

1 **Sediment properties and CO₂ efflux from intact and**
2 **cleared temperate mangrove forests**

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7

8 **Abstract**

9 Temperate mangrove forests in New Zealand have been increasing in area in recent decades.
10 Recreational and amenity values or perceived loss of other estuarine habitats due to
11 expanding temperate mangrove forests have resulted in clearing of temperate mangroves. In
12 this study, we investigated the impact of temperate mangrove clearance on sediment CO₂
13 efflux and associated biotic and abiotic factors. This is the first study to investigate the effect
14 of clearing on sediment CO₂ efflux in temperate *Avicennia marina* forests.

15 Sediment CO₂ efflux rates in intact ($1.95 \pm 0.53 \mu\text{mol m}^{-2} \text{s}^{-1}$) and cleared ($1.55 \pm 0.43 \mu\text{mol}$
16 $\text{m}^{-2} \text{s}^{-1}$) mangrove forests did not differ significantly ($1.55 \pm 0.43 \mu\text{mol m}^{-2} \text{s}^{-1}$) did not differ
17 significantly, and showed high between-site variability. Pre-shading the sediment for > 30
18 minutes prior to dark CO₂ efflux measurements was found to have no significant effect on
19 sediment CO₂ efflux. Mangrove above ground biomass, chlorophyll α concentration and
20 sediment temperature were the main factors explaining the variability in sediment CO₂ efflux
21 in intact mangrove forests. In contrast, sediment organic carbon and nitrogen concentration
22 and sediment grain size were the main factors explaining the variability in sediment CO₂
23 efflux in cleared mangrove sites. Our results show that sediment CO₂ efflux from intact and
24 cleared temperate mangrove forest is comparable to rates measured in tropical mangrove
25 forests.

26

27 **1. Introduction**

28 Mangrove forests are generally confined to the tropics, between latitudes 30°N and 30°S.
29 However, approximately 1.4% of the global mangrove forests are located outside this
30 latitudinal range, growing in conditions which may be broadly characterised as temperate
31 (Morrisey et al., 2010). Temperate mangrove forests mainly occur in Australia, New Zealand,
32 the United States of America and South Africa (Morrisey et al., 2010; Giri et al., 2011).
33 Temperate mangrove forests are subject to colder and generally more variable climatic
34 conditions, and are typically associated with lower diversity of tree species and lower faunal
35 abundance and diversity than in the tropics (Alfaro, 2006; Morrisey et al., 2010). To date,
36 little is known of the biogeochemical processes in temperate mangroves (Livesley and
37 Andrusiak, 2012).

38 Temperate mangrove forest coverage has increased significantly over the last 50-60 years
39 (Morrisey et al., 2010; Saintilan et al., 2014). A landward expansion of mangroves into salt
40 marsh is observed in Australia and USA (Cavanaugh et al., 2014; Saintilan et al., 2014) while
41 mangrove expansion into tidal flats is typically observed in New Zealand (Stokes et al., 2009;
42 Lundquist et al., 2014a). In addition, there is evidence of mangrove expansion from tropical
43 areas northwards and southwards to temperate regions (Saintilan et al., 2014). The expansion
44 of mangroves in New Zealand has been linked to increased sedimentation leading to vertical
45 accretion of tidal flats (Swales et al., 2007; Stokes, 2010), increased nutrient inputs (Saintilan
46 and Williams, 1999), and climatic factors (Burns and Ogden, 1985; Lovelock et al., 2010).

47 The recent expansion of mangrove has led to a push towards mangrove removal in New
48 Zealand, largely from local communities concerned about the loss of diversity of estuarine
49 habitats, or for human amenities such as recreational access and water views (Harty, 2009).
50 Numerous legal and illegal clearings have occurred in recent decades, ranging in scale from
51 small < 0.1 ha clearings to clearances exceeding 100 ha (Morrisey et al., 2010; Lundquist et
52 al., 2014a).

53 Carbon (C) cycling and storage are important ecosystem services provided by mangrove
54 forests (Twilley et al., 1992; Bouillon et al., 2008; Kristensen et al., 2008; Alongi, 2014).
55 Global net primary productivity in mangrove forest has been estimated at $218 \pm 72 \text{ Tg C a}^{-1}$,
56 which includes the rate of litterfall, above- and below-ground biomass production (Bouillon
57 et al., 2008). An important component of the carbon cycle is the efflux of carbon dioxide
58 (CO_2) from the sediment into the atmosphere (Raich and Schlesinger, 1992). Sediment CO_2

59 efflux (also called soil/sediment respiration) is the total of CO₂ released through
60 root/mycorrhizae respiration (autotrophic respiration) and microbial respiration
61 (heterotrophic respiration) associated with the decomposition of organic matter (Bouillon et
62 al., 2008).

63 Clearing will have an impact on the tree and sediment carbon storage and fluxes (Lovelock et
64 al., 2011; Sidik and Lovelock, 2013; Lang'at et al., 2014). For example, the accumulation of
65 mangrove-derived carbon from living mangrove into the sediment is halted following
66 mangrove clearance, yet the release of CO₂ from the sediment continues (Lovelock et al.,
67 2011; Sidik and Lovelock, 2013). The rates of sediment CO₂ efflux from cleared tropical
68 mangrove peat forest have been shown to be significantly higher compared to intact
69 mangrove forests (Lovelock et al., 2011). However, the impact of clearance on sediment
70 carbon storage and sediment CO₂ efflux has not been investigated in temperate mangrove.
71 Quantifying sources of carbon has become increasingly important due to the rapid rise in
72 atmospheric CO₂ concentrations and associated impact on global climate (IPCC, 2013).

73 Studies from tropical mangrove forests have shown that sediment CO₂ efflux is influenced by
74 sediment carbon and nutrient quantity (Chen et al., 2010; Chen et al., 2012; Leopold et al.,
75 2013; Chen et al., 2014) and quality (Kristensen, 2000), sediment grain size (Chen et al.,
76 2010), sediment water content (Alongi, 2009), redox potential (Chen et al., 2010; Chen et al.,
77 2012; Leopold et al., 2013) and sediment temperature (Chen et al., 2012). Conducting
78 measurements in temperate and tropical mangroves, Lovelock (2008) found a positive
79 correlation between leaf area index and sediment CO₂ efflux. Further, sediment microbial
80 communities present on the sediment surface, also called biofilm communities, comprised of
81 cyanobacteria, diatoms, and other microalgae, may also play an important role in mediating
82 CO₂ exchange from the sediment (Alongi et al., 2012; Leopold et al., 2013; Leopold et al.,
83 2015). However, the relative contribution of abiotic and biotic factors on sediment CO₂ efflux
84 from cleared temperate mangrove forest remains to be tested.

85 The aim of this study was to assess the effect of temperate mangrove forest clearance on
86 sediment CO₂ efflux and sediment characteristics. The specific objectives were to quantify
87 the sediment CO₂ efflux from intact and cleared mangrove forest and to investigate the
88 relationship between abiotic and biotic factors and sediment CO₂ efflux. The effect of pre-
89 shading the sediment prior to dark chamber measurements was also investigated. This was
90 due to the observation of CO₂ uptake during dark chamber measurements. The uptake might
91 be attributed to the continuation of photosynthetic activity by surface biofilm communities at

92 the onset of dark measurements until coenzymes were depleted (NADPH, ATP) (Leopold et
93 al. (2015).

94 **2. Materials and methods**

95 **2.1 Study species**

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

102 **2.2 Study area and selection of study sites**

103 This study was conducted at 23 sites covering a large proportion of the geographic range of
104 mangroves (35°43' S to 37° 41' S) in New Zealand (Figure 1). We investigated cleared (n =
105 23) and, where possible, adjacent intact mangrove forest sites (n = 13). The time since
106 mangrove removal ranged from 1 month to over 8 years. Cleared mangrove sites ranged in
107 area from < 0.1 ha to > 13 ha. Besides the difference in time since clearing and area of the
108 clearing the sites differed in shape, hydrodynamic exposure, and method of clearance
109 (Supplementary table 1). Mean air temperature ranges from 19°C during summer to 11°C
110 during winter. Mean monthly rainfall varies from 77 to 152 mm, respectively (NIWA, 2014).
111 Tides for the sites are semi diurnal with a range of 1.3 – 4.1 m (LINZ, 2014).

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

116 **2.3 Sediment CO₂ efflux measurements**

117 **2.3.1 Shading experiment**

118 Frames (0.5 m²) were located approximately 20 cm above the sediment surface at Hatea 1.
119 The frame was completely covered by layered cloth to exclude light penetration. Three
120 frames were deployed throughout the mangrove forest, at least 10 m from each other and the
121 mangrove edge. After 30 minutes of shading, two CO₂ efflux measurements using a dark
122 respiration chamber were conducted at different locations within the 0.5 m² area, before and

123 after the removal of the surface biofilm. The biofilm (top ~2 mm of surface sediment) was
124 scraped off using a spatula. Biofilm removed measurements were conducted immediately
125 following biofilm intact measurements at the same location. Corresponding dark CO₂ efflux
126 measurements were also conducted at locations that had not been pre-shaded (control)
127 adjacent to each shaded measurement, as well as corresponding biofilm removed
128 measurements to account for heterogeneity in sediment conditions.

129 *2.3.2 Sediment CO₂ efflux from intact and cleared temperate mangrove*

130 Sediment CO₂ efflux was measured in the centre of the cleared sites at three randomly
131 selected locations. Locations in the intact mangrove forest were > 10 m from the cleared
132 areas. No pre-shading of the sediment was undertaken prior to measurements.

133 The sediment CO₂ efflux was measured at low tide, between 8 am and 6 pm local time, using
134 an infrared CO₂ analyser (Environmental Gas Monitor (EGM-4) with a dark sediment
135 respiration chamber (SRC-1, PP Systems Ltd., Amesbury, MA, USA). Using a dark chamber
136 prevents the photosynthetic activity of benthic microbial communities which results in the
137 uptake of CO₂. A PVC collar (10 cm height) was attached to the base of the respiration
138 chamber to protect the chamber from potential flooding. The collar was inserted
139 approximately 5 mm into the sediment, avoiding damage to surface roots. Sediment within
140 the chamber included crab burrows and pneumatophores < 7 cm which fit within the
141 respiration chamber. The sediment area covered by each chamber was 0.00785 m². Chamber
142 height was measured during each measurement as collar insertion varied based on sediment
143 characteristics. Total chamber volume varied between 1.72 and 1.98 l depending on the depth
144 of collar insertion. The CO₂ concentration in the chamber was measured at 5 second intervals
145 over a 90 second period. Air and sediment temperature (Novel Ways temperature probe) and
146 moisture (CS620, Campbell Scientific, Logan, UT, USA) to a depth of 12 cm was measured
147 with each CO₂ efflux measurement.

148 In addition to measuring CO₂ efflux in intact (undisturbed) sediment, sediment CO₂ efflux
149 was re-measured at the same location after the removal of the surface biofilm. Measurements
150 were made within 30 seconds following the removal of the surface biofilm.

151 The sediment CO₂ efflux rate was calculated as follows.

$$152 \quad \text{CO}_2 \text{ flux } (\mu\text{mol m}^{-2} \text{ s}^{-1}) = (\Delta\text{CO}_2/\Delta t) \times (P \times V/R \times T \times A) \quad (1)$$

153 Where $\Delta\text{CO}_2/\Delta t$ is the change in CO₂ concentration over time, based on the slope of the linear
154 regression ($\mu\text{mol mol}^{-1}$), t is time (s), P is the atmospheric pressure (Pa), V is the volume of

155 the chamber including collar (m^3), A is the surface area covered by each chamber (0.007854
156 m^2), T is the temperature (K), R is the ideal gas constant, $8.20528 \text{ m}^3 \text{ PaK}^{-1} \text{ mol}^{-1}$).

157 Sediment CO_2 efflux was only calculated if the linear regression of CO_2 concentration vs.
158 time had r^2 values ≥ 0.8 .

159 **2.4 Sediment characteristics**

160 At each site three sediment samples, next to the location of the sediment CO_2 efflux
161 measurements, were collected using two small sediment cores (2 cm deep, 2 cm in diameter).
162 The sediment samples were kept frozen and stored in the dark prior to being analysed.

163 *Sediment carbon and nitrogen concentration:* Samples were dried (60°C for 48 hours) and
164 then pulverised using mortar and pestle. Total carbon (C) and nitrogen (N) concentration was
165 determined using an elemental analyser (TruSpec LECO CNS, Leco Corporation, St. Joseph,
166 MI). A subset of samples ($n = 40$, ranging from 0.17 to 12.63% total C) were acidified to
167 remove the inorganic C (Brodie et al., 2011). Briefly, 300 mg sediment was mixed with 0.5
168 ml dionized water and 1.5 ml of 20% HCl and then dried on a hot plate. Organic carbon
169 concentration was then determined using the elemental analyser.

170 *Grain size:* One sediment sample per site was analysed for grain size. The samples were
171 homogenised and a subsample of approximately 5 g of sediment was taken and digested in ~
172 9% hydrogen peroxide until bubbling ceased (Day, 1965). The sediment sample was then
173 wet sieved through 2000 μm and 63 μm mesh sieves. Pipette analysis was used to separate
174 the $< 63 \mu\text{m}$ fraction into $> 3.9 \mu\text{m}$ and $\leq 3.9 \mu\text{m}$. All fractions were then dried at 60°C until a
175 constant weight was achieved (fractions were weighed at ~ 40 h and then again at 48 h).
176 Grain size fractions were calculated as percentage weight of gravel/shell hash ($>2000 \mu\text{m}$),
177 sand (63 – 2000 μm), silt (3.9 – 62.9 μm) and clay ($\leq 3.9 \mu\text{m}$).

178 *Chlorophyll α :* One sediment sample per site was analysed for chlorophyll α . Within one
179 month of sampling, the sample was freeze dried, weighed, then homogenised and a
180 subsample (~5 g) taken for analysis. Chlorophyll α was extracted by boiling the sediment in
181 90% ethanol, and the extract processed using a spectrophotometer (Spectrophotometer UV-
182 1800, Shimadzu, Kyoto, Japan) measuring absorption at wavelengths 665 and 750 nm. An
183 acidification step was used to separate degradation products from chlorophyll α (Hansson,
184 1988; Moed and Hallegraeff, 1978). Chlorophyll α concentration was calculated based on the
185 following equation:

186 Chlorophyll α ($\mu\text{g g}^{-1}$ sediment) = $\frac{((750_a - 665_a) - (750 - 665)) \times \text{Abs} \times \frac{\text{Ethanol in extraction (l)}}{\text{Sediment analysed (ug)}}}{(2)}$
 187 (2)

188 Where 750 and 665 is the absorption at wavelengths 750 and 665 nm, 750a and 665a is the
 189 absorption at wavelengths 750 and 665 nm after acidification with 0.05 mL 1 mol HCl and
 190 Abs is the absorbance correction for chlorophyll in ethanol (28.66)

191 **2.5 Tree and root biomass**

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

196
$$\text{Total above ground biomass}^{-1/3} \text{ (g dry weight)} = -4.215 + 0.121 \times \text{Height (cm)} \text{ (3)}$$

197 At two sites, Mangere 1 (Auckland) and Hatea 1 (Northland) mangrove height exceeded the
 198 range the allometric equation was designed for (determined from trees ranging in height from
 199 40 to 248 cm) and measures of trunk diameter were instead used to estimate biomass (based
 200 on the trunk diameter at 30 cm height of the closest 5 mangrove trees to each sampling
 201 point):

202
$$\text{Total above ground biomass}^{-1/3} \text{ (g dry weight)} = 0.264 + 2.597 \times \text{Diameter (cm)} \text{ (4)}$$

203 At each clearance site a quadrat (0.5 m x 0.5 m) was sampled at three haphazardly placed
 204 locations (within a 10 m radius). The following metrics were recorded within each quadrat:
 205 the proportion of surface covered by mangrove leaf litter, proportion of surface covered by
 206 macroalgae, number of mangrove seeds and seedlings, and number of pneumatophores.
 207 Further, three randomly located root biomass cores (13 cm diameter, 15 cm depth) were
 208 collected at each clearance site. After sorting, all vegetative material was air dried for one
 209 week on aluminium trays, and then oven dried at 70 °C for approximately 4 days until dry
 210 weight stabilised. No cores were collected from intact mangrove forest sites.

211 **2.6 Data analysis**

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

215 Data were tested for normality using the Shapiro-Wilk test. As sediment CO₂ efflux rates in
 216 the shading experiment were normally distributed, paired t-tests were used to determine

217 significant differences between shaded and control measurements. A Mann-Whitney Rank
218 Sum Test was used to determine significant differences in sediment CO₂ efflux, tree and
219 sediment characteristics, between intact and cleared mangrove sites, as data did not conform
220 to normality.

221 Backward multiple linear regression analysis was used to identify the sediment and
222 ecosystem characteristics that predicted CO₂ efflux. Levene's test was used to verify the
223 homogeneity of variance. Sediment CO₂ efflux values from intact mangrove forest site Matua
224 and cleared mangrove forest site Waiuku 2 were considered outliers (mean values were > 3
225 fold the overall mean and > 2 fold the next highest value) and not included in the regression
226 analysis.

227 Significance levels of 0.05 and 0.01 were used. All statistical analyses were conducted using
228 SPSS statistics software version 17 (SPSS Inc. Chicago, IL, USA).

229

230 **3. Results**

231 *Shading experiment*

232 No significant difference ($p > 0.05$) was detected in mean CO₂ efflux between shaded and
233 control treatments (Figure 2). Removing the surface biofilm resulted in significantly higher
234 CO₂ efflux ($p < 0.01$) for both shaded and control treatments (Figure 2).

235 *Sediment CO₂ efflux and sediment characteristics from intact and cleared mangrove forest* 236 *sites*

237 Sediment CO₂ efflux varied considerably within and among sites. However, the mean
238 variability within sites (CV = 0.55 for intact mangrove forests and 1.1 for cleared mangrove
239 forests) was lower than mean variability among sites (CV = 0.99 for intact mangrove forests
240 and 1.34 for cleared mangrove forests).

241 No significant difference in sediment CO₂ efflux was found between intact and cleared
242 mangrove sites ($p > 0.05$) (Figure 3). The mean sediment CO₂ efflux rates for intact and
243 cleared mangrove forest sites was $1.55 \pm 0.43 \mu\text{mol m}^{-2} \text{s}^{-1}$ ($n = 13$) and $1.95 \pm 0.53 \mu\text{mol m}^{-2}$
244 s^{-1} ($n = 23$), respectively. Removing the surface biofilm resulted in a higher CO₂ efflux at
245 intact (2.34 fold increase) and cleared (1.66 fold increase) mangrove forest sites ($p < 0.05$)
246 (Figure 3).

247 Mangrove above ground biomass ranged from 0.52 to 13.54 kg dry weight m⁻². Sediment
248 characteristics varied considerably among sites and no significant differences ($p > 0.05$) were
249 detected in sediment characteristics between intact and cleared mangrove forest sites (Table
250 1).

251 Variation in sediment CO₂ efflux was high among sites. Visual analysis indicated two
252 sediment CO₂ efflux clusters within intact mangrove forests: high ($>1.95 \mu\text{mol m}^{-2} \text{s}^{-1}$) and
253 low ($<1.95 \mu\text{mol m}^{-2} \text{s}^{-1}$). Mean sediment CO₂ efflux of the 'high efflux group' (Matua,
254 Tairua 2, Uretara 1, Waikareao, and Welcome Bay 1) was $3.60 \pm 0.94 \mu\text{mol m}^{-2} \text{s}^{-1}$ compared
255 to $0.93 \pm 0.27 \mu\text{mol m}^{-2} \text{s}^{-1}$ measured in the 'low efflux group'. Chlorophyll α concentration
256 was significantly higher in the 'high efflux group' ($53.31 \pm 6.97 \mu\text{g}^{-1} \text{g}^{-1}$ sediment) than in the
257 'low efflux group' ($26.63 \pm 7.03 \mu\text{g}^{-1} \text{g}^{-1}$ sediment) ($p < 0.05$). In addition, sediment
258 temperature ($^{\circ}\text{C}$) was significantly higher in the 'high efflux group' (21.32 ± 0.99) than in the
259 'low efflux group' (17.87 ± 0.81) ($p < 0.05$) (supplementary table 2).

260 Similarly, cleared mangrove forest sites were grouped into two clusters: high ($>1.55 \mu\text{mol m}^{-2} \text{s}^{-1}$) and low ($<1.55 \mu\text{mol m}^{-2} \text{s}^{-1}$). Mean sediment CO_2 efflux of the ‘high efflux group’
261 ($\text{Mangere 1, Pahurehure 4, Waiuku 1, 2 and 3, Welcome Bay 1, Whangamata E}$) was $3.91 \pm$
262 $0.82 \mu\text{mol m}^{-2} \text{s}^{-1}$ compared to $0.52 \pm 0.21 \mu\text{mol m}^{-2} \text{s}^{-1}$ measured in the ‘low efflux
263 group’. Sediment organic carbon concentration ($4.22 \pm 0.84\%$ vs. $2.10 \pm 0.35\%$), nitrogen
264 concentration ($0.45 \pm 0.05\%$ vs. $0.26 \pm 0.04\%$), sediment sand content ($15.46 \pm 9.87\%$ vs.
265 $42.99 \pm 7.99\%$), and sediment clay content ($28.19 \pm 4.30\%$ vs. $15.09 \pm 2.64\%$) were
266 significantly higher in the ‘high efflux group’ than in the ‘low efflux group’ for cleared
267 mangrove forest sites ($p < 0.05$) (supplementary table 3).
268

269 *Regression analysis*

270 Backward multiple linear regression analysis revealed that mangrove biomass was the only
271 significant predictor of CO_2 efflux within intact mangrove forest sites ($r^2 = 0.49$, $F = 9.43$, $p =$
272 0.01) (Figure 4.A). Within the cleared sites, backward multiple linear regression analysis
273 revealed that sediment organic carbon concentration was the only significant predictor of CO_2
274 efflux ($r^2 = 0.32$, $F = 9.23$, $p < 0.01$) (Figure 4.B). No other significant relationships were
275 observed ($p > 0.05$ for individual coefficients).

276

277 **4. Discussion**

278 **4.1 Sediment CO₂ efflux and sediment characteristics from intact temperate mangrove** 279 **forest**

280 Dark sediment CO₂ efflux in intact *Avicennia marina* forests across its distribution range in
281 New Zealand ($1.95 \pm 0.53 \mu\text{mol m}^{-2} \text{s}^{-1}$ which equals $168.4 \pm 45.8 \text{ mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) is
282 similar to values reported for intact *Avicennia marina* forests in New Zealand (Lovelock,
283 2008; Lovelock et al., 2014), Australia (Livesley and Andrusiak, 2012) and New Caledonia (
284 Leopold et al., 2013; Leopold et al., 2015) (Table 2). In contrast, our values are higher than
285 the global estimates of sediment CO₂ efflux from intact mangrove forests including a number
286 of other tropical mangrove species ($0.71 \pm 0.65 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Bouillon et al., 2008); $0.80 \pm$
287 $0.09 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Alongi, 2014)) (Table 2). Higher sediment CO₂ efflux observed within our
288 study may partly be explained by the inclusion of crab burrows and pneumatophores within
289 flux measurements. The omission of crab burrows and pneumatophores has previously been
290 proposed as a potential explanation of why global estimates may be underestimated (Bouillon
291 et al., 2008). Crab burrows have been shown to increase CO₂ efflux by increasing the surface
292 area for sediment-air exchange of CO₂ (Kristensen et al., 2008) and enhancing carbon
293 decomposition processes (Pülmanns et al., 2014). Pneumatophores have been associated with
294 increased CO₂ emissions by efficient translocation of CO₂ exchange from deeper sediments
295 (Bouillon et al., 2008; Kristensen et al., 2008).

296 We found a negative relationship between mangrove above ground biomass and sediment
297 CO₂ efflux across the 13 intact mangrove forests. The above ground biomass across the
298 investigated *Avicennia marina* forests (5.2 to 135 t dry weight ha⁻¹) is considerably lower
299 than the above ground biomass in many tropical mangrove forests (35 to over 400 t dry
300 weight ha⁻¹) (Komiya et al., 2008). Lower tree biomass associated with low forest cover
301 may lead to increased light availability and sediment temperature, which in turn may result in
302 a higher abundance and activity of microbial communities. Respiration from microbial
303 communities growing on the sediment surface contribute a considerable proportion to total
304 CO₂ efflux from mangrove sediments, as shown in a New Caledonian *Avicennia marina*
305 forest (Leopold et al., 2013). High sediment chlorophyll *a* concentrations and the presence of
306 algal mats characterising the ‘high efflux sites’ also suggest that respiration by
307 photosynthetic communities can be a significant contributor to CO₂ efflux by
308 remineralization of organic material (Decho, 2000). Further, higher sediment temperature in

309 the 'high efflux sites' is in line with findings from other mangrove forests (e.g. Leopold et al.,
310 2015) and many terrestrial ecosystems (e.g. Davidson and Janssens, 2006) as temperature
311 influences both the autotrophic and heterotrophic activity (Raich and Schlesinger, 1992).

312 We note that all sediment CO₂ efflux measurements in this study were made at low to mid-
313 tide. The efflux of CO₂ from mangrove sediment during low tide can be up to 40% greater
314 than during tidal immersion as molecular diffusion of CO₂ is faster when sediments are
315 aerated and the surface area for aerobic respiration and chemical oxidation increases (Alongi,
316 2009). However, benthic light availability is also reduced during tidal immersion, which may
317 result in increased respiration by the microphytobenthos (Billerbeck et al., 2007).

318 ***4.2 Sediment CO₂ efflux and sediment characteristics of cleared mangrove forest***

319 Dark sediment CO₂ efflux in cleared *Avicennia marina* forests in New Zealand (1.55 ± 0.43
320 $\mu\text{mol m}^{-2} \text{s}^{-1}$ which equals $133.9 \pm 37.2 \text{ mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) is similar to sediment CO₂ efflux
321 following the clearance of tropical mangrove (Lovelock et al., 2011; Sidik and Lovelock,
322 2013; Lang'at et al., 2014). Higher sediment CO₂ efflux rates (2.1 to 7.6 $\mu\text{mol m}^{-2} \text{s}^{-1}$
323 depending on the time since clearing) were measured in cleared peat mangrove stands in
324 Belize (Lovelock et al., 2011).

325 We did not find a significant difference in sediment CO₂ efflux between intact and cleared
326 mangrove forest sites. Further, we did not find a relationship between time since clearing and
327 sediment CO₂ efflux. In contrast, sediment CO₂ efflux from cleared peat mangrove forests in
328 Belize declined logarithmically over a 20 year period (Lovelock et al., 2011). Two months
329 after the clearing of mangroves in Kenya, sediment CO₂ efflux increased approximately two
330 fold before returning to comparable levels to adjacent intact mangrove forests approximately
331 five months after clearance (Lang'at et al., 2014). A number of factors such as differences in
332 site sediment characteristics, size, exposure, and method of clearance may confound the
333 effect of time since clearing on sediment CO₂ efflux in our study.

334 Sediment CO₂ efflux in cleared sites was positively related to sediment organic carbon
335 concentration. This is in line with the findings reported for the clearing of peat mangroves
336 where the rate of CO₂ efflux was related to the microbial degradation of organic matter in the
337 sediments (Lovelock et al., 2011). Sediment organic carbon concentrations in the cleared
338 sites ($2.74 \pm 0.40\%$) are comparable to the sediment organic carbon concentration measured
339 in a mangrove forest in Auckland, New Zealand (Yang et al., 2013) and *Avicennia marina*
340 forests south of Melbourne, Australia (Livesley and Andrusiak, 2012). The mean sediment

341 carbon concentration in mangrove sediments collected across the globe is 2.2% (Kristensen et
342 al., 2008). The highest sediment CO₂ efflux rates were measured at sites where large areas
343 were cleared (>1 ha) using mechanical diggers and where the mulch was left in place.
344 Increased sediment organic carbon and nitrogen concentrations resulting from the mulch
345 input explain higher sediment CO₂ efflux at these locations. High clay content found at these
346 sites may have also contributed to the accumulation of sediment carbon, which has been
347 shown to be associated with higher CO₂ efflux in tropical mangrove forests (Leopold et al.,
348 2013; Chen et al., 2010; Chen et al., 2012; Chen et al., 2014). Nitrogen enrichment has also
349 been found to result in increased sediment CO₂ efflux, in particular dwarf/stunted mangrove
350 forests (Lovelock et al., 2014). While no significant correlation was observed between CO₂
351 efflux and mangrove root biomass in our study, increased CO₂ efflux following mangrove
352 clearance has previously been attributed to the rapid decomposition of fine root material
353 related to increased sediment temperatures following the loss of canopy cover (Lang'at et al.,
354 2014).

355 The clearance process typically includes considerable sediment disturbance, particularly
356 when mechanical diggers are used (Lundquist et al., 2014a). The tracking and raking of the
357 sediment creates compacted and mixed areas where deeper anoxic sediment is brought to the
358 surface (*pers. obs*). Increased sediment CO₂ efflux has been observed within intact mangrove
359 forest following disturbance of the top 30 cm of the sediment, however the effect was
360 transitory, returning to pre disturbed levels within two days (Lovelock et al., 2011).

361 The area of clearing, shape and exposure may also influence CO₂ efflux as these factors
362 influence site recovery. For example, smaller more exposed clearance sites at the edge of
363 mangrove forests may be more likely to transition towards tidal flat characteristics (i.e.
364 coarser sediment grain size, lower organic carbon and chlorophyll α concentration) than
365 larger, less exposed sites where limited sediment mobilisation occurs (Lundquist et al.,
366 2014b). Higher sediment carbon concentrations have been measured in older mangrove
367 forests, growing further inland compared to younger mangrove forests, growing at the
368 expanding seaward edge (Lovelock et al., 2010). This may also be related to the protection
369 offered by seaward mangroves, enabling greater accumulation of carbon enriched mangrove
370 detritus within the centre of the stand (Yang et al., 2013).

371 **4.3 Sediment CO₂ uptake**

372 Sediment CO₂ uptake (negative flux) was observed at one intact (Hatea 1) and three cleared
373 (Tairua 3, Whangamata 1, Hatea 1) mangrove forest sites. CO₂ uptake has also been reported
374 in other mangrove efflux studies (Lovelock, 2008; Lovelock et al., 2014; Leopold et al.,
375 2015). CO₂ uptake has been explained by the presence of biofilm microbial communities, as
376 CO₂ uptake changed to efflux following biofilm removal (Leopold et al. (2015). In other
377 habitats, CO₂ uptake from terrestrial shrub sediment has been attributed to sediment effusion-
378 dissolution processes driven by sediment pH and moisture (Ma et al., 2013). CO₂ uptake
379 from wetland sediment has been attributed to the drawdown of CO₂ into the sediment during
380 large ebbing or very low tides (Krauss and Whitbeck, 2012).

381 Microphytobenthos have been shown to be significant contributors to benthic primary
382 productivity (Kristensen and Alongi, 2006; Bouillon et al., 2008; Oakes and Eyre, 2014).
383 Due to the short duration of our measurements (90 seconds), CO₂ uptake might be explained
384 by the continuation of photosynthetic activity by surface biofilm communities at the onset of
385 dark measurements until coenzymes are depleted (NADPH, ATP) (Leopold et al. (2015).
386 However, the results from our shading results suggest that this was not the case, as we did not
387 see significantly higher CO₂ efflux from sediment that was pre-shaded compared to sediment
388 which had not been pre shaded.

389 Another possibility is that the decrease in CO₂ concentration within the chamber observed at
390 these sites is driven by the leakage of CO₂ from dark chamber measurements, via cracks,
391 fissures or burrows in the surface sediment. The removal of the surface biofilm resulted in
392 CO₂ emission even at the sites where CO₂ uptake was previously observed. This is possibly
393 related to homogenising the sediment surface following biofilm removal, with cracks or
394 burrows covered by scraped sediment, minimising CO₂ leakage to adjacent non-shaded
395 microphytobenthos. Other studies have suggested that the biofilm may also act as a barrier to
396 the flow of CO₂ from deeper sediment, which when removed results in a rapid increase in
397 CO₂ efflux (Leopold et al., 2013; Leopold et al., 2015).

398 Chemoautotrophs have also been shown to fix carbon in intertidal sediment under dark
399 conditions (Lenk et al., 2011; Boschker et al., 2014). In particular, at the interface of aerobic
400 and anaerobic zones where large amounts of reduced compounds, such as sulphur,
401 accumulate (Thomsen and Kristensin, 1997; Lenk et al., 2011; Santoro et al., 2013; Boschker
402 et al., 2014). This is consistent with what is observed in mangrove sediment, where aerobic

403 to anaerobic transitions typically occur close to the sediment surface, with sulphur driven
404 processes likely to dominate in anaerobic conditions (Kristensen et al., 2008).

405 **4.4 Conclusions**

406 Mangrove deforestation is occurring at a rapid rate and the impacts of clearance are of
407 immediate environmental concern. This is the first study to investigate the effect of clearing
408 on sediment CO₂ efflux in temperate *Avicennia marina* forests. We found that rates of
409 sediment CO₂ efflux from cleared and intact temperate *Avicennia marina* forests are
410 comparable to rates observed in the tropics. High variability between sites due to age, size
411 and methodology of clearings, and underlying (and resulting) environmental characteristics
412 (e.g., sediment grain size, organic content) resulted in no significant differences between
413 intact and cleared sites. Regardless, our results suggest that greater consideration should be
414 made regarding the rate of carbon released from mangrove forest following clearance and the
415 relative contribution to the atmosphere.

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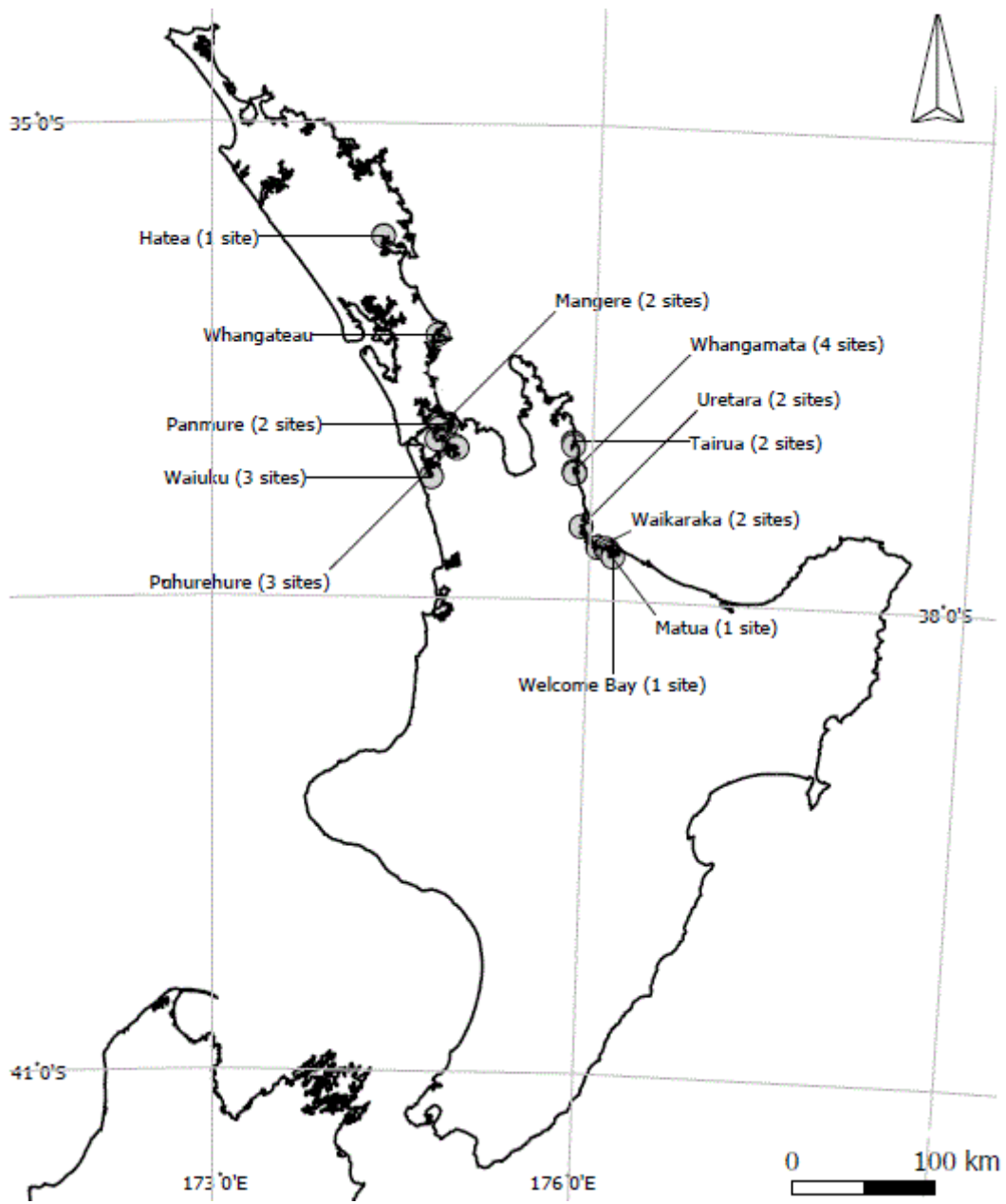
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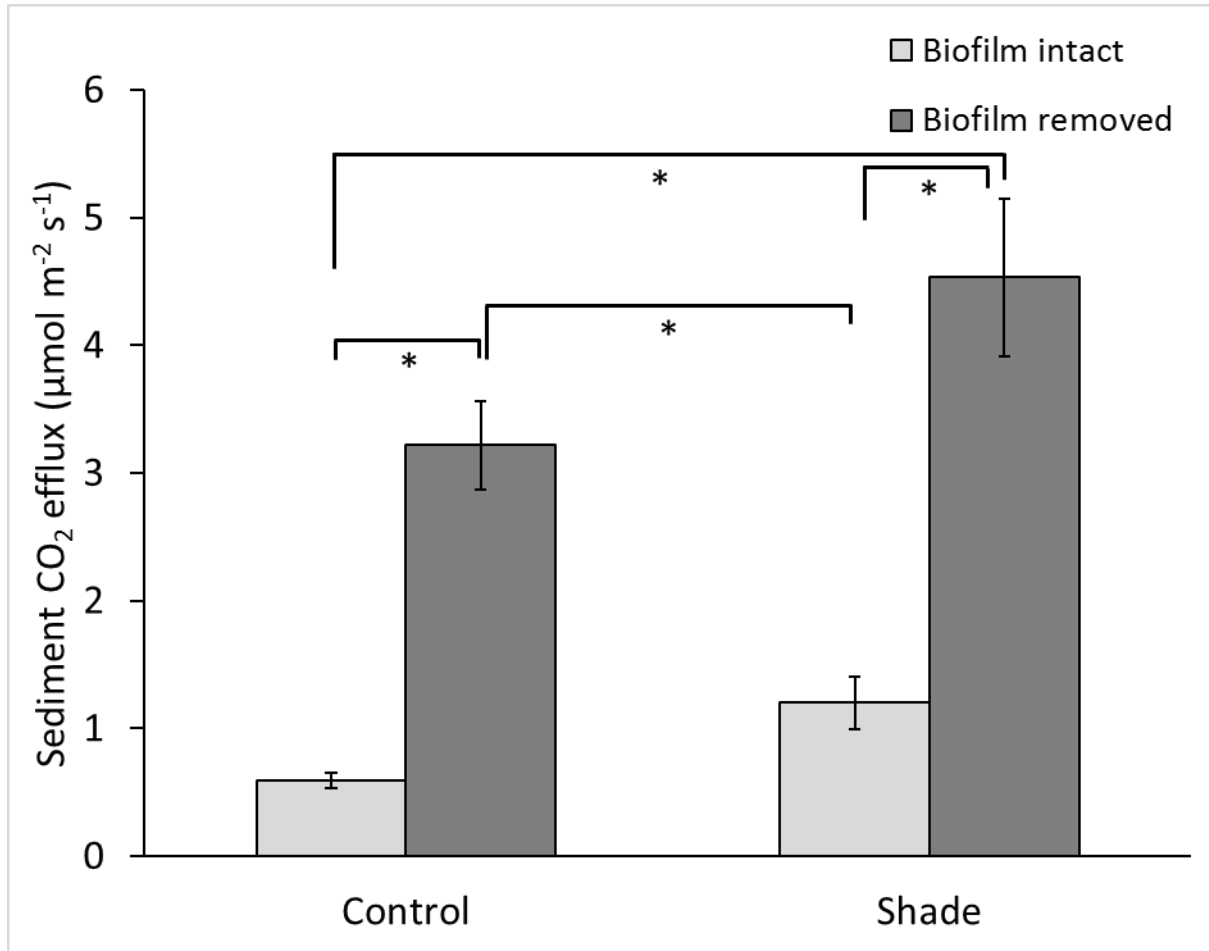
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568

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

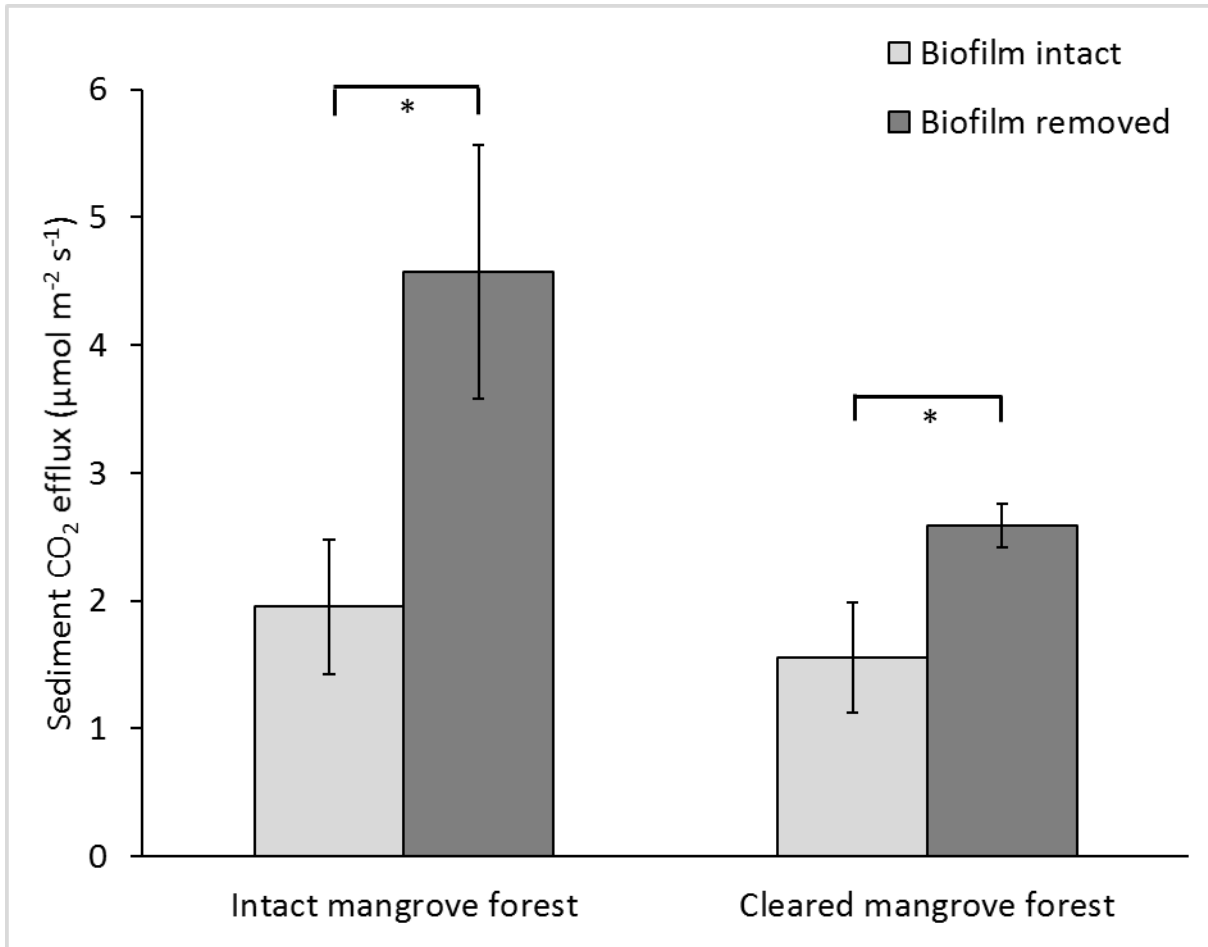
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572

573 Figure 2: Mean sediment (\pm SE) CO_2 efflux ($\mu\text{mol m}^{-2} \text{s}^{-1}$) before and after surface biofilm was
574 removed, from control ($n = 6$), and pre-shaded sediment ($n = 6$) at intact mangrove site Hatea 1.
575 *significant difference ($p < 0.05$)

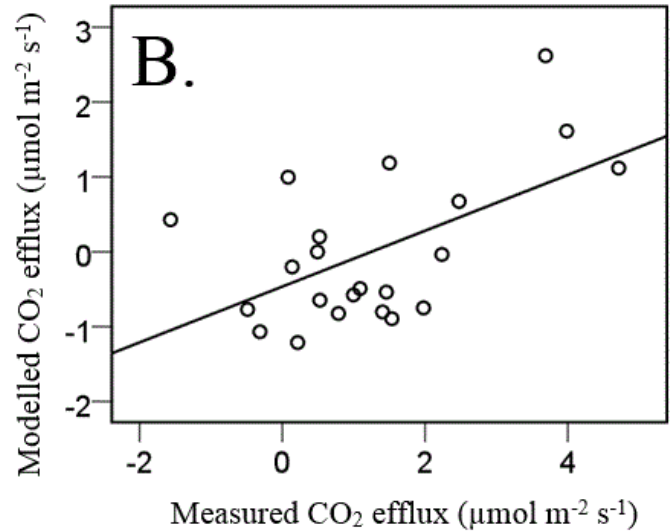
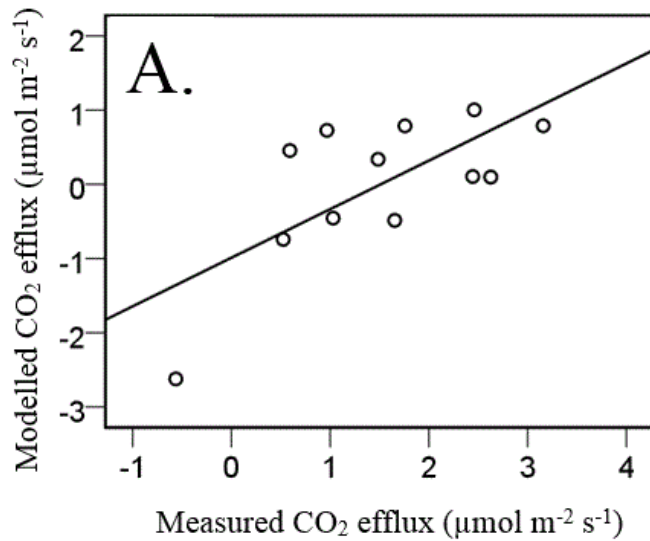
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577

578 Figure 3: Mean sediment (\pm SE) CO₂ efflux ($\mu\text{mol m}^{-2} \text{s}^{-1}$) before and after surface biofilm was
579 removed, from intact mangrove forest (13 sites), and cleared mangrove forest (23 sites). *significant
580 difference ($p < 0.05$).

581



582

583 Figure 4: Model A. Modelled values of mangrove forest CO₂ efflux compared to measured CO₂ efflux
 584 ($y = -0.73 + 0.59x$ mangrove biomass, $r^2 = 0.49$, $p < 0.01$). Model B. Modelled values of cleared
 585 mangrove forest CO₂ efflux compared to measured CO₂ efflux ($y = -0.47 + 0.37x$ sediment organic
 586 carbon concentration, $r^2 = 0.32$, $p < 0.01$).

587

588 Table 1: Mean site characteristics from intact and cleared mangrove sites, \pm SE.

| | Mangrove (n = 13) | Clearance (n = 23) |
|--|----------------------|-----------------------|
| Mangrove biomass (kg dry weight m ⁻²) | 4.35 \pm 0.93 | 0 |
| Mangrove root mass (kg dry weight m ⁻³ , 15 cm depth) | <i>no data</i> | 9.45 \pm 1.00 |
| Mangrove pneumatophore abundance (n m ⁻²) | <i>no data</i> | 257.32 \pm 86.72 |
| Time since clearance (yr ⁻¹) | - | 2.89 \pm 0.44 |
| <i>Sediment characteristics</i> | | |
| Organic carbon (%) | 3.60 \pm 0.73 | 2.74 \pm 0.40 |
| Nitrogen (%) | 0.47 \pm 0.10 | 0.32 \pm 0.04 |
| Gravel (%) | 3.71 \pm 2.25 | 1.54 \pm 0.89 |
| Sand (%) | 29.44 \pm 10.56 | 34.61 \pm 6.76 |
| Silt (%) | 47.46 \pm 7.07 | 44.78 \pm 5.24 |
| Clay (%) | 16.61 \pm 2.66 | 19.08 \pm 2.55 |
| Chlorophyll α (μ g ⁻¹ g ⁻¹ sediment) | 36.89 \pm 6.16 | 26.82 \pm 4.35 |
| Sediment temperature ($^{\circ}$ C) | 19.20 \pm 0.17 | 20.20 \pm 0.45 |

589

590

591 Table 2: Comparison of mean estimates of sediment CO₂ efflux from a range of intact and cleared
 592 mangrove forests, ± SE. * indicates no overall mean values provided

| Intact Mangrove Forests | | | | |
|---------------------------------------|----------------------------------|--|--|-------------------------------|
| Species | Location, number of sites | Overall mean CO₂ efflux ± SE (mmol CO₂ m⁻² d⁻¹) | Overall mean CO₂ efflux ± SE (μmol CO₂ m⁻² s⁻¹) | Reference |
| <i>Avicennia marina</i> | New Zealand , 13 | 168.4 ± 45.8 | 1.95 ± 0.53 | This study |
| <i>Avicennia marina</i> | New Zealand , 4 | 114.0 ± 19.9 | 1.32 ± 0.23 | Lovelock et al, (2014) |
| <i>Avicennia marina</i> | South and North Australia , 4 | 107.1 ± 45.8 | 1.24 ± 0.53 | Lovelock et al, (2014) |
| <i>Avicennia marina</i> | New Caledonia, 1 | 88.2 ± 23.7 | 1.02 ± 0.27 | Leopold et al., (2013) |
| <i>Avicennia marina</i> | South Australia, 3 | *Ranging from 73.73 to 117.89 throughout the year | *Ranging from 0.85 to 1.36 throughout the year | Livesley and Andrusiak (2012) |
| | Global estimate, 82 | 61 ± 56 | 0.71 ± 0.65 | Bouillon et al., (2008) |
| | Global estimate, 140 | 69 ± 8 | 0.80 ± 0.09 | Alongi, (2014) |
| Cleared Mangrove Forests | | | | |
| Species | Location, number of sites | Overall mean CO₂ efflux ± SE (mmol CO₂ m⁻² d⁻¹) | Overall mean CO₂ efflux ± SE (μmol CO₂ m⁻² s⁻¹) | Source |
| <i>Avicennia marina</i> | New Zealand , 23 | 133.9 ± 37.2 (0 - 8 years since clearing) | 1.55 ± 0.43 (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 | *Declining from 2.10 to 7.72 over 20 years | Lovelock et al., (2011) |
| Tropical mangrove | Bali, Indonesia, 1 | *Shrimp pond floors: 99.4; Shrimp pond walls: 272.2 | *Shrimp pond floors: 1.15; Shrimp pond walls: 3.15 | Sidik and Lovelock, (2013) |
| Tropical mangrove | Gazi Bay, Mombasa, Kenya | 88.62 (343 days since clearing) | 1.03 (343 days since clearing) | Lang'at et al., (2014) |

593