

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

3

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## 9 Abstract

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

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

31

32 **Keywords:** *Avicennia marina*, biofilm, chlorophyll  $\alpha$ , mangrove biomass, pre-shading,  
33 sediment organic carbon, New Zealand

34

## 35 **1. Introduction**

36 Mangroves are generally confined to the tropics, between latitudes 30°N and 30°S. However,  
37 approximately 1.4% of the global mangrove forests are located outside this latitudinal range,  
38 growing in conditions which may be broadly characterised as temperate (Morrisey et al.,  
39 2010). Temperate mangrove forests mainly occur in Australia, New Zealand, the United  
40 States of America and South Africa (Morrisey et al., 2010; Giri et al., 2011). These forests  
41 are subject to colder and generally more variable climatic conditions, and are typically  
42 associated with lower diversity of tree species and lower faunal abundance and diversity than  
43 in the tropics (Alfaro, 2006; Morrisey et al., 2010). However, little is known about sediment  
44 properties and the factors driving the storage and exchange of carbon (C) in temperate  
45 mangrove sediments (Livesley and Andrusiak, 2012).

46 Temperate mangrove forest cover has increased significantly over the last 50-60 years  
47 (Morrisey et al., 2010; Saintilan et al., 2014). A landward expansion of mangroves into salt  
48 marsh has been observed in Australia and the USA (Cavanaugh et al., 2014; Saintilan et al.,  
49 2014) while mangrove expansion into tidal flats is typically observed in New Zealand (Stokes  
50 et al., 2009; Lundquist et al., 2014b). The expansion of mangroves in New Zealand has been  
51 linked to increased sedimentation leading to vertical accretion of tidal flats (Swales et al.,  
52 2007; Stokes, 2010), increased nutrient inputs (Lovelock et al., 2007), and climatic factors  
53 (Burns and Ogden, 1985).

54 The recent expansion of temperate mangrove forests has led to a push towards mangrove  
55 removal in New Zealand, largely from local communities concerned about the loss of  
56 diversity of estuarine habitats caused by mangrove expansion, or for human amenities such as  
57 recreational access and water views (Harty, 2009). Numerous legal and illegal mangrove  
58 clearings have occurred in recent decades, ranging in scale from < 0.1 to > 100 ha (Morrisey  
59 et al., 2010; Lundquist et al., 2014b).

60 Carbon cycling and storage are important ecosystem services provided by mangrove forests  
61 (Twilley et al., 1992; Bouillon et al., 2008; Kristensen et al., 2008; Alongi, 2014). The global  
62 net primary productivity in mangrove forests has been estimated at  $218 \pm 72 \text{ Tg C a}^{-1}$ , which  
63 includes the rate of litterfall and above- and below-ground biomass production (Bouillon et  
64 al., 2008). An important component of the C cycle is the efflux of carbon dioxide (CO<sub>2</sub>) from  
65 the sediment into the atmosphere (Raich and Schlesinger, 1992). Sediment CO<sub>2</sub> efflux (also  
66 called soil/sediment respiration) is the total of CO<sub>2</sub> released through root/mycorrhizae

67 respiration (autotrophic respiration) and microbial respiration (heterotrophic respiration)  
68 associated with the decomposition of organic matter (Bouillon et al., 2008). Quantifying C  
69 emissions and understanding the factors influencing C storage and exchange has become  
70 increasingly important due to the rapid rise in atmospheric CO<sub>2</sub> concentrations and associated  
71 impact on global climate (IPCC, 2013).

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

80 Studies from tropical mangrove forests have shown that sediment CO<sub>2</sub> efflux is influenced by  
81 abiotic and biotic sediment characteristics including sediment C and nutrient quantity and  
82 quality (Kristensen, 2000), sediment grain size (Chen et al., 2010), redox potential (Chen et  
83 al., 2010; Chen et al., 2012; Leopold et al., 2013), sediment water content (Alongi, 2009) and  
84 sediment temperature (Chen et al., 2012). A study by Lovelock (2008) on temperate and  
85 tropical mangrove forests reported a positive correlation between leaf area index and  
86 sediment CO<sub>2</sub> efflux. Further, biofilm communities, which are present on the sediment  
87 surface, may play an important role in mediating CO<sub>2</sub> flux from the sediment (Alongi et al.,  
88 2012; Leopold et al., 2013; Leopold et al., 2015). Biofilm communities include a wide variety  
89 of diatoms, bacteria, fungi, and microfauna (Decho, 2000). The autotrophic biofilm  
90 communities contribute significantly to the primary productivity in estuarine ecosystems and  
91 supply energy to biofilm and other primary and secondary consumers, whereas the  
92 heterotrophic biofilm communities mineralize organic matter (Van Colen et al., 2014).

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

## 100 **2. Materials and methods**

### 101 **2.1 Study species**

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

### 108 **2.2 Study area and selection of study sites**

109 This study was conducted at 23 sites covering a large proportion of the geographic range of  
110 mangroves (35°43' S to 37° 41' S) in New Zealand (Figure 1). We investigated cleared (n =  
111 23) and, where possible, adjacent intact mangrove forest sites (n = 13). The time since  
112 mangrove removal ranged from 1 month to over 8 years. Cleared mangrove sites ranged in  
113 size from < 0.1 ha to > 13 ha. Besides the difference in size and time since clearing, the sites  
114 differed in shape of cleared area, hydrodynamic conditions (sheltered: protected from direct  
115 wind and wave action, generally located in the upper reaches of the estuary; exposed:  
116 exposed to wind and wave action, generally located in the lower reaches of the estuary), and  
117 method of mangrove removal (Supplementary table 1). Mean air temperature ranges from  
118 19°C during summer to 11°C during winter. Mean monthly rainfall varies from 77 to 152  
119 mm, respectively (NIWA, 2014). Tides for the sites are semi diurnal with a range of 1.3 – 4.1  
120 m (LINZ, 2014).

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

### 125 **2.3 Sediment CO<sub>2</sub> efflux measurements**

#### 126 **2.3.1 Pre-shading the sediment**

127 The effect of pre-shading the sediment prior to dark chamber measurements was investigated  
128 at site Hatea 1. Three frames (0.5 m<sup>2</sup>) were deployed throughout the mangrove forest, at least  
129 10 m from each other and the mangrove edge. Frames were located approximately 20 cm  
130 above the sediment surface. The frame was completely covered by layered cloth to exclude  
131 light penetration. After 30 minutes of shading, two CO<sub>2</sub> efflux measurements using a dark

132 respiration chamber were conducted at different locations within the 0.5 m<sup>2</sup> area, before and  
133 after the removal of the surface biofilm. The biofilm (top ~2 mm of surface sediment) was  
134 scraped off using a spatula. Biofilm **removal** measurements were collected immediately  
135 following biofilm intact measurements in the identical location. Corresponding dark CO<sub>2</sub>  
136 efflux measurements were also conducted at locations that had not been pre-shaded (control)  
137 adjacent to each shaded measurement, as well as corresponding biofilm **removal**  
138 measurements to account for heterogeneity in sediment conditions.

### 139 2.3.2 Sediment CO<sub>2</sub> efflux from intact and cleared temperate mangrove

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

143 The sediment CO<sub>2</sub> efflux was measured at low tide, between 8 am and 6 pm local time, using  
144 an infrared CO<sub>2</sub> analyser (Environmental Gas Monitor (EGM-4) with a dark sediment  
145 respiration chamber (SRC-1, PP Systems Ltd., Amesbury, MA, USA). Using a dark chamber  
146 prevents the photosynthetic activity of biofilm communities which results in the uptake of  
147 CO<sub>2</sub>. A PVC collar (10 cm height) was attached to the base of the respiration chamber to  
148 protect the chamber from potential flooding. The collar was inserted approximately 5 mm  
149 into the sediment, avoiding damage to surface roots. Sediment within the chamber included  
150 crab burrows and pneumatophores < 7 cm which fit within the respiration chamber. The  
151 sediment area covered by each chamber was 0.00785 m<sup>2</sup>. Chamber height was measured  
152 during each measurement as collar insertion varied based on sediment characteristics. Total  
153 chamber volume varied between 1.72 and 1.98 l depending on the depth of collar insertion.  
154 The CO<sub>2</sub> concentration in the chamber was measured at 5 second intervals over a 90 second  
155 period. Air and sediment temperature (Novel Ways temperature probe) and moisture (CS620,  
156 Campbell Scientific, Logan, UT, USA) at a depth of 12 cm was measured with each CO<sub>2</sub>  
157 efflux measurement.

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

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

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

164 
$$\text{Sediment CO}_2 \text{ efflux} = (\Delta\text{CO}_2 / \Delta t) \times ((P \times V) / (R \times T) / A) \quad (1)$$

165 Where  $\Delta\text{CO}_2/\Delta t$  is the change in  $\text{CO}_2$  concentration over time, based on the slope of the linear  
166 regression ( $\mu\text{mol mol}^{-1} \text{ s}^{-1} = \text{ppm s}^{-1}$ ),  $t$  is time (s),  $P$  is the atmospheric pressure (mbar),  $V$  is  
167 the volume of the chamber including collar (L),  $A$  is the surface area covered by each  
168 chamber ( $\text{m}^2$ ),  $T$  is the temperature (K),  $R$  is the ideal gas constant ( $83.144621 \text{ L mbar}$   
169  $\text{K}^{-1} \text{ mol}^{-1}$ ). Daily sediment  $\text{CO}_2$  efflux ( $\text{mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ ) were estimated by multiplying the  
170 measured efflux rates, assuming constant efflux rates.

171

## 172 **2.4 Sediment characteristics**

173 At each site three sediment samples, next to the location of the sediment  $\text{CO}_2$  efflux  
174 measurements, were collected using two small sediment cores (2 cm deep, 2 cm in diameter).  
175 After collection the samples were immediately frozen and stored in the dark before analysis.

176 *Sediment carbon and nitrogen concentration:* Samples were dried ( $60^\circ\text{C}$  for 48 hours) and  
177 then pulverised using mortar and pestle. Total carbon (C and nitrogen (N) concentration was  
178 determined using an elemental analyser (TruSpec LECO CNS, Leco Corporation, St. Joseph,  
179 MI). A subset of samples (14% of samples, ranging from 0.17 to 12.63% total C) were  
180 acidified to remove the inorganic C (Brodie et al., 2011). Briefly, 300 mg sediment was  
181 mixed with 0.5 ml distilled water and 1.5 ml of 20% HCl and then dried on a hot plate at  
182  $60^\circ\text{C}$ . Organic C concentration was then determined using the elemental analyser. A linear  
183 regression function between total C and organic C ( $r^2 = 0.98$ ,  $p < 0.001$ ) was used to calculate  
184 organic C concentrations of non-treated samples.

185 *Grain size:* One sediment sample per site was analysed for grain size. The samples were  
186 homogenised and a subsample of approximately 5 g of sediment was taken and digested in ~  
187 9% hydrogen peroxide until bubbling ceased (Day, 1965). The sediment sample was then wet  
188 sieved through 2000  $\mu\text{m}$  and 63  $\mu\text{m}$  mesh sieves. Pipette analysis was used to separate the <  
189 63  $\mu\text{m}$  fraction into  $> 3.9 \mu\text{m}$  and  $\leq 3.9 \mu\text{m}$ . All fractions were then dried at  $60^\circ\text{C}$  until a  
190 constant weight was achieved (fractions were weighed at ~ 40 h and then again at 48 h).  
191 Grain size fractions were calculated as percentage weight of gravel/shell hash ( $>2000 \mu\text{m}$ ),  
192 sand (63 – 2000  $\mu\text{m}$ ), silt (3.9 – 62.9  $\mu\text{m}$ ) and clay ( $\leq 3.9 \mu\text{m}$ ).

193 *Chlorophyll  $\alpha$ :* One sediment sample per site was analysed for chlorophyll  $\alpha$ . The samples  
194 were freeze dried within a month of sampling, weighed, then homogenised and a subsample  
195 (~5 g) was taken for extraction. Chlorophyll  $\alpha$  was extracted by boiling the sediment in 90%

196 ethanol. The absorption of the extract was measured at 665 and 750 nm using a  
197 spectrophotometer (Spectrophotometer UV-1800, Shimadzu, Kyoto, Japan). Immediately  
198 after the absorbance reading 0.05 mL 1 mol HCl were added to separate degradation products  
199 from chlorophyll  $\alpha$ . The absorption of the acidified extract was re-measured after 30 seconds  
200 (Hansson, 1988; Moed and Hallegraeff, 1978). Chlorophyll  $\alpha$  concentration was calculated  
201 based on the following equation:

$$202 \text{ Chlorophyll } \alpha \text{ (}\mu\text{g g}^{-1} \text{ sediment)} = ((750a - 665a) - (750 - 665) \times \text{Abs} \times (\text{ethanol in extraction} \\ 203 \text{ (l)/Sediment analysed (}\mu\text{g)})) \quad (2)$$

204 Where 750 and 665 are the absorptions at wavelengths 750 and 665 nm, 750a and 665a are  
205 the absorptions at wavelengths 750 and 665 nm after acidification, and Abs is the absorbance  
206 correction factor for chlorophyll  $\alpha$  in ethanol (28.66)

### 207 **2.5 Tree and root biomass**

208 Within intact mangrove forests the tree height of the closest 5 mangrove trees to each  
209 measurement/sampling point and the density (number of mangroves within a 2 m x 2 m area)  
210 was recorded. Above-ground biomass was estimated using the allometric equations  
211 developed for *Avicennia marina* in New Zealand (Woodroffe, 1985):

$$212 \text{ Total above-ground biomass}^{-1/3} \text{ (g dry weight)} = -4.215 + 0.121 \times \text{Height (cm)} \quad (3)$$

213 At two sites, Mangere 1 (Auckland) and Hatea 1 (Northland) mangrove height exceeded the  
214 range the allometric equation was designed for (determined from trees ranging in height from  
215 40 to 248 cm). Here, trunk diameter (at 30 cm height) of the closest 5 mangrove trees to each  
216 sampling point was used to estimate biomass **for all trees** at Mangere 1 and Hatea 1:

$$217 \text{ Total above-ground biomass}^{-1/3} \text{ (g dry weight)} = 0.264 + 2.597 \times \text{Diameter (cm)} \quad (4)$$

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



227 **2.6 Data analysis**

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

231 Data were tested for normality using the Shapiro-Wilk test. The Mann-Whitney Rank Sum  
232 Test was used to determine differences in sediment CO<sub>2</sub> efflux and other site characterises  
233 between shaded and control measurements and between intact and cleared mangrove sites as  
234 data did not conform to normality.

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

242 Statistical analyses were conducted using SigmaPlot Version 12.5 (Systat Software Inc., San  
243 Jose, CA, USA) and SPSS statistics software version 17 (SPSS Inc. Chicago, IL, USA).

244

245 **3. Results**

246 *Shading experiment*

247 No significant difference was detected in mean CO<sub>2</sub> efflux between shaded ( $103.6 \pm 17.8$   
248  $\text{mmol m}^{-2} \text{d}^{-1}$ ) and control ( $51.1 \pm 5.5 \text{ mmol m}^{-2} \text{d}^{-1}$ ) treatments ( $p > 0.05$ ) (Figure 2).

249 Removing the surface biofilm resulted in significantly higher CO<sub>2</sub> efflux for both shaded  
250 ( $391.5 \pm 53.1 \text{ mmol m}^{-2} \text{d}^{-1}$ ) and control ( $278.0 \pm 29.9 \text{ mmol m}^{-2} \text{d}^{-1}$ ) treatments ( $p < 0.01$ )  
251 (Figure 2).

252 *Sediment CO<sub>2</sub> efflux and sediment characteristics from intact and cleared mangrove forest*  
253 *sites*

254 No significant difference in sediment CO<sub>2</sub> efflux was found between intact ( $168.5 \pm 45.8$   
255  $\text{mmol m}^{-2} \text{d}^{-1}$ ,  $n = 13$ ) and cleared mangrove ( $133.9 \pm 37.2 \text{ mmol m}^{-2} \text{d}^{-1}$ ,  $n = 23$ ) sites ( $p >$   
256  $0.05$ ) (Figure 3). Removing the surface biofilm resulted in significantly higher CO<sub>2</sub> efflux at  
257 intact (2.34 fold increase) and cleared (1.66 fold increase) mangrove forest sites ( $p < 0.01$ )  
258 (Figure 3).

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

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

267 Individual sites were grouped based on whether CO<sub>2</sub> efflux exceeded ('high efflux group') or  
268 was below ('low efflux group') the mean CO<sub>2</sub> efflux rate for intact mangrove forests ( $168.5 \pm$   
269  $45.8 \text{ mmol m}^{-2} \text{d}^{-1}$ ), to determine whether site characteristics were significantly different  
270 between high and low efflux groups. Mean sediment CO<sub>2</sub> efflux of the 'high efflux group'  
271 (Matua, Tairua 2, Uretara 1, Waikareao, and Welcome Bay 1) was  $310.8 \pm 80.7 \text{ mmol m}^{-2} \text{d}^{-1}$   
272  $\text{d}^{-1}$ , significantly higher ( $p < 0.05$ ) than  $80.1 \pm 23.4 \text{ mmol m}^{-2} \text{d}^{-1}$  measured in the 'low efflux  
273 group'. Chlorophyll  $\alpha$  concentration was significantly higher in the 'high efflux group' ( $53.3$   
274  $\pm 7.0 \mu\text{g}^{-1} \text{g}^{-1}$  sediment) than in the 'low efflux group' ( $26.6 \pm 7.0 \mu\text{g}^{-1} \text{g}^{-1}$  sediment) ( $p <$   
275  $0.05$ ). In addition, sediment temperature ( $^{\circ}\text{C}$ ) was significantly higher in the 'high efflux

276 group' ( $21.3 \pm 1.0$ ) than in the 'low efflux group' ( $17.9 \pm 0.8$ ) ( $p < 0.05$ ) (Supplementary  
277 table 2).

278 Similarly, cleared mangrove sites were grouped based on whether CO<sub>2</sub> efflux exceeded  
279 ('high efflux group') or was below ('low efflux group') the mean CO<sub>2</sub> efflux rate for cleared  
280 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'  
281 (Mangere 1, Pahurehure 4, Waiuku 1, 2 and 3, Welcome Bay 1, Whangamata E) was  $338.0 \pm$   
282  $71.3 \text{ mmol m}^{-2} \text{ d}^{-1}$ , significantly higher ( $p < 0.05$ ) than  $45.2 \pm 18.3 \text{ mmol m}^{-2} \text{ d}^{-1}$  measured in  
283 the 'low efflux group'. Sediment organic C concentration ( $4.2 \pm 0.8\%$  vs.  $2.1 \pm 0.4\%$ ), N  
284 concentration ( $0.5 \pm 0.1\%$  vs.  $0.3 \pm 0.1\%$ ), sediment sand content ( $15.5 \pm 9.9\%$  vs.  $43.0 \pm$   
285  $8.0\%$ ), and sediment clay content ( $28.2 \pm 4.3\%$  vs.  $15.1 \pm 2.6\%$ ) were significantly higher in  
286 the 'high efflux group' than in the 'low efflux group' for cleared mangrove forest sites ( $p <$   
287  $0.05$ ) (Supplementary table 3).

#### 288 *Regression analysis*

289 Backward multiple linear regression analysis revealed that mangrove biomass was the only  
290 significant predictor of sediment CO<sub>2</sub> efflux within intact mangrove forest sites ( $r^2 = 0.49$ ,  $F$   
291  $= 9.43$ ,  $p = 0.01$ ) (Figure 3.A). Within the cleared sites, backward multiple linear regression  
292 analysis revealed that sediment organic C concentration was the only significant predictor of  
293 CO<sub>2</sub> efflux ( $r^2 = 0.32$ ,  $F = 9.23$ ,  $p < 0.01$ ) (Figure 3.B). No other significant relationships  
294 were observed ( $p > 0.05$  for individual coefficients).

295

## 296 4. Discussion

### 297 4.1 Sediment CO<sub>2</sub> efflux and sediment characteristics from intact temperate mangrove 298 forest

299 The magnitude of dark sediment CO<sub>2</sub> efflux in intact *Avicennia marina* forests measured in  
300 this study ( $168.5 \pm 45.8 \text{ mmol m}^{-2} \text{ d}^{-1}$ ) is similar to values reported for intact *Avicennia*  
301 *marina* forests in New Zealand (Lovelock, 2008; Lovelock et al., 2014), Australia (Livesley  
302 and Andrusiak, 2012) and tropical locations (New Caledonia: Leopold et al. (2013), 2015)  
303 (Table 2). However, our values are higher than the global estimates of sediment CO<sub>2</sub> efflux  
304 from intact tropical mangrove forests ( $75 \text{ mmol m}^{-2} \text{ d}^{-1}$ , Kristensen et al., 2008;  $61 \pm 56 \text{ mmol}$   
305  $\text{m}^{-2} \text{ d}^{-1}$ , Bouillon et al., 2008;  $69 \pm 8 \text{ mmol m}^{-2} \text{ d}^{-1}$ , Alongi, 2014; Table 2). The differences in  
306 CO<sub>2</sub> efflux may be related to the methods applied. The global estimates were primarily  
307 determined in the laboratory by incubating sediment cores extracted from the field  
308 (Kristensen et al., 2008). CO<sub>2</sub> efflux is generally lower in these studies than that observed in  
309 studies using chamber based techniques where CO<sub>2</sub> is measured continuously over a short  
310 period of time in the field (this study; Lovelock, 2008; Lovelock et al., 2014; Livesley and  
311 Andrusiak, 2012; Leopold et al., 2013; Leopold et al., 2015). Higher sediment CO<sub>2</sub> efflux  
312 observed in our study may also be explained by the inclusion of crab burrows and short  
313 pneumatophores in the flux measurements. The omission of crab burrows and  
314 pneumatophores has previously been proposed as a potential explanation of why global  
315 estimates may be underestimated (Bouillon et al., 2008). Crab burrows have been shown to  
316 increase CO<sub>2</sub> efflux by increasing the surface area for sediment-air exchange of CO<sub>2</sub>  
317 (Kristensen et al., 2008) and enhancing organic matter decomposition (Pülmanns et al.,  
318 2014). Pneumatophores have been associated with increased CO<sub>2</sub> emissions by efficient  
319 translocation of CO<sub>2</sub> exchange from deeper sediments (Bouillon et al., 2008; Kristensen et  
320 al., 2008).

321 Sediment organic C concentrations in the intact mangrove sites ( $3.6 \pm 0.7\%$ ) are comparable  
322 to the sediment organic C concentration measured in mangrove forests in New Zealand  
323 (Auckland, Yang et al., 2013; Firth of Thames, Lovelock et al., 2010) and *Avicennia marina*  
324 forests south of Melbourne, Australia (Livesley and Andrusiak, 2012). The mean sediment  
325 organic C concentration in mangrove sediments collected across the globe is 2.2%  
326 (Kristensen et al., 2008). The main sources of organic C in intact mangrove sediments are  
327 litter and root material and suspended matter from other terrestrial and estuarine sources

328 (Bouillon et al., 2003). The relative contribution of each source has been shown to vary  
329 considerably depending on site characteristics and histories (Bouillon et al., 2003).

330 The above-ground biomass across the investigated *Avicennia marina* forests (5 - 135 t dry  
331 weight ha<sup>-1</sup>) is lower than the above-ground biomass in many tropical mangrove forests (35 -  
332 400 t dry weight ha<sup>-1</sup>). This is in line with previous findings reporting a decrease in mangrove  
333 biomass with increasing latitude (Saenger and Snedaker, 1993; Komiyama et al., 2008). We  
334 found a negative relationship between mangrove above-ground biomass and sediment CO<sub>2</sub>  
335 efflux across the 13 intact mangrove forests. Lower tree biomass associated with lower forest  
336 cover may result in increased light availability and sediment temperature (Lovelock, 2008).  
337 Higher sediment temperature may in turn lead to a higher abundance and activity of the  
338 sediment microbial decomposer community (Zogg et al., 1997) and higher sediment CO<sub>2</sub>  
339 efflux.

340 Respiration from heterotrophic biofilm communities also contribute a considerable  
341 proportion to total CO<sub>2</sub> efflux from mangrove sediments, as shown in a New Caledonian  
342 *Avicennia marina* forest (Leopold et al., 2013). High sediment chlorophyll  $\alpha$  concentrations  
343 and the presence of algal mats characterising the intact ‘high efflux sites’ suggests that  
344 respiration by heterotrophic biofilm communities may be a significant contributor to CO<sub>2</sub>  
345 efflux (Decho, 2000). Further, higher sediment temperature resulting in higher sediment CO<sub>2</sub>  
346 efflux in the ‘high efflux sites’ is in line with findings from other mangrove forests (e.g.  
347 Leopold et al., 2015) and many terrestrial systems (e.g. Davidson and Janssens, 2006). Soil  
348 temperature is one of the key abiotic factors influencing both the autotrophic and  
349 heterotrophic activity (Raich and Schlesinger, 1992).

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

#### 358 *4.2 Sediment CO<sub>2</sub> efflux and sediment characteristics of cleared mangrove forest*

359 Our results show that dark sediment CO<sub>2</sub> efflux rates from cleared *Avicennia marina* forests  
360 ( $133.9 \pm 37.2$  mmol CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>) are similar to sediment CO<sub>2</sub> efflux following mangrove  
361 clearing in the tropics (Lovelock et al., 2011; Sidik and Lovelock, 2013; Lang'at et al., 2014).  
362 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  
363 clearing) were measured in cleared peat mangrove forests in Belize, Central America  
364 (Lovelock et al., 2011). The mangroves in New Zealand grow on mineral sediments which  
365 may explain lower CO<sub>2</sub> emissions compared to the Belize study where mangroves are  
366 growing on carbon rich peat soils (Lovelock, 2008).

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

377 Sediment CO<sub>2</sub> efflux in cleared sites was positively related to sediment organic C  
378 concentration. This was also observed following the clearing of peat mangroves in Belize,  
379 where the rate of CO<sub>2</sub> efflux was related to the microbial degradation of organic matter in the  
380 sediments (Lovelock et al., 2011). While no significant regression coefficient was found  
381 between CO<sub>2</sub> efflux and mangrove root biomass in our study, increased CO<sub>2</sub> efflux following  
382 mangrove clearing has previously been attributed to the rapid decomposition of fine root  
383 material related to increased sediment temperatures following the loss of canopy cover  
384 (Lang'at et al., 2014).

385 The highest sediment CO<sub>2</sub> efflux rates were measured at sites where large areas were cleared  
386 (>1 ha) using mechanical diggers and the tree mulch was left in place. Increased sediment  
387 organic C and N concentrations resulting from the mulch input may explain higher sediment  
388 CO<sub>2</sub> efflux at these locations. Decomposition and thus sediment CO<sub>2</sub> efflux rates are not only  
389 controlled by the amount of C and N but also by the quality of the substrate and activity of  
390 the decomposer community (Kristensen, 2000). As C quality was not measured in this study

391 it remains unknown whether the observed positive correlation between sediment organic C  
392 concentration and sediment CO<sub>2</sub> efflux is driven by C quality or quantity.

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

399 The mangrove clearance process typically includes considerable sediment disturbance,  
400 particularly when mechanical diggers are used (Lundquist et al., 2014b). The tracking and  
401 raking of the sediment creates areas where deeper anoxic sediment is brought to the surface  
402 (*personal observation*). Elsewhere, increased sediment CO<sub>2</sub> efflux has been observed within  
403 intact mangrove forests following disturbance of the top 30 cm of the sediment; however the  
404 effect was transitory, returning to pre disturbed levels within two days (Lovelock et al.,  
405 2011).

406 Hydrodynamic conditions and the area and shape of clearings may also influence CO<sub>2</sub> efflux  
407 as these factors influence site recovery. For example, smaller more exposed cleared sites at  
408 the edge of mangrove forests may transition towards tidal flat characteristics (i.e. coarser  
409 sediment grain size, lower organic C and chlorophyll  $\alpha$  concentration) than larger, less  
410 exposed sites where limited sediment mobilisation occurs (Lundquist et al., 2014a). Higher  
411 sediment organic C concentrations have been measured in older mangrove forests, growing  
412 further inland compared to younger mangrove forests, growing at the expanding seaward  
413 edge (Lovelock et al., 2010).

#### 414 **4.3 Sediment CO<sub>2</sub> uptake**

415 Sediment CO<sub>2</sub> uptake (negative flux) was observed at one intact (Hatea 1) and three cleared  
416 (Tairua 3, Whangamata 1, Hatea 1) mangrove forest sites. CO<sub>2</sub> uptake has also been reported  
417 in other mangrove CO<sub>2</sub> efflux studies (Lovelock, 2008; Leopold et al., 2015; Lovelock et al.,  
418 2014). CO<sub>2</sub> uptake has been explained by the presence of autotrophic biofilm communities,  
419 as net CO<sub>2</sub> uptake changed to net CO<sub>2</sub> loss through efflux following biofilm removal  
420 (Leopold et al., (2015).

421 Autotrophic biofilm communities have been shown to be significant contributors to CO<sub>2</sub>  
422 uptake and thus benthic primary productivity (Oakes and Eyre, 2014; Kristensen and Alongi,

423 2006; Bouillon et al., 2008). CO<sub>2</sub> uptake may occur at the onset of dark measurements as  
424 photosynthetic activity by autotrophic biofilm communities continues until coenzymes are  
425 depleted (NADPH, ATP) (Leopold et al., (2015). Due to the short duration of our  
426 measurements (90 seconds) the proportion of CO<sub>2</sub> uptake versus loss may be higher  
427 compared the studies where the dark chamber is left in place for longer. However, the results  
428 from our shading experiment suggest that this was not the case, as we did not see  
429 significantly higher sediment CO<sub>2</sub> efflux rates after pre-shading compared to control. We  
430 note that spatial variation in sediment CO<sub>2</sub> efflux may partly explain the lack of a pre-shading  
431 effect. Further, our shading experiment was restricted to an intact mangrove forest site. A  
432 study by Granek and Ruttenberg (2008) investigating the effect of mangrove clearing on  
433 abiotic and biotic factors in Panama showed that cleared mangrove sediments are exposed to  
434 higher light levels. Thus the activity and the response of photosynthesising biofilm  
435 communities to pre-shading may differ in cleared mangrove forests.

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

#### 448 ***4.3 Biofilm removal***

449 Sediment CO<sub>2</sub> efflux was consistently higher across both intact and cleared mangrove sites  
450 following the removal of the top 2 mm of sediment. Other studies have suggested that the  
451 surface biofilm may act as a barrier to the flow of CO<sub>2</sub> from deeper sediment, which when  
452 removed results in a rapid increase in CO<sub>2</sub> efflux (Leopold et al., 2015; Leopold et al., 2013).  
453 It is also possible that the increase in CO<sub>2</sub> efflux following biofilm removal is related to the  
454 modification of sediment profiles, changing the oxygen distribution and anoxic/oxic  
455 interface, and resulting in increasing diffusion gradients (Kristensen, 2000). Our findings



456 demonstrate that relatively small disturbances to the sediment column such as biofilm  
457 removal have significant impacts on sediment CO<sub>2</sub> efflux. This illustrates the complexity of  
458 processes influencing sediment CO<sub>2</sub> efflux in coastal wetlands and generates further  
459 questions (for example, what is the duration of this effect? Does the magnitude of the effect  
460 change depending on the clearance method? What effect does wind or wave disturbance have  
461 on efflux rates?).

#### 462 **4.4 Conclusions**

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

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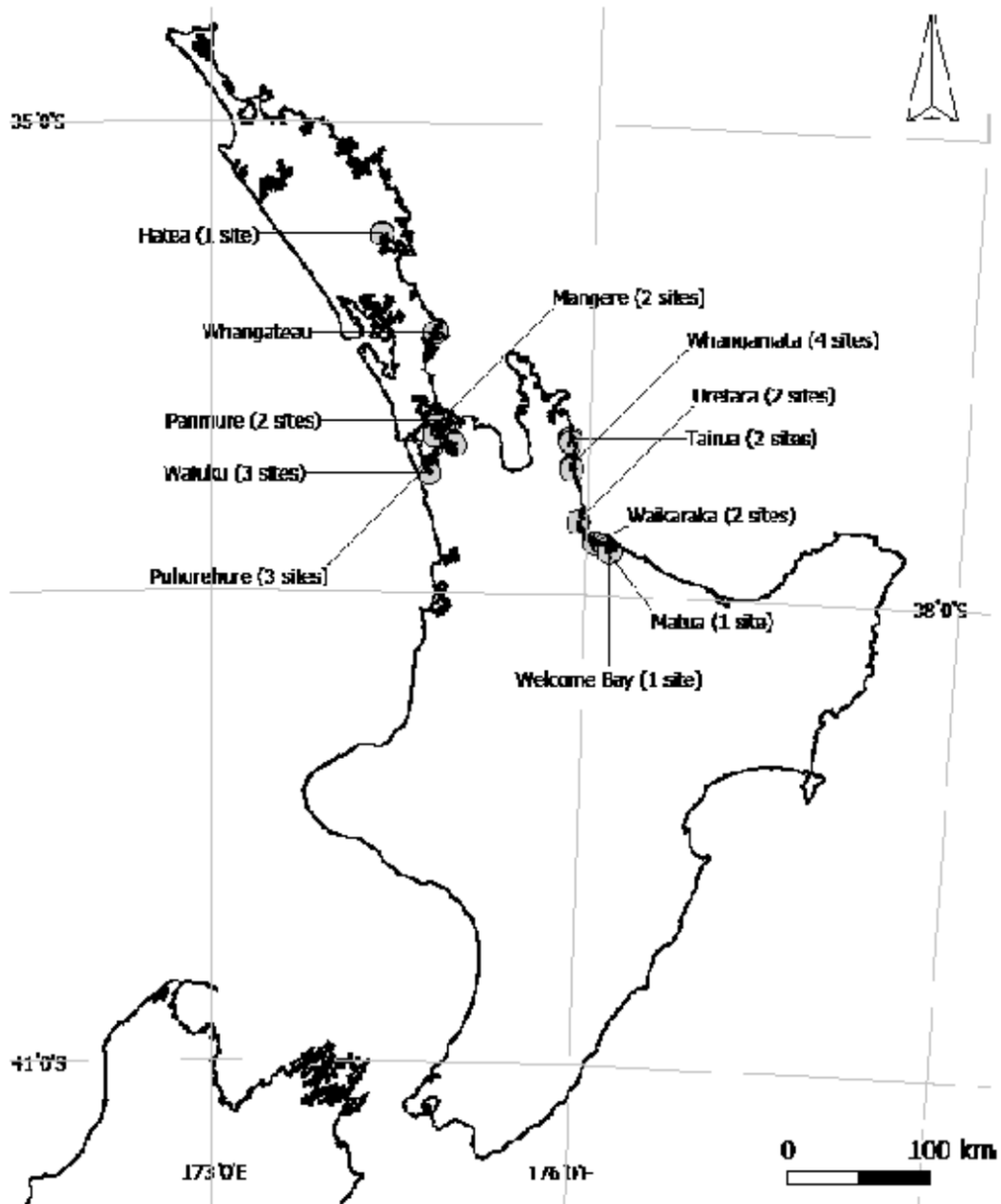
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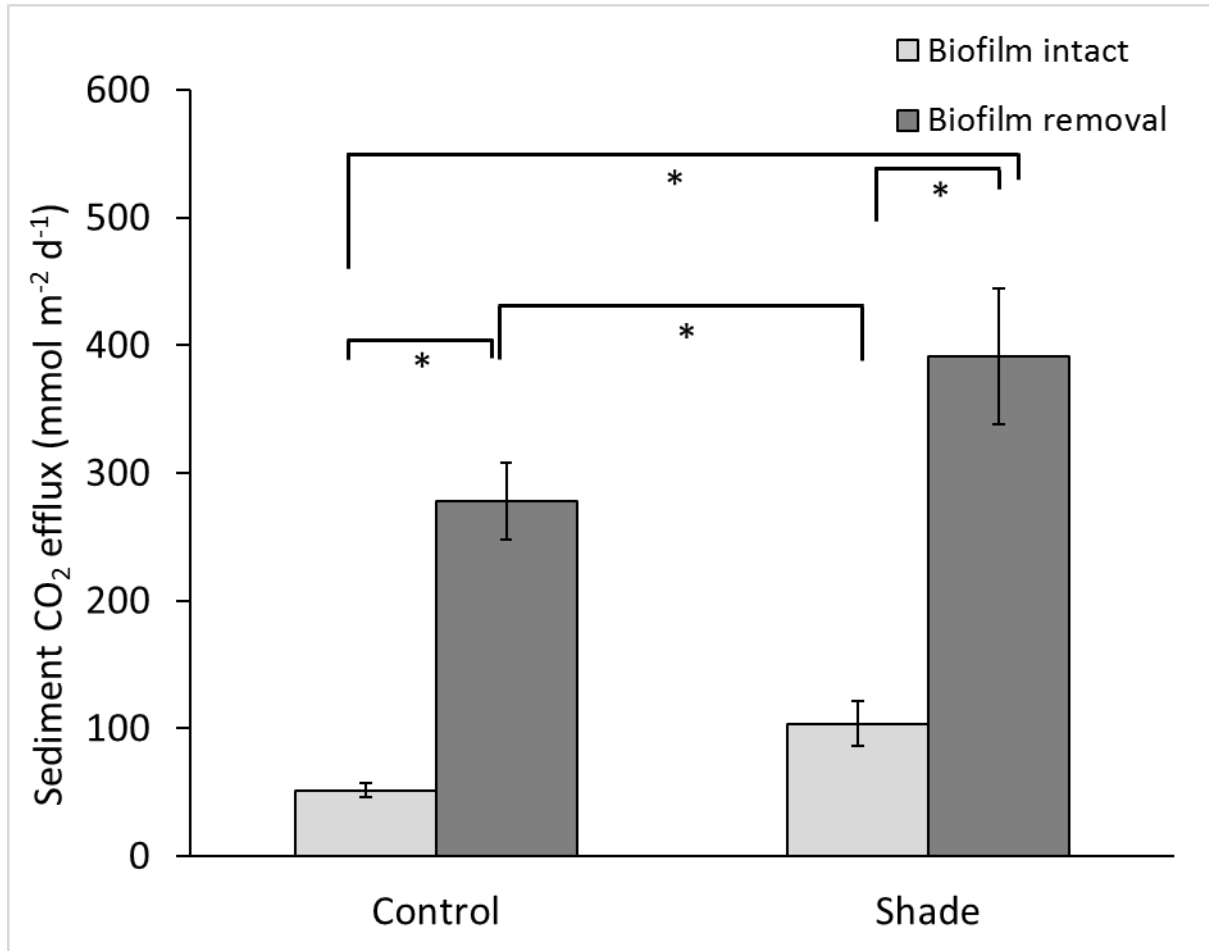
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632 Figure 1: Location of the cleared mangrove sites (•) and estuary locations, throughout North  
633 Island, New Zealand.

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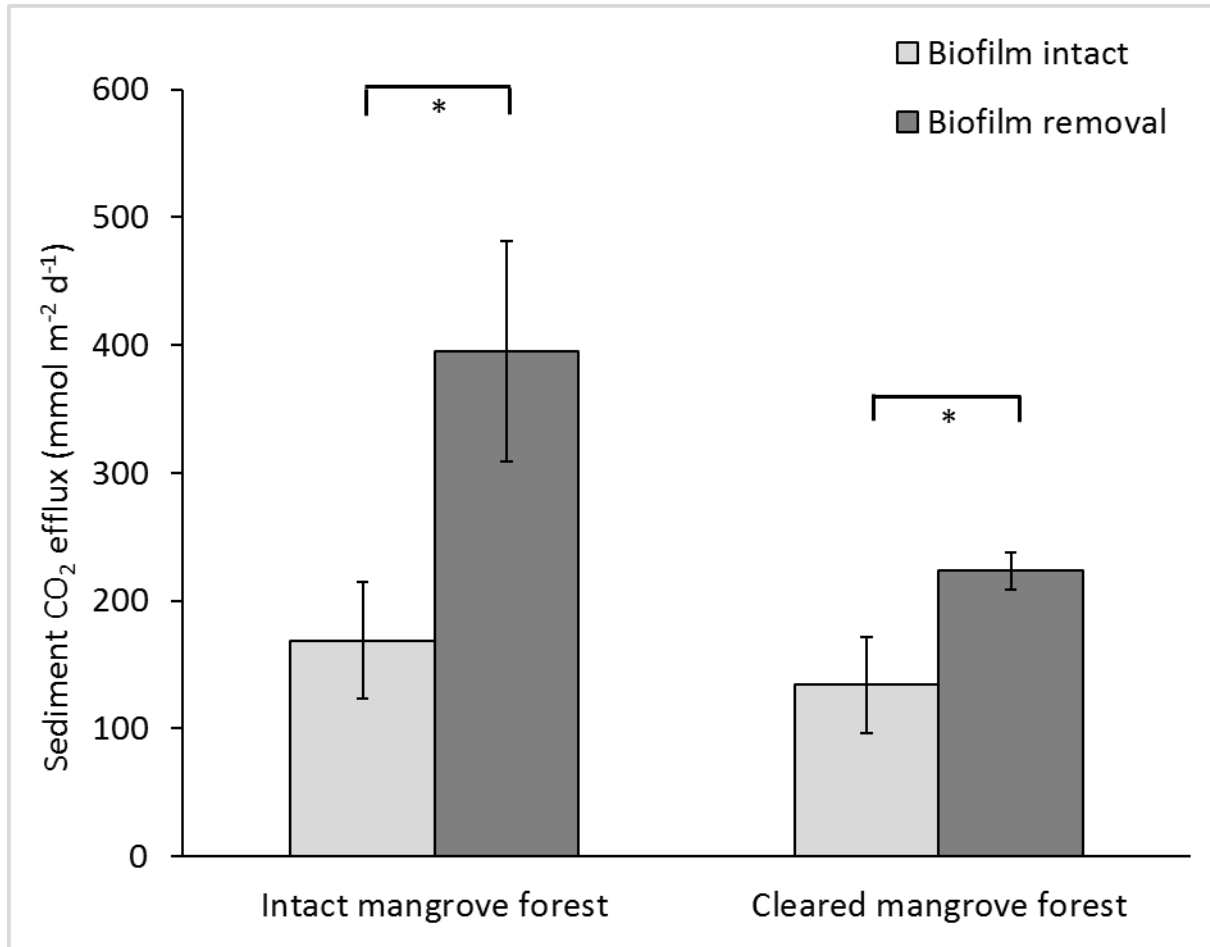
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636 Figure 2: Mean sediment ( $\pm$  SE) CO<sub>2</sub> efflux (mmol m<sup>-2</sup> d<sup>-1</sup>) before and after surface biofilm removal,  
637 from control (n = 6), and pre-shaded sediment (n = 6) at intact mangrove site Hatea 1. \*significant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

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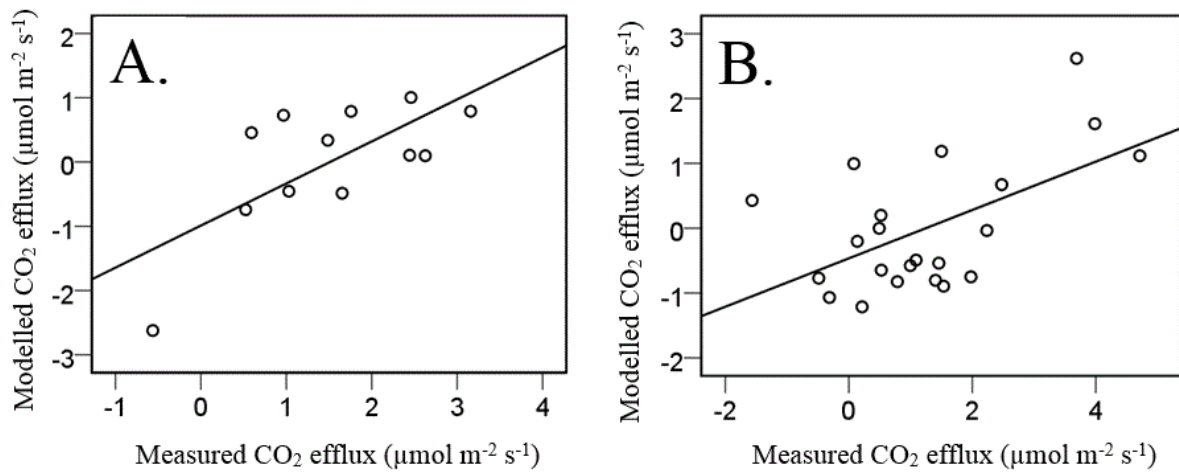
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642 Figure 3: Mean sediment ( $\pm$  SE) CO<sub>2</sub> efflux (mmol m<sup>-2</sup> d<sup>-1</sup>) before and after surface biofilm removal,  
643 from intact mangrove forest (13 sites), and cleared mangrove forest (23 sites). \*significant difference  
644 ( $p < 0.01$ ).

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649 Figure 3: Model A. Modelled values of mangrove forest CO<sub>2</sub> efflux compared to measured CO<sub>2</sub> efflux  
 650 (Modelled CO<sub>2</sub> efflux (µmol m<sup>-2</sup> s<sup>-1</sup>) = 2.454 - 0.215 x mangrove biomass, r<sup>2</sup> = 0.49, p < 0.05). Model  
 651 B. Modelled values of cleared mangrove forest CO<sub>2</sub> efflux compared to measured CO<sub>2</sub> efflux  
 652 (Modelled CO<sub>2</sub> efflux (µmol m<sup>-2</sup> s<sup>-1</sup>) = 0.0713 + (0.430 x sediment organic carbon concentration, r<sup>2</sup> =  
 653 0.32, p < 0.05).

654

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

	Intact (n = 13)	Cleared (n = 23)
<i>Tree characteristics</i>		
Aboveground biomass (kg dry weight m <sup>-2</sup> )	4.35 $\pm$ 0.9	0
Mangrove root mass (kg dry weight m <sup>-3</sup> )	<i>no data</i>	9.5 $\pm$ 1.0
Mangrove pneumatophore abundance (n m <sup>-2</sup> )	<i>no data</i>	257.3 $\pm$ 86.7
Time since clearance (yr <sup>-1</sup> )	-	2.9 $\pm$ 0.4
<i>Sediment characteristics</i>		
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 $\alpha$ ( $\mu$ g <sup>-1</sup> g <sup>-1</sup> sediment)	36.9 $\pm$ 6.2	26.8 $\pm$ 4.4
Sediment temperature ( $^{\circ}$ C)	19.2 $\pm$ 0.2	20.2 $\pm$ 0.5

657 Table 2: Comparison of mean estimates of sediment CO<sub>2</sub> efflux in intact and cleared mangrove forests. Values are means ± SE.

658

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
<b>Intact Mangrove Forests</b>			
<i>Avicennia marina</i>	New Zealand, 13	168.5 ± 45.8	This study
<i>Avicennia marina</i>	New Zealand, 4	114.0 ± 19.9	Lovelock et al. 2014
<i>Avicennia marina</i>	South and North Australia, 4	107.1 ± 45.8	Lovelock et al. 2014
<i>Avicennia marina</i>	New Caledonia, 1	88.2 ± 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 ± 56	Bouillon et al. 2008
Mixed species	Global estimate, 140	69 ± 8	Alongi 2014
<b>Cleared Mangrove Forests</b>			
<i>Avicennia marina</i>	New Zealand, 23	133.9 ± 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

659 \* no overall mean values provided