pm 2.6\%$ ) were significantly higher and sediment sand content ( $15.5 \pm 9.9\%$  vs.  $43.0 \pm 8.0\%$ ) was significantly lower in the high-efflux group than in the low-efflux group for cleared mangrove forest sites ( $p < 0.05$ ; Table S3).

### 3.3 Regression analysis

Backward multiple linear regression analysis revealed that mangrove biomass was the only significant predictor of sediment CO<sub>2</sub> efflux within intact mangrove forest sites ( $r^2 = 0.49$ ,  $F = 9.43$ ,  $p = 0.01$ ; Fig. 4a). Within the cleared sites, backward multiple linear regression analysis revealed that sediment organic C concentration was the only significant predictor of CO<sub>2</sub> efflux ( $r^2 = 0.32$ ,  $F = 9.23$ ,  $p < 0.01$ ; Fig. 4b). No other significant relationships were observed ( $p > 0.05$  for individual coefficients).

## 4 Discussion

### 4.1 Sediment CO<sub>2</sub> efflux and sediment characteristics from intact temperate mangrove forests

The magnitude of dark sediment CO<sub>2</sub> efflux in intact *Avicennia marina* forests measured in this study ( $168.5 \pm 45.8 \text{ mmol m}^{-2} \text{d}^{-1}$ ) is similar to values reported for intact *Avicennia marina* forests in New Zealand (Lovelock, 2008; Lovelock et al., 2014), Australia (Livesley and Andrusiak, 2012) and tropical locations (New Caledonia: Leopold et al., 2013, 2015; Table 2). However, our values are higher than the global estimates of sediment CO<sub>2</sub> efflux from intact tropical mangrove forests ( $75 \text{ mmol m}^{-2} \text{d}^{-1}$ : Kristensen et al., 2008;  $61 \pm 56 \text{ mmol m}^{-2} \text{d}^{-1}$ : Bouillon et al., 2008;  $69 \pm 8 \text{ mmol m}^{-2} \text{d}^{-1}$ : Alongi, 2014; Table 2). The differences in CO<sub>2</sub> efflux may be related to the methods applied. The global estimates were primarily determined in the laboratory by incubating sediment cores extracted from the field (Kristensen et al., 2008). CO<sub>2</sub> efflux is generally lower in these studies than that observed in studies using chamber-based techniques where CO<sub>2</sub> is measured continuously over a short period of time in the field (this study; Lovelock, 2008; Lovelock et al., 2014; Livesley and Andrusiak, 2012; Leopold et al., 2013; Leopold et al., 2015). Higher sediment CO<sub>2</sub> efflux observed in our study may also be explained by the inclusion of crab burrows and short pneumatophores in the flux measurements. The omission of crab burrows and pneumatophores has previously been proposed as a potential explanation of why global estimates may be underestimated (Bouillon et al., 2008). Crab burrows have been shown to increase CO<sub>2</sub> efflux by increasing the surface area for sediment–air exchange of CO<sub>2</sub> (Kristensen et al., 2008) and enhancing organic matter decomposition (Pülmanns et al., 2014). Pneumatophores have been associated with increased CO<sub>2</sub> emissions by efficient translocation of CO<sub>2</sub> exchange from deeper sediments (Bouillon et al., 2008; Kristensen et al., 2008).

Sediment organic C concentrations in the intact mangrove sites ( $3.6 \pm 0.7\%$ ) are comparable to the sediment organic C concentration measured in mangrove forests in New Zealand (Auckland: Yang et al., 2013; Firth of Thames: Lovelock et al., 2010) and *Avicennia marina* forests south of Melbourne, Australia (Livesley and Andrusiak, 2012). The mean sediment organic C concentration in mangrove sediments collected across the globe is  $2.2\%$  (Kristensen et al., 2008). The main sources of organic C in intact mangrove sediments are litter and root material and suspended matter from other terrestrial and estuarine sources (Bouillon et al., 2003). The relative contribution of each source has been shown to vary considerably depending on site characteristics and histories (Bouillon et al., 2003).

The above-ground biomass across the investigated *Avicennia marina* forests ( $0.5\text{--}13.5 \text{ kg dry weight m}^{-2}$ ) is lower than the above-ground biomass in many tropical mangrove

**Table 1.** Tree and sediment characteristics from intact and cleared mangrove sites. Values are means  $\pm$  SE.

	Intact ( <i>n</i> = 13)	Cleared ( <i>n</i> = 23)
Tree characteristics		
Above-ground biomass (kg dry weight m <sup>-2</sup> )	4.35 $\pm$ 0.9	0
Mangrove root mass (kg dry weight m <sup>-3</sup> )	no data	9.5 $\pm$ 1.0
Mangrove pneumatophore abundance (n m <sup>-2</sup> )	no data	257.3 $\pm$ 86.7
Time since clearance (yr <sup>-1</sup> )	–	2.9 $\pm$ 0.4
Sediment characteristics		
Organic carbon (%)	3.6 $\pm$ 0.7	2.7 $\pm$ 0.4
Nitrogen (%)	0.5 $\pm$ 0.1	0.3 $\pm$ 0.1
Gravel (%)	3.7 $\pm$ 2.3	1.5 $\pm$ 0.9
Sand (%)	29.4 $\pm$ 10.6	34.6 $\pm$ 6.8
Silt (%)	47.5 $\pm$ 7.8	44.8 $\pm$ 5.2
Clay (%)	16.6 $\pm$ 2.7	19.1 $\pm$ 2.6
Chlorophyll <i>a</i> ( $\mu\text{g}^{-1} \text{g}^{-1}$ sediment)	36.9 $\pm$ 6.2	26.8 $\pm$ 4.4
Sediment temperature (°C)	19.2 $\pm$ 0.2	20.2 $\pm$ 0.5

**Table 2.** Comparison of mean estimates of sediment CO<sub>2</sub> efflux in intact and cleared mangrove forests. Values are means  $\pm$  SE.

Species	Location, number of sites	Sediment CO <sub>2</sub> efflux (mmol CO <sub>2</sub> m <sup>-2</sup> d <sup>-1</sup> )	Reference
Intact mangrove forests			
<i>Avicennia marina</i>	New Zealand, 13	168.5 $\pm$ 45.8	This study
<i>Avicennia marina</i>	New Zealand, 4	114.0 $\pm$ 19.9	Lovelock et al. (2014)
<i>Avicennia marina</i>	South and north Australia, 4	107.1 $\pm$ 45.8	Lovelock et al. (2014)
<i>Avicennia marina</i>	New Caledonia, 1	88.2 $\pm$ 23.7	Leopold et al. (2013)
<i>Avicennia marina</i>	New Caledonia, 1	*Ranging from –17.3 to 212.4 throughout the year	Leopold et al. (2013)
<i>Avicennia marina</i>	South Australia, 3	*Ranging from 73.7 to 117.9 throughout the year	Livesley and Andrusiak (2012)
Mixed species	Global estimate, 16	75	Kristensen et al. (2008)
Mixed species	Global estimate, 82	61 $\pm$ 56	Bouillon et al. (2008)
Mixed species	Global estimate, 140	69 $\pm$ 8	Alongi (2014)
Cleared mangrove forests			
<i>Avicennia marina</i>	New Zealand, 23	133.9 $\pm$ 37.2; 0–8 years since clearing	This study
<i>Rhizophora mangle</i> – peat soils	Twin Cays, Belize, 5	*Declining from 658.3 to 181.4 over 20 years	Lovelock et al. (2011)
Tropical mangrove	Bali, Indonesia, 1	*Shrimp pond floors: 99.4; Shrimp pond walls: 272.2	Sidik and Lovelock (2013)
Tropical mangrove	Gazi Bay, Mombasa, Kenya	88.6, 343 days since clearing	Lang'at et al. (2014)

\* Note: no overall mean values provided.

forests (3.5–40 kg dry weight m<sup>-2</sup>). This is in line with previous findings reporting a decrease in mangrove biomass with increasing latitude (Saenger and Snedaker, 1993; Komiyama et al., 2008). We found a negative relationship between mangrove above-ground biomass and sediment CO<sub>2</sub> efflux across the 13 intact mangrove forests. Lower tree biomass associated with lower forest cover may result in increased light availability and sediment temperature (Lovelock, 2008). Higher sediment temperature may in turn lead to a higher abundance and activity of the sediment microbial decomposer community (Zogg et al., 1997) and higher sediment CO<sub>2</sub> efflux.

Respiration from heterotrophic biofilm communities also contributes a considerable proportion to total CO<sub>2</sub> efflux from mangrove sediments, as shown in a New Caledonian *Avicennia marina* forest (Leopold et al., 2013). High sediment chlorophyll *a* concentrations and the presence of algal mats characterising the intact “high-efflux sites” suggest that respiration by heterotrophic biofilm communities may be a significant contributor to CO<sub>2</sub> efflux (Decho, 2000). Further, higher sediment temperature resulting in higher sediment CO<sub>2</sub> efflux in the high-efflux sites is in line with findings from other mangrove forests (e.g. Leopold et al., 2015) and many terrestrial systems (e.g. Davidson and Janssens,

2006). Soil temperature is one of the key abiotic factors influencing both the autotrophic and heterotrophic activity (Raich and Schlesinger, 1992).

We note that all sediment CO<sub>2</sub> efflux measurements in this study were made at low to mid-tide while surface sediments were exposed to air and that they likely overestimate maximum efflux rates across a tidal cycle. Mangrove sediment CO<sub>2</sub> efflux during low tide can be up to 40% greater than during tidal immersion as molecular diffusion of CO<sub>2</sub> is faster when sediments are aerated and the surface area for aerobic respiration and chemical oxidation increases (Alongi, 2009). Further, benthic light availability is also reduced during tidal immersion, which may result in increased respiration by heterotrophic biofilm communities (Billerbeck et al., 2007).

#### 4.2 Sediment CO<sub>2</sub> efflux and sediment characteristics of cleared mangrove forests

Our results show that dark sediment CO<sub>2</sub> efflux rates from cleared *Avicennia marina* forests ( $133.9 \pm 37.2$  mmol CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>) are similar to sediment CO<sub>2</sub> efflux following mangrove clearing in the tropics (Lovelock et al., 2011; Sidik and Lovelock, 2013; Lang'at et al., 2014). Higher sediment CO<sub>2</sub> efflux rates (181.4 to 656.6 mmol m<sup>-2</sup> d<sup>-1</sup> depending on the time since clearing) were measured in cleared peat mangrove forests in Belize, Central America (Lovelock et al., 2011). The mangroves in New Zealand grow on mineral sediments, which may explain lower CO<sub>2</sub> emissions compared to those from the study in Belize, where mangroves are growing on carbon-rich peat soils (Lovelock, 2008).

We did not find a significant difference in sediment CO<sub>2</sub> efflux between intact and cleared mangrove forest sites. Further, there was no relationship to be found between time since clearing and sediment CO<sub>2</sub> efflux. It is likely that a number of factors (such as differences in site sediment characteristics, size, hydrodynamic conditions, and method of clearing) are concealing the effect of time since clearing on sediment CO<sub>2</sub> efflux in our study. In contrast, sediment CO<sub>2</sub> efflux from cleared peat mangrove forests in Belize declined logarithmically over a 20-year period (Lovelock et al., 2011). In Kenya, 2 months after mangrove removal, sediment CO<sub>2</sub> efflux increased approximately 2-fold compared to intact mangroves. However, 5 months after clearing, sediment CO<sub>2</sub> efflux rates returned to levels similar to adjacent intact mangrove forests (Lang'at et al., 2014).

Sediment CO<sub>2</sub> efflux in cleared sites was positively related to sediment organic C concentration. This was also observed following the clearing of peat mangroves in Belize, where the rate of CO<sub>2</sub> efflux was related to the microbial degradation of organic matter in the sediments (Lovelock et al., 2011). While no significant correlation was found between CO<sub>2</sub> efflux and mangrove root biomass in our study, increased CO<sub>2</sub> efflux following mangrove clearing has previously been attributed to the rapid decomposition of fine root material re-

lated to increased sediment temperatures following the loss of canopy cover (Lang'at et al., 2014).

The highest sediment CO<sub>2</sub> efflux rates were measured at sites where large areas were cleared (> 1 ha) using mechanical diggers and the tree mulch was left in place. Increased sediment organic C and N concentrations resulting from the mulch input may explain higher sediment CO<sub>2</sub> efflux at these locations. Decomposition and thus sediment CO<sub>2</sub> efflux rates are controlled not only by the amount of C and N but also by the quality of the substrate and activity of the decomposer community (Kristensen, 2000). As C quality was not measured in this study, it remains unknown whether the observed positive correlation between sediment organic C concentration and sediment CO<sub>2</sub> efflux is driven by C quality or quantity.

High clay content and sediment organic C concentration characterised the high-efflux sites. Spatial covariation of clay and organic C has been found in terrestrial soils (Davidson, 1995) but also applies to coastal sediments (Hu et al., 2006). For example, both clay and organic C settle out on the sediment surface in areas where there is low current velocity. Clay content has been shown to be associated with higher CO<sub>2</sub> efflux in tropical mangrove forests (Leopold et al., 2013; Chen et al., 2010; Chen et al., 2012; Chen et al., 2014).

The mangrove clearance process typically includes considerable sediment disturbance, particularly when mechanical diggers are used (Lundquist et al., 2014a). The tracking and raking of the sediment creates areas where deeper anoxic sediment is brought to the surface (personal observation, 2015). Elsewhere, increased sediment CO<sub>2</sub> efflux has been observed within intact mangrove forests following disturbance of the top 30 cm of the sediment; however, the effect was transitory, returning to pre-disturbed levels within 2 days (Lovelock et al., 2011).

Hydrodynamic conditions and the area and shape of clearings may also influence CO<sub>2</sub> efflux as these factors influence site recovery. For example, smaller more exposed cleared sites at the edge of mangrove forests may transition towards tidal flat characteristics (i.e. coarser sediment grain size, lower organic C and chlorophyll *a* concentration) than larger, less exposed sites where limited sediment mobilisation occurs (Lundquist et al., 2014b). Higher sediment organic C concentrations have been measured in mangroves located further inland compared to areas at the seaward edge (Lovelock et al., 2010; Yang et al., 2013).

#### 4.3 Sediment CO<sub>2</sub> uptake

Sediment CO<sub>2</sub> uptake (negative flux) was observed at one intact (Hatea 1) and three cleared (Tairua 3, Whangamata 1, Hatea 1) mangrove forest sites. CO<sub>2</sub> uptake has also been reported in other mangrove CO<sub>2</sub> flux studies (Lovelock, 2008; Leopold et al., 2015; Lovelock et al., 2014). CO<sub>2</sub> uptake has been explained by the presence of autotrophic biofilm com-

munities, as net CO<sub>2</sub> uptake changed to net CO<sub>2</sub> loss through efflux following biofilm removal (Leopold et al., 2015).

Autotrophic biofilm communities have been shown to be significant contributors to CO<sub>2</sub> uptake and thus benthic primary productivity (Oakes and Eyre, 2014; Kristensen and Alongi, 2006; Bouillon et al., 2008). CO<sub>2</sub> uptake may occur at the onset of dark measurements as photosynthetic activity by autotrophic biofilm communities continues until coenzymes are depleted (NADPH, ATP; Leopold et al., 2015). Due to the short duration of our measurements (90 s) the proportion of CO<sub>2</sub> uptake versus loss may be higher compared to studies where the dark chamber is left in place for longer. However, the results from our shading experiment suggest that this was not the case, as we did not see significantly higher sediment CO<sub>2</sub> efflux rates after pre-shading compared to control. We note that spatial variation in sediment CO<sub>2</sub> efflux may partly explain the lack of a pre-shading effect. A higher number of replicates may have resulted in significant differences in CO<sub>2</sub> efflux between control and shaded locations. However, even with a significant difference we cannot rule out that higher sediment CO<sub>2</sub> efflux in the shaded treatment was due to other factors associated with the shade structure such as differences in sediment temperature, moisture, or the behaviour of shaded fauna. Further, our shading experiment was restricted to an intact mangrove forest site. A study by Granek and Ruttenberg (2008) investigating the effect of mangrove clearing on abiotic and biotic factors in Panama showed that cleared mangrove sediments are exposed to higher light levels. Thus the activity and the response of photosynthesising biofilm communities to pre-shading may differ in cleared mangrove forests.

Other processes for CO<sub>2</sub> uptake include drawdown of CO<sub>2</sub> into the sediment during large ebbing or very low tides (Krauss and Whitbeck, 2012). In terrestrial shrub ecosystems, sediment CO<sub>2</sub> uptake has been attributed to sediment effusion–dissolution processes driven by sediment pH and moisture (Ma et al., 2013). Chemoautotrophs have also been shown to fix C in intertidal sediment under dark conditions (Boschker et al., 2014; Lenk et al., 2011) and may contribute to the decrease in CO<sub>2</sub> concentration measured in the dark chamber, in particular at the interface of aerobic and anaerobic zones, where large amounts of reduced compounds, such as sulfur, accumulate (Santoro et al., 2013; Boschker et al., 2014; Thomsen and Kristensen, 1997; Lenk et al., 2011). This is consistent with what is observed in mangrove sediments, where aerobic to anaerobic transitions typically occur close to the sediment surface, with sulfur-driven processes likely to dominate in anaerobic conditions (Kristensen et al., 2008).

#### 4.4 Biofilm removal

Sediment CO<sub>2</sub> efflux was consistently higher across both intact and cleared mangrove sites following the removal of the top 2 mm of sediment. Other studies have suggested that the

surface biofilm may act as a barrier to the flow of CO<sub>2</sub> from deeper sediment, which when removed results in a rapid increase in CO<sub>2</sub> efflux (Leopold et al., 2015; Leopold et al., 2013). It is also possible that the increase in CO<sub>2</sub> efflux following biofilm removal is related to the modification of sediment profiles, changing the oxygen distribution and anoxic–oxic interface, and resulting in increasing diffusion gradients (Kristensen, 2000). Our findings demonstrate that relatively small disturbances to the sediment column such as biofilm removal have significant impacts on sediment CO<sub>2</sub> efflux. This illustrates the complexity of processes influencing sediment CO<sub>2</sub> efflux in coastal wetlands and generates further questions (for example, what is the duration of this effect, does the magnitude of the effect change depending on the clearance method, and what effect does wind or wave disturbance have on efflux rates?).

## 5 Conclusions

Rates of mangrove clearing are increasing in temperate forests, and the impacts on C cycling and sediment properties are of potential environmental concern. This is the first study investigating the effect of clearing on sediment CO<sub>2</sub> efflux in temperate *Avicennia marina* forests grown on mineral sediments. We found that rates of sediment CO<sub>2</sub> efflux from cleared and intact temperate *Avicennia marina* forests are comparable to rates observed in other temperate and tropical forests. No significant differences were found in sediment CO<sub>2</sub> efflux between cleared and intact mangrove forests due to high spatial variability in sediment characteristics and environmental factors. However, mangrove forest clearing resulted in a long-term modification of the sediment carbon cycle. Our results show that greater consideration should be given regarding the rate of carbon released from mangrove forest following clearance and the relative contribution to global carbon emissions.

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