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Discussions

Sediment CO$_2$ efflux from cleared and intact temperate mangroves and tidal flats

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Abstract

Temperate mangroves in Southern Australia and New Zealand have been increasing in area over the past 50 years, whereas tropical mangroves have declined by 30–50 % over a similar time frame. Tropical mangroves are understood to be an important car-
5 bon sink and carbon dioxide (CO$_2$) emissions following clearance are estimated to be comparable or greater than CO$_2$ emissions following the clearance of many terrestrial forest systems. Recreational and amenity values or perceived loss of other estuarine habitats due to expanding temperate mangrove forests have resulted in clearing of temperate mangroves. In this study, we investigated the impact of temperate mangrove
10 clearance on CO$_2$ efflux from the sediment to the atmosphere along with a range of other biotic and abiotic factors.

Significantly higher CO$_2$ efflux rates were measured in cleared (1.34 ± 0.46 µmol m^2 s^{-1}) and intact mangrove sites (2.31 ± 0.72 µmol m^2 s^{-1}) than in tidal flats (−0.23 ± 0.27 µmol m^2 s^{-1}). Site and sediment characteristics such as sediment carbon
15 and nitrogen concentration, chlorophyll α concentration, grain size, mangrove height, macrofaunal abundance, sediment temperature and moisture were strongly correlated with sediment CO$_2$ efflux. Our results suggest that carbon stored within temperate mangrove sediment is released over a period of years to decades after mangrove clearance. CO$_2$ efflux from intact and cleared temperate mangroves was found to be comparable
20 to rates observed in the tropics. Disturbance of the surface biofilm resulted in elevated CO$_2$ efflux across all habitats, suggesting the important role of surface biofilm communities in mediating CO$_2$ efflux.

1 Introduction

Mangroves are generally confined to the tropics, between latitudes 30° N and 30° S.
25 However, an estimated 0.2 to 1.4 % of mangroves are located outside this latitudinal range, growing in conditions which may be broadly characterised as temperate (Mor-

risey et al., 2010). Approximately 50 % of temperate mangrove forests are located in Southern Australia, 45 % in New Zealand, 3 % in Louisiana, and 0.5 % in South Africa (Morrisey et al., 2010; Alongi et al., 2012).

Temperate mangroves are subject to different climactic conditions, are characterised by a lower diversity of tree species and lower faunal abundance and diversity than in the tropics (Alfaro, 2006; Morrisey et al., 2010). While the area of tropical mangrove has declined by 30–50 % worldwide over the past 50 years (Duke et al., 2007; Donato et al., 2011; Giri et al., 2011; Spalding et al., 2010), the area of temperate mangroves has increased in many locations in Southern Australia and New Zealand (Morrisey et al., 2010). Rates of mangrove expansion, primarily based on aerial imagery from the 1940's and 1950's onwards, have been estimated at 2.1 % yr^{-1} (0.7–9.1 % yr^{-1}) in south-eastern Australian estuaries, and 4.1 % yr^{-1} (0–20.2 % yr^{-1}) in New Zealand estuaries (Morrisey et al., 2010).

Landward expansion of mangrove into salt marshes is typically observed in South Australia while mangrove expansion into tidal flats is typically observed in New Zealand (Morrisey et al., 2010). The expansion of New Zealand mangrove has been linked to sedimentation and vertical accretion of tidal flats (Swales et al., 2007; Stokes et al., 2010), as well as other factors such as increased nutrient input (Saintilan and Williams, 1999), climate (Burns and Ogden, 1985), and changes in sea level (Rogers et al., 2006).

The recent expansion of mangrove 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 clearings have occurred over the past 60 years, ranging in scale from small < 0.1 ha clearings to clearances exceeding 100 ha (Morrisey et al., 2010; Lundquist et al., 2014b).

Tropical mangrove ecosystems store an estimated 937 t C ha^{-1}, approximately 25 % within their tree biomass and 75 % within the sediment (Alongi, 2012). Only a few studies have been conducted which measure the carbon storage of temperate mangrove

sediment (Yang et al., 2013; Lovelock et al., 2010; Howe et al., 2009) or tree biomass (Woodroffe, 1985; Mackey, 1993; Comley and McGuinness, 2005; Clough et al., 1997). Further, the impact of clearing temperate mangrove on carbon storage and emission of carbon dioxide (CO_2) from the sediment has not been investigated. Quantifying sources and sinks of carbon has become increasingly important due to the rapid rise in atmospheric CO_2 concentrations and associated impact on global climate (IPCC, 2013).

Sediment CO_2 efflux from mangroves and adjacent tidal flats originates from photosynthetic and chemoautotrophic microbial degradation of organic matter within the sediment (Lovelock, 2008; Leopold et al., 2015), as well as respiration of living roots (Bouillon et al., 2008a). When cleared, the accumulation of mangrove-derived carbon is halted, other than from adjacent intact mangrove, yet the release of CO_2 from the system continues. The rates of sediment CO_2 efflux from cleared tropical mangroves have been shown to be significant (Lovelock et al., 2011; Sidik and Lovelock, 2013). It is estimated that tropical mangrove deforestation generates emissions of 0.02–0.12 Pg carbon per year, approximately 10 % of emissions from deforestation globally, yet account for only 0.7 % of tropical forest area (Donato et al., 2011; Giri et al., 2011; Van der Werf et al., 2009).

Numerous abiotic and biotic factors may influence the CO_2 efflux from mangrove sediments, such as sediment carbon concentration (Leopold et al., 2013; Chen et al., 2010, 2012, 2014), sediment nitrogen concentration (Lovelock et al., 2014; Chen et al., 2010, 2012), sediment grain size (Chanda et al., 2014; Chen et al., 2010), mangrove respiration (Chanda et al., 2013; Lovelock, 2008; Lovelock et al., 2014; Poungparn et al., 2009), sediment water content (Alongi, 2009), redox potential (Leopold et al., 2013; Chen et al., 2010, 2012; Chanda et al., 2014), and sediment temperature (Chen et al., 2012).

Sediment microbial communities present on the sediment surface, also called biofilm communities, comprised of cyanobacteria, diatoms, and other microalgae, are important contributors to primary production (Bouillon et al., 2008b) and may also play an important role in mediating CO_2 exchange from the sediment (Leopold et al., 2013,

2015; Alongi et al., 2012). Anaerobic mineralisation processes within mangrove sediments may lead to the accumulation of high amounts of reduced compounds, such as sulphides and ammonium (Jorgensen, 1978), which may fuel chemoautotrophic activity. Chemoautotrophic organisms have been shown to be a major component of the carbon cycle in coastal sediments (Boschker et al., 2014; Lee et al., 2015; Evrard et al., 2008). In addition, macrofauna may influence CO_2 efflux through the consumption of mangrove detritus, sediment and associated organic material or by irrigation and reworking of the sediment and supporting increased aerobic degradation of carbon and other geochemical processes (Kristensen, 2001; Dean, 2008; Chareonpanich et al., 1993).

The aim of this study was to assess the effect of temperate mangrove clearance on sediment CO_2 efflux and sediment characteristics. The specific objectives were: to quantify the sediment CO_2 efflux from intact and cleared mangroves and adjacent tidal flats; to investigate the relationship between abiotic and biotic factors and sediment CO_2 efflux; and to estimate short and long-term effects of temperate mangrove clearance on CO_2 efflux.

2 Materials and methods

2.1 Study species

Only one species of mangrove occurs in New Zealand, *Avicennia marina* subsp. *australasica*, found from the top of the North Island to the central North Island (Morrisey et al., 2010). The southernmost limit (38°) is most likely restricted by a combination of low temperatures (Duke, 1990), lack of suitable conditions for propagule dispersal, and lack of suitable habitat (de Lange and De Lange, 1994). Mature mangrove trees have been documented ranging in size from less than 1 m 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 40 clearance sites covering a large proportion of the geographic range of mangroves in northern New Zealand (35°43′ to 37°41′ S) (Fig. 1). At each site we sampled at mangrove clearance (40 sites), adjacent intact mangroves (18 sites), and tidal flats (30 sites) where existing/accessible. The proximity of some cleared mangrove sites (< 500 m apart) meant that adjacent mangroves or tidal flats were shared at 19 locations. The time since mangrove clearance within our study ranged from 1 month to over 13 years. Clearance sites ranged in size from < 0.1 ha to > 13 ha. Besides the difference in years since clearing and size the sites differed in shape, hydrodynamic exposure, and method of clearance (Table 1 in the Supplement). Mean air temperature for the sites ranged from 19 °C during summer to 11 °C during winter, and mean monthly rainfall ranged 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).

Sampling was undertaken during late spring and summer (November 2013–January 2014). Weather conditions during sampling were sunny or overcast, with no rainfall.

2.3 Sediment CO_2 efflux measurements

Three sediment CO_2 efflux measurements were conducted within each habitat type (mangrove, clearance, tidal flat) at each site. CO_2 efflux was measured in the centre of the clearance, adjacent mangroves (> 10 m from clearance) and adjacent tidal flats (> 10 m from clearance) if existing/accessible.

The sediment CO_2 efflux was measured at low tide, between 8 a.m. and 6 p.m. local time, using an infrared CO_2 analyser (Environmental Gas Monitor (EGM-4) with a soil respiration chamber (SRC-1, PP Systems Ltd., Amesbury, MA, USA). 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. Chamber height was measured during

each measurement as collar insertion varied based on sediment characteristics. Air and soil temperature (Novel Ways temperature probe) and moisture (CS620, Campbell Scientific, Logan, UT, USA) to a depth of 12 cm was measured with each CO_2 efflux measurement. In addition to measuring CO_2 efflux in intact (undisturbed) sediment, soil CO_2 efflux was re-measured at the same location after the removal of the surface biofilm, by removing the top ~ 2 mm of surface sediment using a spatula.

Sediment CO_2 efflux was calculated from linear regression of the CO_2 concentration within the chamber over time; chamber CO_2 concentration was measured at 5 s intervals over a 90 s period. For each habitat the mean CO_2 efflux rate was calculated from the three chamber flux measurements.

Measurements of sediment CO_2 flux from mangrove and tidal flats using dark chambers represent net CO_2 fluxes from heterotrophic and autotrophic processes. Our measurements of CO_2 flux were conducted using dark chambers, and therefore include uptake of CO_2 from chemoautotrophs but exclude the uptake of CO_2 by benthic microbial photoautotrophic processes. However, Leopold et al. (2013) observed no significant difference between light and dark measurements of sediment CO_2 efflux within *Avicennia marina*.

The relationship between CO_2 efflux and years since removal is likely to be confounded by the sediment carbon concentrations of the site immediately prior to mangrove clearance, as well as the sediment carbon concentrations and CO_2 efflux of the site after the mangrove derived carbon has been depleted. We adjusted for this by expressing clearance values as a proportion of the difference between adjacent mangrove and tidal flat values (CO_2^{Prop}), assuming that adjacent mangrove values represent values from the clearance site immediately prior to clearance, and adjacent tidal flat values represent values after the mangrove derived carbon at the site has been depleted. The following formula was used for this purpose, with output values expressed as a proportion from zero to one; ≥ 1 representing no difference (or higher) sediment CO_2 efflux within clearance than adjacent mangrove sites, and output values ≤ 0 representing no

difference (or lower) CO_2 efflux within clearance than adjacent tidal flat.

$$CO_2^{Prop} = (\text{Clearance} - \text{Tidal flat})/(\text{Mangrove} - \text{Tidalflat})$$

Sites from Auckland Airport, Waiuku and Weiti were not included in CO_2^{Prop} calculations due to an absence of mangrove sediment data.

2.4 Sediment characteristics

At each site three sediment samples were collected using two small sediment cores (2 cm deep, 2 cm in diameter). The sediment samples were kept frozen prior to being analysed.

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 ($n = 40$, ranging from 0.17 to 12.63 % total C) were acidified to remove the inorganic C (Brodie et al., 2011). Briefly, 300 mg sediment was mixed with 0.5 mL dionized water and 1.5 mL of 20 % HCL and then dried on a hot plate. Organic carbon concentration was then determined by running samples through the elemental analyser and subtracted from total C concentration to estimate the inorganic C concentration.

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, 500, 250 and 63 μm mesh sieves. Pipette analysis was used to separate the < 63 μm fraction into > 3.9 μm 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), coarse and very coarse sand (500–2000 μm), medium sand (250–500 μm), fine and very fine sand (63–250 μm), silt (3.9–62.9 μm) and clay (≤ 3.9 μm).

Chlorophyll α: one sediment sample per site was analysed for chlorophyll α. Within one month of sampling, the sample was freeze dried, weighed, then homogenised and a subsample (~ 5 g) taken for analysis. Chlorophyll α was extracted by boiling the sediment in 90 % ethanol, and the extract processed using a spectrophotometer (Shimadzu UV Spectrophotometer UV-1800). An acidification step was used to separate degradation products from chlorophyll α (Hansson, 1988; Moed and Hallegraeff, 1978).

2.5 Tree biomass and habitat characteristics

Within intact mangrove sites the average tree height (based on the height of the closest 5 mangrove trees to each 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 New Zealand *Avicennia marina* (Woodroffe, 1985). At two locations, Mangere (Auckland) and Hatea (Northland) mangrove height exceeded the range the allometric equation was designed for (determined from trees ranging in height from 40 to 248 cm) and measures of trunk circumference were instead used to estimate biomass (based on the trunk circumference at 30 cm height of the closest 5 mangrove trees to each sampling point). Measures of trunk circumference were not collected at all sites.

At each site a quadrat (0.5 m × 0.5 m) was sampled at three haphazardly placed locations (within a 10 m radius). Within each quadrat, visual observations (as defined below) were recorded for surface characteristics and then hand-raked to determine the abundance of infaunal bivalves. The following metrics were recorded for each 0.5 m × 0.5 m area: number of visible crab holes, number and species of epifauna on the surface (including primarily the gastropods *Amphibola crenata, Zeacumantus lutulentus, Diloma subrostrata,* and *Cominella glandiformis*), number of infaunal bivalves > 5 mm (including *Austrovenus stutchburyi and Macomona liliana)*, proportion of surface covered by mangrove leaf litter, proportion of surface covered by macroalgae, number of mangrove seeds and seedlings, and number of pneumatophores. The depth of oxic layer (cm), as a proxy for redox potential discontinuity, was also measured, de-

fined visually as the point at which anoxic sediments were first visually evident, usually determined by a marked colour change from tan to black or grey sediment. The depth of footprints (cm) was also measured as an indicator of sediment compaction.

Thirty four of forty mangrove clearance sites and twenty five of thirty tidal flat sites were sampled for macrofaunal community analysis. At each site, three randomly placed macrofaunal cores (13 cm diameter, 15 cm depth) were collected within 1 m of quadrats sampled for visual information. Macrofaunal cores were sieved through a 500 μm mesh and the residues stained with rose bengal and preserved in 70 % isopropyl alcohol in seawater. Unvegetated samples were then rinsed and sieved through a series of nested sieves, and then sorted and stored in 50 % isopropyl alcohol. Macrofauna were identified to the lowest taxonomic level practicable, usually to species. No macrofauna cores were collected from intact mangrove sites.

Due to the generally large amount of root material, samples from mangrove clearance were extensively rinsed and sieved to remove as many macrofauna as possible from vegetative material. Larger vegetative material, for which rinsing successfully removed 100 % of macrofauna, was removed from root material and set aside and all macrofauna identified. The remaining root mass was subsampled and the macrofauna identified and counted. The subsample proportion varied between samples with range of 9–100 % of remaining root mass subsampled; generally the subsample proportion ranged between 14–25 %. Macrofaunal abundance from root material was estimated by multiplying the counts within the subsample by the proportion of the root material that was sorted; total abundance was calculated as the combined abundance from the primary sample and the root material. Abundance data from individual macrofaunal species was also grouped based on functional traits; suspension feeders; deposit feeders; predators; scavengers; grazers; epifauna; top 2 cm (active in the top 2 cm), deep (active in depths > 2 cm); occupying a permanent burrow; simple hole or pit; or tube structure.

Root biomass in macrofaunal cores (13 cm diam., 15 cm depth) for 3 replicate samples at each site was also quantified. After sorting, all vegetative material was air dried

for one week on aluminium trays, and then oven dried at 70 °C for approximately 4 days until dry weight stabilised. Weights for each mangrove constituent were then recorded.

2.6 Data analysis

As data did not conform to normality, Kruskal–Wallis One Way Analysis of Variance on Ranks was used to determine differences in sediment CO_2 efflux and other site characteristics, between mangrove, clearance and tidal flat sites ($p < 0.05$). Kruskal–Wallis One Way Analysis of Variance on Ranks was also used to determine significant ($p < 0.05$) differences in CO_2 efflux between mangrove, clearance, and tidal flat before and after the biofilm was removed. If significant differences were detected, post-hoc pairwise comparisons were conducted using Dunn's method and Tukey's test, respectively.

Spearman's rank order correlation was used to test the relationships between abiotic and biotic site characteristics and both sediment CO_2 efflux and organic carbon concentration. Step-wise multiple regressions of normalised data was used to identify the contribution of individual site characteristics to CO_2 efflux.

To determine whether macrofaunal community composition was similar across sites (clearance and tidal flat), nonmetric multidimensional scaling and similar percentages analysis (SIMPER) based on Bray Curtis similarities (Clarke and Warwick, 1994) was conducted on the sum of square root transformed macrofauna data collected at each site (clearance and tidal flat).

Analysis of variance and Spearman's rank order correlation was conducted using Sigmaplot software (SYSTAT software Inc). PRIMER software (PRIMER-E Ltd) was used for macrofaunal community composition and regression analysis.

3 Results

Mean sediment CO_2 efflux measured from the intact and cleared mangrove sites was $2.31 \pm 0.72\,\mu\mathrm{mol}\,\mathrm{m}^2\,\mathrm{s}^{-1}$ and $1.34 \pm 0.46\,\mu\mathrm{mol}\,\mathrm{m}^2\,\mathrm{s}^{-1}$, respectively. Mean sediment CO_2 efflux from tidal flat sites was $-0.23 \pm 0.27\,\mu\mathrm{mol}\,\mathrm{m}^2\,\mathrm{s}^{-1}$. Significant differences were found between intact mangroves and tidal flats ($p < 0.01$) and cleared mangrove sites and tidal flats ($p < 0.01$) (Fig. 2).

Tree and sediment characteristics varied widely among sites (Table 1). Mangrove density ranged from 0.25 to 3 trees m^{-2}, mangrove height ranged from 103 to 410 cm, and mangrove above ground biomass ranged from 0.52 to 13.54 kg dry weight m^{-2} (5.2 to 135 t dry weight ha^{-1}). Organic carbon and nitrogen concentrations, clay content, and chlorophyll α concentrations were significantly higher in mangrove sites (intact and cleared) compared to the tidal flat sites ($p < 0.05$, Table 1).

Macrofaunal abundance was significantly ($p < 0.01$) higher in cleared sites compared to tidal flat sites, while Shannon–Wiener diversity index was significantly lower ($p = 0.03$). No significant difference was detected in number of taxa (Table 2). While there was overlap in macrofaunal community composition between clearance and tidal flat sites, SIMPER results indicate the average dissimilarity between clearance and tidal flat sites was 71.46 %. The top 10 species contributing 49.35 % of dissimilarity between clearance and tidal flat sites were *Potamopyrgus estuarinis*, Oligochaetes, *Paracorophium* sp., *Ceratonereis* sp., *Scolecolepides benhami*, Capitellidae, and *Zeacumantus lutulentus* which were all more abundant within clearance sites, and *Arthritica bifurca*, *Scoloplos cylindrifer* and *Prionospio aucklandica* which were more abundance within tidal flat sites (Table 2 in the Supplement).

Within intact mangrove, sediment CO_2 efflux and organic carbon content were negatively correlated with mangrove tree height (-0.54, $p = 0.02$, -0.47, $p = 0.05$, respectively), while sediment organic carbon content was positively correlated to mangrove density (0.57, $p = 0.01$). Sediment chlorophyll α concentration was also negatively correlated with mangrove tree height (-0.66, $p < 0.01$). Regression analysis indicated that

22.8 % of the CO_2 efflux from mangrove sites could be explained by soil temperature ($p < 0.05$).

Within cleared mangrove, CO_2 efflux was positively correlated to sediment organic carbon (0.36, $p = 0.02$) and nitrogen concentration (0.39 $p = 0.02$), silt (0.46, $p < 0.01$) and clay (0.48, $p < 0.01$) content, and negatively correlated to soil temperature (−0.35, $p = 0.03$), with similar correlations occurring between sediment organic carbon concentration and other sediment characteristics. CO_2 efflux and sediment organic carbon content were also correlated to a number of macrofaunal species and sediment organic carbon concentration was correlated with the abundance of macrofaunal suspension feeders (0.35, $p = 0.04$), deposit feeders (0.36, $p = 0.04$), predators (0.38, $p = 0.03$) and grazers (0.50, $p < 0.01$). Regression analysis revealed that 25.2 % of the CO_2 efflux from clearance sites could be explained by sediment clay content ($p < 0.01$).

Sediment organic carbon concentration was negatively correlated to years since clearance (−0.39, $p = 0.01$), yet no correlation between age of clearance and CO_2 efflux was observed. However, by expressing clearance CO_2 efflux as a proportion of the difference between adjacent mangrove and tidal flat efflux (CO_2^{Prop}) a significant correlation was observed (−0.65, $p < 0.05$); CO_2 efflux declining logarithmically over time ($p < 0.05$) (Fig. 3).

Similar to clearance sites, CO_2 efflux within tidal flat sites was correlated to sediment organic carbon (0.52, $p < 0.01$) and nitrogen (0.42, $p = 0.03$) concentration, silt (0.52, $p < 0.01$) and clay (0.55, $p < 0.01$) content, soil temperature (−0.40, $p = 0.03$) and moisture (0.42, $p = 0.02$). A number of correlations were observed between CO_2 efflux and macrofaunal species abundance, as well as the abundance of macrofaunal species occupying permanent burrows (−0.43, $p = 0.03$) and tube structures (0.45, $p = 0.02$). Sediment organic carbon concentration was also correlated with the abundance of a number of macrofaunal species, as well as macrofaunal grazers (0.56, $p < 0.01$). Multiple regression analysis revealed that 39.7 % of the CO_2 efflux from tidal flat sites was explained by sediment chlorophyll *a* and silt content ($p < 0.01$).

Removing the surface biofilm resulted in up to 2.98 fold higher sediment CO_2 efflux at all sites ($P < 0.01$) (Fig. 2). Following the removal of the surface biofilm, mean sediment CO_2 efflux was significantly higher at mangrove and mangrove clearance sites than at tidal flat sites ($P < 0.01$).

4   Discussion

Our mean CO_2 efflux values (intact: $2.31 \pm 0.72\,\mu mol\,m^2\,s^{-1}$, cleared: $1.34 \pm 0.46\,\mu mol\,m^2\,s^{-1}$, tidal flats: $-0.23 \pm 0.27\,\mu mol\,m^2\,s^{-1}$) are within the range reported from other temperate and tropical *Avicennia marina* and other mangroves; though higher than previously reported (Lovelock, 2008; Lovelock et al., 2014; Leopold et al., 2013, 2015; Chen et al., 2010, 2012, 2014; Chanda et al., 2014). Our surface sediment organic carbon concentrations (3.18 ± 0.57 %, 2.35 ± 0.28 %, and 0.89 ± 0.14 %, respectively) are comparable to other temperate and tropical mangrove locations (Yang et al., 2013; Livesley and Andrusiak, 2012; Kristensen et al., 2008), yet lower than values observed at many tropical mangrove locations (Leopold et al., 2013; Chen et al., 2010, 2012, 2014; Chanda et al., 2014; Lang'at et al., 2014).

4.1 CO_2 efflux from temperate mangrove sediment

The primary factors effecting CO_2 efflux from temperate mangrove sediment are the sediment and biological characteristics of the site, including microbial and macrofaunal activity, as well as respiration from living root material (Chanda et al., 2013; Lovelock, 2008; Lovelock et al., 2014; Poungparn et al., 2009; Leopold et al., 2013; Chen et al., 2014). The considerable variation in sediment CO_2 efflux among sites, from -0.94 ± 1.10 to $12.47 \pm 2.78\,m^2\,s^{-1}$, appears to be associated with differences in these factors. High variability in mangrove sediment CO_2 efflux was also reported by Chen et al. (2010, 2012) and was associated with elevated nutrient levels enhancing soil

microbial respiration and nitrogen metabolism, along with tidal position and soil characteristics (soil organic matter, nitrogen and phosphorous concentrations).

In our study CO_2 efflux was higher beneath shorter mangroves. This might be related to differences in light or nutrient availability, stimulating the growth and activity of photosynthetic (Lovelock, 2008; Leopold et al., 2013) or chemoautotrophic microbial communities (Boschker et al., 2014; Lee et al., 2015; Evrard et al., 2008). This is supported by higher chlorophyll α concentrations in these stands, an indicator of increased microphytobenthic activity (Leopold et al., 2013; Bishop et al., 2007). In addition, CO_2 efflux was found to increase with increasing soil temperature, which may also be related to increased light penetration and associated microbial activity. Our findings are consistent with Alongi et al. (2012) who observed increasing belowground net primary productivity at sites with shorter mangrove and declining canopy cover.

The locations with the highest CO_2 efflux values could be broadly characterised as impacted; close to large human populations (Matua, Waiuku, Welcome Bay), and with elevated sediment organic carbon, nitrogen and chlorophyll α concentration, silt and clay content. The locations where CO_2 uptake was observed (Tairua, Whangamata, Hatea) showed no consistent trends in sediment characteristics measured. However, sediment organic carbon and the fraction of silt and clay at Tairua and Hatea were elevated compared to other mangrove sites. A dense algal matt was also present on the sediment surface at Tairua and Hatea, possibly acting as a barrier to CO_2 being released from the sediment, or influencing CO_2 efflux rates through chemoautotrophic activity. CO_2 uptake has also been reported in other studies (Lovelock, 2008; Chanda et al., 2014; Leopold et al., 2015) which Leopold et al. (2015) suggested was related to the presence of biofilm microbial communities, as CO_2 uptake changed to efflux following biofilm removal.

4.2 Effect of mangrove clearance on sediment CO_2 efflux

Sediment CO_2 efflux and organic carbon concentration from cleared mangroves appeared lower than from intact mangrove, although the difference was not significant

($p > 0.05$, Fig. 2). Lower sediment CO_2 efflux within cleared mangrove is likely due to lower organic carbon concentrations within clearance sediment (Table 1), as well as the absence of respiration from living roots.

CO_2 efflux from cleared mangrove was found to increase with increased organic carbon, nitrogen and chlorophyll α concentration, silt and clay content and microbial and macrofauna activity. Capitellidae have previously been identified as potential indicators for high organic material and other pollutants (Dean, 2008), and were associated increased CO_2 efflux within mangrove clearance in our study. However, CO_2 efflux declined with increasing abundance of many other polychaete species, which have been positively associated with increased sediment CO_2 efflux in other studies (Kristensen, 2001; Dean, 2008; Chareonpanich et al., 1993). This is likely due to the sensitivity of polychaetes to the sediment conditions of the site, with lower abundance of many polychaetes at sites with greater disturbance or organic enrichment (and higher CO_2 efflux) rather than a measurable impact of polychaete abundance on CO_2 efflux. This is consistent with other studies which have shown that temperate mangrove and mangrove clearance typically possess high proportions of disturbance tolerant species such as oligochaetes and *Capitella* spp., with an absence of infaunal bivalves, when compared to tidal flat which typically supports higher proportions of bivalves and spionid polycheates (Lundquist et al., 2012, 2014a; Bulmer and Lundquist, 2014).

Other factors likely to influence sediment CO_2 efflux from cleared sites include the site histories prior to clearance, the clearance method, and other site characteristics. The highest CO_2 efflux was observed at sites where mechanical mulchers were used to clear above ground biomass and the mulch was left on the sediment to disperse (Welcome Bay and Waiuku). The increased CO_2 efflux is likely related to the increased sediment organic carbon concentration at these sites. Higher sediment carbon concentrations have also previously been observed in older mangrove than younger mangrove growing at the edge of the stand (Lovelock et al., 2010). This suggests that the clearance of older mangrove is likely to result in higher CO_2 efflux than the clearance of younger, less established, mangrove. This may also be related to the protection offered

by seaward mangroves, enabling greater accumulation of carbon within the centre of the stand (Yang et al., 2013). At clearance sites where large areas of sediment are disturbed, increased CO_2 efflux may occur due to increased oxygenation of the sediment (Lovelock et al., 2011) or disturbance of the sediment microbial communities (Leopold et al., 2013). Site size, shape and exposure may also influence CO_2 efflux, due to impact of these characteristics on site recovery. For example, smaller more exposed clearance sites at the edge of mangrove may be more likely to transition towards tidal flat characteristics than larger, less exposed sites (Lundquist et al., 2012, 2014a; Bulmer and Lundquist, 2014).

While sediment organic carbon concentration declined with the age of clearance, no significant correlation between age of clearance and CO_2 efflux was observed. This is likely due to differences in site sediment characteristics, size, exposure, and method of removal that confound our ability to see temporal differences. By adjusting for variation in sediment characteristics between clearance sites, expressing clearance CO_2 efflux as a proportion of the difference between adjacent mangrove and tidal flat CO_2 efflux (CO_2^{Prop}) we observed a significant logarithmic decline in CO_2 efflux from clearance habitat over time, suggesting that the majority of CO_2 efflux from cleared temperate mangrove occurs during the first 6 years following clearance. This is consistent with other studies which have shown a decline in CO_2 efflux from tropical mangrove clearance sediment following clearing (Lovelock et al., 2011; Lang'at et al., 2014). Lovelock et al. (2011) observed that CO_2 efflux from cleared mangrove growing in peat soils declined logarithmically with time, from 7.6 to 2.1 $\mu mol\, m^{-2}\, s^{-1}$ over a 20 year period, reaching a relatively constant level at around 2 $\mu mol\, m^{-2}\, s^{-1}$ four years after clearing. The rate of CO_2 efflux was related to the microbial degradation of organic matter in the soils. Lang'at et al. (2014) observed CO_2 efflux from tropical mangrove sediment increased two months after mangrove clearance by approximately three fold before returning to comparable levels to adjacent mangrove approximately five months after removal. The increase in CO_2 efflux was attributed to rapid decomposition of fine root

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

4.3 CO_2 efflux from tidal flat sediment

Sediment CO_2 efflux from tidal flats was significantly compared to intact and cleared mangrove sites. This is likely due to the absence of respiration from mangrove roots as well as lower microbial activity, reflected by significantly lower sediment organic carbon, nitrogen, and chlorophyll concentrations, and coarser sediment grain size. Similar observations were made by Leopold et al. (2013), who observed lower sediment CO_2 efflux within tidal flats than intact *Avicennia marina* stands in New Caledonia and attributed this primarily to lower organic matter within the tidal flat sediment.

The CO_2 efflux from tidal flat sites was driven by similar factors observed within clearance sites such as increasing organic carbon, nitrogen and chlorophyll a concentration, silt and clay content and microbial activity. CO_2 efflux from tidal flats was also related to macrofaunal abundance, increasing with crab burrows abundance, likely related to the consumption and collection of organic material, including mangrove detritus and microalgal matts, as well as turning over sediment by digging and maintaining burrows by crabs (Kristensen, 2008; Pülmanns et al., 2014). As observed within cleared mangrove sites, CO_2 efflux was negatively correlated to the abundance of a number of species of polychaetes, suggesting the measurable effect of polychaetes on CO_2 efflux have been confounded by other factors.

4.4 Effect of biofilm (removal) on sediment CO_2 efflux

The removal of the surface biofilm resulted in elevated sediment CO_2 efflux across all sites measured (Fig. 2) as well as resulting at efflux at all sites where CO_2 uptake had previously occurred. Similar findings have been documented in other studies, indicating that surface biofilm communities play an important role in mediating sediment-atmosphere CO_2 exchange in mangroves and tidal flats (Leopold et al., 2013, 2015;

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Alongi et al., 2012). Microorganisms firmly attached to surface sediment by means of an extracellular polymeric substance may form a biofilm matt which acts as a barrier to the flow of CO_2 from the sediment, which when removed results in a rapid increase in CO_2 efflux (Leopold et al., 2013). Aerating the surface sediment by removing the biofilm results in an increase in CO_2 efflux due to the oxidisation of relatively labile fractions exposed to increased oxygen concentration (Lovelock et al., 2011). This fraction is quickly depleted before the slower decomposition of refractory pools dominates CO_2 efflux (Lallier-Vergas et al., 2008), with CO_2 efflux returning to pre-disturbed levels within days after disturbance in sediment core incubations (Lovelock et al., 2011).

5 Conclusions

Sediment CO_2 efflux varied considerably across sites, representing differences in site characteristics and history. Our results suggest that CO_2 efflux from temperate mangrove sediment is strongly affected by microbial activity, particularly the activity of sediment biofilm communities. We found that carbon stored within temperate mangrove sediment is released over a period of years to decades after mangrove clearance, in rates comparable to clearance of tropical mangrove.

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Table 1. Mean sediment characteristics from intact and cleared mangrove and tidal flat sites, ±SE.

	Mangrove ($n = 18$)	Clearance ($n = 40$)	Tidal flat ($n = 30$)
Remaining mangrove root mass (g core^{-1})	nd	19.3 ± 1.73	na
Organic Carbon (%)	3.18 ± 0.57[c]	2.35 ± 0.28[c]	0.89 ± 0.14[ab]
Nitrogen (%)	0.42 ± 0.06[c]	0.31 ± 0.03[c]	0.20 ± 0.02[ab]
Gravel (%)	2.72 ± 1.66	1.10 ± 0.53	0.82 ± 0.27
Coarse Sand (%)	2.88 ± 0.83	3.95 ± 0.94	4.37 ± 0.97
Medium Sand (%)	9.98 ± 3.25	10.94 ± 2.03	16.36 ± 3.36
Fine Sand (%)	27.45 ± 5.23	29.45 ± 3.39	39.81 ± 4.83
Silt (%)	41.49 ± 5.94	39.33 ± 3.76	29.26 ± 5.11
Clay (%)	15.47 ± 2.09[c]	15.23 ± 1.88[c]	9.37 ± 1.66[ab]
Chlorophyll α (mg^{-1} g^{-1} sediment)	43.08 ± 8.44[c]	27.02 ± 2.96[c]	17.26 ± 2.19[ab]
Phaeophytin (mg^{-1} g^{-1} sediment)	4.97 ± 0.58	3.90 ± 0.46[c]	2.95 ± 0.51[b]
Air temperature (°C)	23.84 ± 0.18	24.03 ± 0.08	23.83 ± 0.14
Soil Temperature (°C)	19.41 ± 0.56	20.44 ± 0.37	20.65 ± 0.44

[a] Significantly different to mangrove sites,
[b] significantly different to clearance sites,
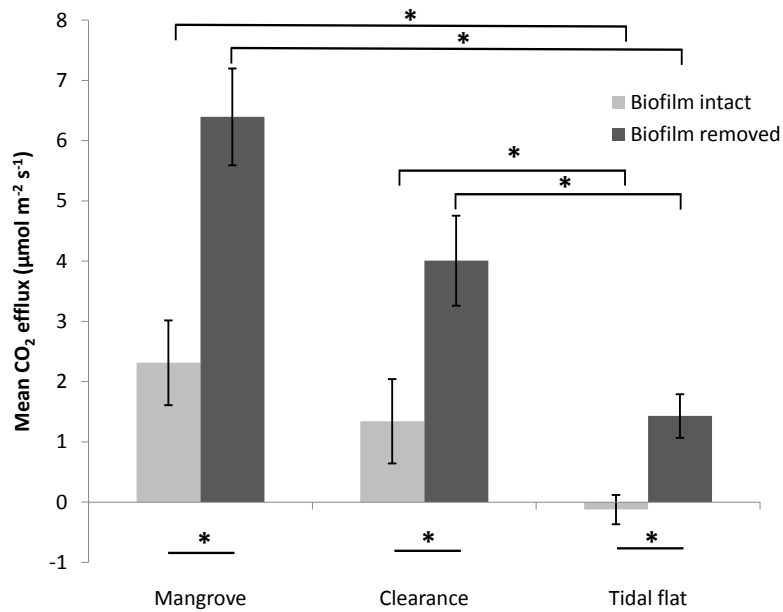[c] significantly different to tidal flat sites ($p < 0.05$).

Table 2. Mean benthic macrofaunal community characteristics from clearance and tidal flat sites, ±SE.

	Clearance ($n = 34$)	Tidal flat ($n = 25$)
Macrofauna abundance (individuals/core)[*]	258.61 ± 61.66	89.03 ± 20.97
Number of taxa	16.32 ± 0.86	15.88 ± 1.05
Shannon–Wiener Diversity Index[*]	1.65 ± 0.09	1.95 ± 0.09

[*] Significant difference between clearance and tidalflat sites ($p < 0.05$).

Figure 1. Location of the study sites (•), throughout North Island, New Zealand.

Figure 2. Mean sediment ($\pm$ SE) CO_2 efflux ($\mu mol\, m^{-2}\, s^{-1}$) before and after surface biofilm was removed, from intact mangrove ($n = 18$), mangrove clearance ($n = 40$), and tidal flat ($n = 30$) sites. * Significant difference ($p < 0.05$).
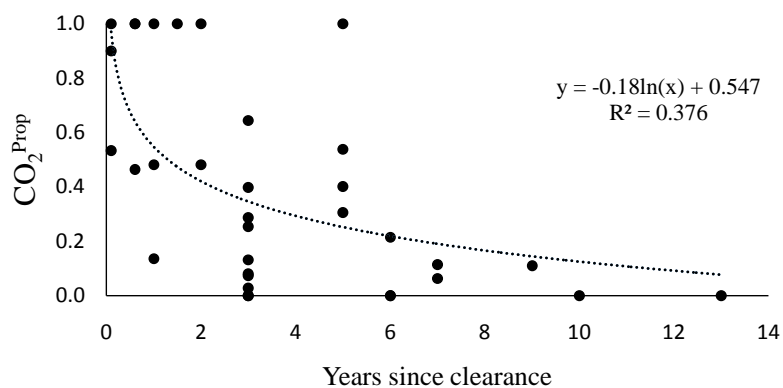
$$y = -0.18\ln(x) + 0.547$$
$$R^2 = 0.376$$

Figure 3. CO_2 efflux ($\mu mol\, m^{-2}\, s^{-1}$) from clearance sites expressed as a proportion of the difference between adjacent mangrove and tidal flat sites (CO_2^{Prop}), $n = 34$.