

Overview comment (to all referees)

We would like to acknowledge the helpful comments received by the referees. Here we address two of the main concerns expressed by the referees. We note that the referees expressed a recommendation that while the manuscript contained a large amount of valuable information, it should focus on the main factors influencing CO₂ efflux. In addition the referees asked for a more detailed description of the methods. We have addressed these concerns and suggestions by:

- Omitted the tidal flat data to concentrate on CO₂ efflux from intact and cleared mangrove forest sites and the main factors influencing the sediment CO₂ efflux.
- Removed the macrofaunal data
- We have reassessed the criteria for including flux data. In the revised version only fluxes where the r^2 of the linear regression (increase of CO₂ concentration vs time) exceeds 0.8. In general, r^2 values of less than 0.8 occurred at sites where there was minimal change in CO₂ efflux, typically less than $\pm 0.4 \mu\text{mol m}^{-2} \text{s}^{-1}$. While it is possible that the flux at these sites exhibits a non-linear trend, we have removed them to in order to strengthen the interpretation of the remaining dataset.
- This resulted in a decline in the number of clearance sites from 40 to 23, and intact mangrove forest sites from 18 to 13.
- While working on the calculations we identified an error in the CO₂ efflux calculation script (the chamber volume was overestimated by about 40 %) and we re-calculated all sediment CO₂ efflux values, re-did all related statistical tests, corrected the tables and figures.

The second point raised by referee#3 was in regards to the procedure of the CO₂ flux measurements, i.e. the possible continuation of photosynthesis if measurements were made immediately after the chamber deployment. Based on this we undertook additional measurements to test the impact of pre shading the sediment for > 30 minutes prior to dark CO₂ efflux measurements. We selected an existing location (Hatea 1) where CO₂ uptake had previously been measured. The manuscript has been modified to include the results of this experiment.

We compared control and biofilm removed measurements using identical methodology to that described in the manuscript. Relevant sections are included below:

2.3.1 Pre-shading the sediment

Frames (0.5 m²) were located approximately 20 cm above the sediment surface. The frame was completely covered by layered cloth to exclude light penetration. At site Hatea 1, three frames were deployed throughout the mangrove forest, at least 10 m from each other and the mangrove edge. After 30 minutes of shading, two CO₂ efflux measurements using a dark

respiration chamber were conducted at different locations within the 0.5 m² area, before and after the removal of the surface biofilm. The biofilm (top ~2 mm of surface sediment) was scraped off using a spatula. Biofilm removed measurements were collected immediately following biofilm intact measurements in the identical location. Corresponding dark CO₂ efflux measurements were also conducted at locations that had not been pre-shaded (control) adjacent to each shaded measurement, as well as corresponding biofilm removed measurements to account for heterogeneity in sediment conditions.

2.3.2 Sediment CO₂ efflux from intact and cleared temperate mangrove

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

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

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

Sediment CO₂ efflux was calculated from linear regression of the CO₂ concentration within the chamber over time. Only regressions with r^2 values ≥ 0.8 were used for flux calculations.

The sediment CO₂ efflux rate was calculated as follows.

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

Where $\Delta\text{CO}_2/\Delta t$ is the change in CO_2 concentration over time, based on the slope of the linear regression ($\mu\text{mol mol}^{-1}$), t is time (s), P is the atmospheric pressure (Pa), V is the volume of the chamber including collar (m^3), A is the surface area covered by each chamber (0.007854 m^2), T is the temperature (K), R is the ideal gas constant, $8.20528 \text{ m}^3 \text{ PaK}^{-1} \text{ mol}^{-1}$.

We note that as part of a separate study we also undertook similar testing within intact mangrove at a new location (Whangateau 2), with similar results which we include in the response to referees but not the manuscript. A total of 18 measurements were collected for each treatment at Whangateau 2 (control biofilm intact, and control biofilm removed, shaded biofilm intact, shaded biofilm removed).

Statistical analysis used:

A Shapiro-Wilk test was used to test normality. As data conformed to normality, paired t-tests were used to determine significant differences ($p < 0.05$) in shaded and control measurements of sediment CO_2 efflux within intact mangrove at Hatea 1.

Results of the additional testing at Hatea 1:

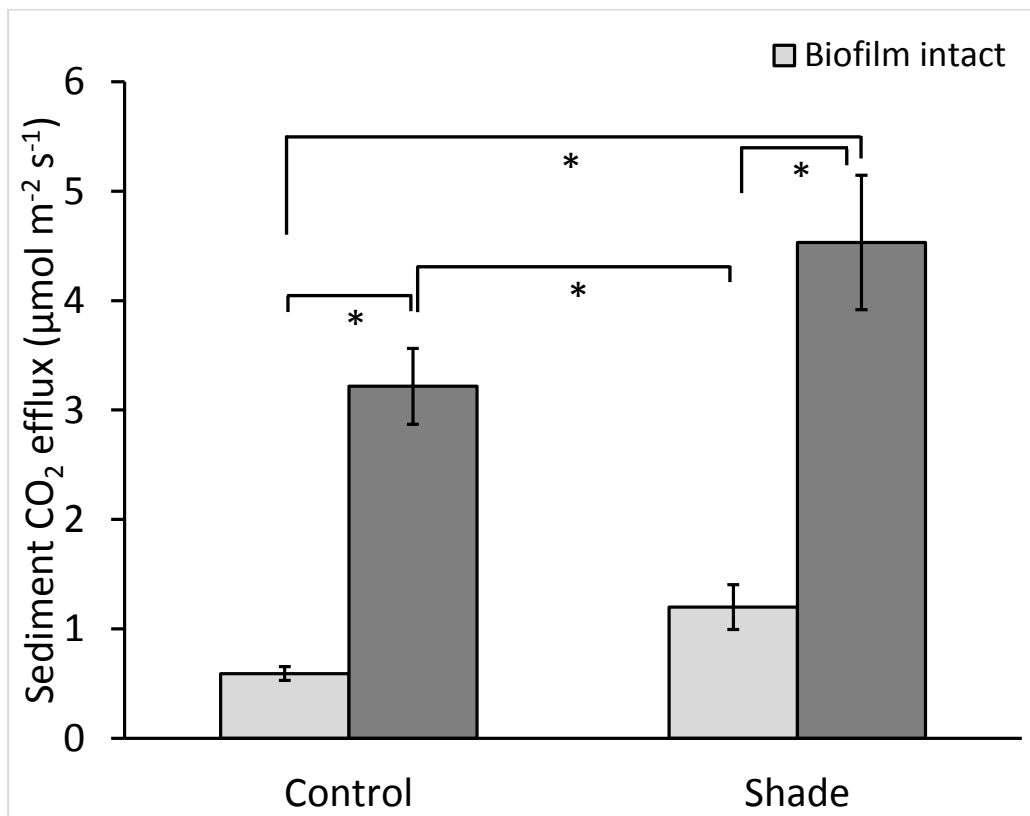


Figure 1. Mean sediment (\pm SE) CO_2 efflux ($\mu\text{mol m}^{-2} \text{ s}^{-1}$) before and after surface biofilm was removed, from control ($n = 6$), and pre-shaded sediment ($n = 6$) at intact mangrove site Hatea 1. *significant difference ($p < 0.05$)

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

Results of the additional testing at Whangateau 2:

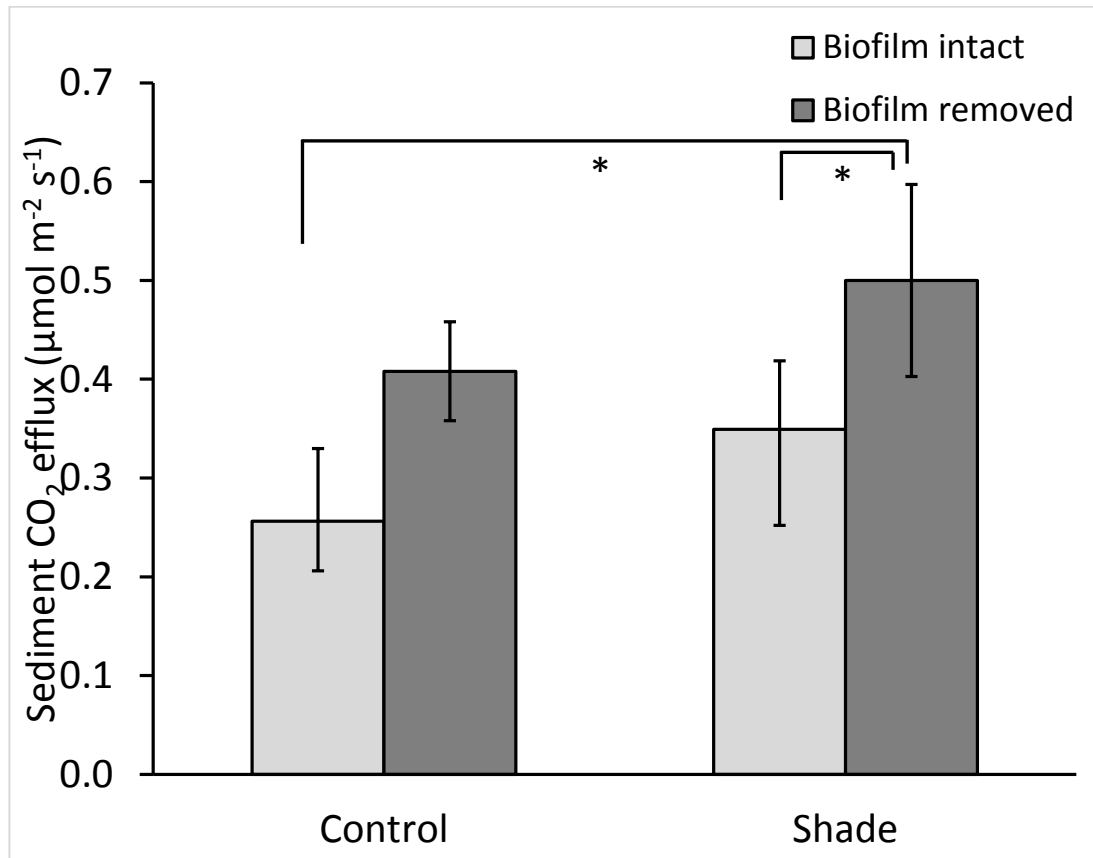


Figure 2. Mean sediment (\pm SE) CO₂ efflux ($\mu\text{mol m}^{-2} \text{s}^{-1}$) before and after surface biofilm was removed, from control ($n = 18$), and pre-shaded sediment ($n = 18$) at intact mangrove site Whangateau 2. *significant difference ($p < 0.05$)

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

Based on these results we derive the following conclusions.

- Our procedure to measure dark CO₂ efflux (which do not include > 30 minutes of pre shading) are valid.
- Lagged photosynthetic processes within the sediment of the dark incubation chamber are unlikely to be resulting in the CO₂ uptake observed at certain sites, or the significant increase in CO₂ efflux following biofilm removal.

We have included the following in the discussion as a potential explanation of the CO₂ uptake observed at certain sites in our study.

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

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

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

Chemoautotrophs have also been shown to fix carbon in intertidal sediment under dark conditions (Boschker et al., 2014; Lenk et al., 2011). In particularly at the interface of aerobic and anaerobic zones where large amounts of reduced compounds, such as sulphur, accumulate (Boschker et al., 2014; Lenk et al., 2011; Santoro et al., 2013; Thomsen and Kristensen, 1997)). This is consistent with what is observed in mangrove sediment, where aerobic to anaerobic transitions typically occur close to the sediment surface, with sulphur driven processes likely to dominate in anaerobic conditions (Kristensen et al., 2008).

Below is the response to individual referee's feedback.

Referee 3

Comment from referee: This manuscript presents a study on CO₂ emissions from exposed mangrove and tidal sediments with emphasis on the role of mangrove clearing. Measurements of CO₂ emissions were done at low tide during daytime at 18 to 40 sites depending on the environment. The fluxes were then correlated with a variety of sediment, flora and fauna parameters. Based on these correlations, it was concluded that sediment organic content, chlorophyll, grain size, mangrove height, macrofaunal abundance, temperature and sediment water content controlled the emissions. It was also concluded that stored organic carbon in the sediment is released within a few years, and that the surface biofilm of the sediment prevents release of CO₂.

The study is in principle very interesting and relevant, but the approach is not so good. Many of the methods used are not described adequately and some of them appear flawed (see below). I wonder why so much effort is put into the analysis of fauna communities, while the results on these are not used very much. The results section is poor as it only describes a wealth of correlations. Correlations can of course be an important tool to see if various parameters show the same trend, but they are not a proof for any causal relationship. Many of the correlations found here may very well be spurious.

Author's response: We appreciate the referee's helpful comments. We agree that greater consideration should be made regarding the rate of carbon released from mangrove forest following clearance and the relative contribution to the atmosphere. The manuscript has been modified to include a more detailed explanation of the methods, as well as the inclusion of significant linear regressions. We also modified the discussion substantially.

Comment from referee: I feel that the authors are benthic ecologists trying to do biogeochemistry. Some of the biogeochemical arguments are simply wrong. For example line 64-65, where it is stated that "CO₂ efflux originates from photosynthetic and chemoautotrophic microbial degradation of organic matter within the sediment". This is simply nonsense as all autotrophic processes fix CO₂ into organic carbon and not the other way around.

Author's response: We revised this statement

Changes in manuscript: An important component of the carbon cycle is the efflux of carbon dioxide (CO₂) from the sediment into the atmosphere (Raich and Schlesinger, 1992). Sediment CO₂ efflux (also called soil/sediment respiration) is the total of CO₂ released through root/mycorrhizae respiration (autotrophic respiration) and microbial respiration (heterotrophic respiration) associated with the decomposition of organic matter (Bouillon et al., 2008).

Comment from referee: Another example is line 211-213, where it is stated that the oxic layer in sediments is defined as the depth of the upper tan colored sediment and the anoxic zone is the black sediment below. This is not true. The tan colored sediment is oxidized and show where oxidized iron dominates. The oxic zone in mangrove sediments is only 2-3 mm deep and cannot be determined visually.

Author's response: We removed the oxic depth measurements from the manuscript.

Comment from referee: The authors have also difficulties with the terminology. They use both sediment and soil to denote the substratum. They must be consistent, and I prefer sediment. They should also use the term “mangrove” to denote the trees in a “mangrove forest”. Thus use the latter term to describe the environment.

Author's response: The manuscript has been modified to consistently use the terms sediment and mangrove forest.

Comment from referee: Another major (the most important) concern is the reliability of CO₂ flux measurements. I don't trust the obtained rates and believe that they are flawed. When CO₂ flux measurements are made on intertidal sediments at low tide in the middle of the day, it is required that the sediment must be pre-darkened for at least 30 minutes before initiating measurements. Otherwise, the benthic microalgae present may still assimilate CO₂ from the energy gained in light before the incubation. They can in fact continue with that for some time. As I understand the approach used here, the darkened chambers were placed on the sediment and fluxes were measured during a 90 second period right after. This will certainly lead to an underestimate and explain the uptake of CO₂ in the intertidal flats, which cannot occur in darkness. Chemoautotrophic carbon fixation is much too slow to account for such uptake. This flaw can certainly also explain the difference in fluxes found after removing the biofilm. Then the benthic microalgae are removed and no such delayed CO₂ assimilation occurs.

Author's response: Please refer to the earlier sections where this point is addressed.

Comment from referee: Abstract. Line 7: Here and throughout the MS, I recommend denoting the environment “mangrove forest” as “mangrove” refers to the trees only.

Author's response: The manuscript has been modified as recommended.

Comment from referee: Line 16-17: Here and throughout the MS, I recommend using the standard biogeochemical units for fluxes “mmol m⁻² d⁻¹”. At least, it must be “m⁻²” and not “m2”.

Introduction.

Author's response: Different units are used to express CO₂ efflux in terrestrial and coastal soil/sediment studies. We feel that the units $\mu\text{mol m}^{-2} \text{s}^{-1}$ are more appropriate given that the measurements were conducted over short period of time (90 sec) during low tide. However, we converted $\mu\text{mol m}^{-2} \text{s}^{-1}$ into $\text{mmol m}^{-2} \text{d}^{-1}$ to compare with other studies.

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

Intact Mangrove Forests				
Species	Location, number of sites	Overall mean CO₂ efflux \pm SE (mmol CO₂ m⁻² d⁻¹)	Overall mean CO₂ efflux \pm SE ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	Reference
<i>Avicennia marina</i>	New Zealand , 13	168.4 \pm 45.8	1.95 \pm 0.53	This study
<i>Avicennia marina</i>	New Zealand , 4	114.0 \pm 19.9	1.32 \pm 0.23	Lovelock et al, (2014)
<i>Avicennia marina</i>	South and North Australia , 4	107.1 \pm 45.8	1.24 \pm 0.53	Lovelock et al, (2014)
<i>Avicennia marina</i>	New Caledonia, 1	88.2 \pm 23.7	1.02 \pm 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 \pm 56	0.71 \pm 0.65	Bouillon et al., (2008)
	Global estimate, 140	69 \pm 8	0.80 \pm 0.09	Alongi, (2014)
Cleared Mangrove Forests				
Species	Location, number of sites	Overall mean CO₂ efflux \pm SE (mmol CO₂ m⁻² d⁻¹)	Overall mean CO₂ efflux \pm SE ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	Source
<i>Avicennia marina</i>	New Zealand , 23	133.9 \pm 37.2 (0 - 8 years since clearing)	1.55 \pm 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)

Comments from referee: Line 34: Change to “Temperate mangrove forests are subject to harsh climatic condition leading to a lower. . .”

Author’s response: The sentence has been modified. We note that while tropical mangrove habitat is subject to cyclones and typhoons, temperate mangroves are subject to frosts, which by comparison may not be considered harsh.

Changes to the manuscript: Temperate mangrove forests are subject to colder and generally more variable climatic conditions, and are typically associated with lower diversity of tree species and lower faunal abundance and diversity than in the tropics (Alfaro, 2006; Morrissey et al., 2010).

Comment from referee: Line 46-48: Isn’t vertical accretion and sea level rise of opposite direction and the latter will most likely not lead to mangrove expansion.

Author’s response: We modified this paragraph.

Changes to the manuscript: A landward expansion of mangroves into salt marsh is observed in Australia and USA (Cavanaugh et al., 2014; Saintilan et al., 2014) while mangrove expansion into tidal flats is typically observed in New Zealand (Lundquist et al., 2014; Stokes et al., 2009). In addition, there is evidence of mangroves expansion from tropical areas northwards and southwards to temperate regions (Saintilan et al., 2014). The expansion of mangroves in New Zealand have been linked to increased sedimentation leading to vertical accretion of tidal flats (Stokes, 2010; Swales et al., 2007), increased nutrient inputs (Saintilan and Williams, 1999), and climatic factors (Burns and Ogden, 1985).

Comment from referee: Here and throughout the MS the authors focus very much on organic carbon concentration in sediments. They should also consider the quality – i.e. the composition and lability of the organic matter.

Author’s response: The manuscript has been modified as recommended.

Changes to manuscript introduction:

Studies from tropical mangrove forests have shown that sediment CO₂ efflux is influenced by sediment carbon and nutrient quantity (Chen et al., 2012; Chen et al., 2010; Chen et al., 2014; Leopold et al., 2013) and quality (Kristensen, 2000), sediment grain size ((Chanda et al., 2014; Chen et al., 2010), sediment water content (Alongi, 2009), redox potential (Chanda et al., 2014; Chen et al., 2012; Chen et al., 2010; Leopold et al., 2013), and sediment temperature (Chen et al., 2012).

Comment from referee: Line 88: The reference here is old and not related to mangrove environments. Please use one of the several publications on the issue by Alongi or Kristensen

Author's response: We revised this section

Changes to manuscript:

Chemoautotrophs have also been shown to fix carbon in intertidal sediment under dark conditions (Boschker et al., 2014; Lenk et al., 2011). In particular at the interface of aerobic and anaerobic zones where large amounts of reduced compounds, such as sulphur, accumulate (Boschker et al., 2014; Lenk et al., 2011; Santoro et al., 2013; Thomsen and Kristensen, 1997)). This is consistent with what is observed in mangrove sediment, where aerobic to anaerobic transitions typically occur close to the sediment surface, with sulphur driven processes likely to dominate in anaerobic conditions (Kristensen et al., 2008).

Comments from referee/author's response: Material and Methods

Line 104: Change to “. . .from the top to the central North Island. . .” ; *changed accordingly*

Line 113: Change to “. . .we sampled at cleared (40 sites) and adjacent intact (18 sites) mangrove locations, as well as tidal flats (30 sites) where existing.” ; *section was revised*

Line 132: What was the area covered by the chamber? This is important information. ; *We revised this section “The sediment area covered by each chamber was 0.00785 m². Total chamber volume varied between 1.72 and 1.98 l depending on the depth of collar insertion.”*

Line 139: Here we have one of the places where sediment and soil terms are mixed. Please delete “soil” here.; *soil was replaced by sediment throughout the manuscript*

Line 146: It is quite late to inform about the darkened chambers here. It must be done earlier.; *modified accordingly*

Line 148-150: I disagree that the approach used excludes photoautotrophic contribution. I have found that CO₂ fixation occurs during the first 30 minutes after darkening. It is a very serious flaw. *Please refer to the comments earlier in regards to the impact of pre-shading the sediment.*

Line 152: Change “years” to “time” here and throughout.” ; *changed accordingly*

Line 154-155: This statement is not clear to readers because it refers to one of the conclusions of the paper. Please omit.; *statement was deleted*

Line 155-165: I am not sure that I trust this proportion of difference adjustment – and I certainly don't like it. It seems to be a kind of data manipulation to obtain the expected results. It is also weird to have output values between 0 and 1 – and then the explanation of what they mean includes an option to have values below 0 and above 1.” ; *we removed the CO₂prop calculation*

Line 176: What do you use the inorganic carbon concentration for?; *The reference to inorganic carbon concentration has been removed*

Line 179: This hydrogen peroxide approach is used very much by geologists. However, it removes the biologically important particles. Biogeochemists usually include these particles in their grain size distribution; *we will modify the methods in future studies.*

Line 186- 187: How were the samples for chlorophyll stored during the month before analysis? This is important.; *samples were frozen and stored in the dark prior to analysis. We modified the methods accordingly*

Line 202-223: There seems to be two methods to obtain infauna by either raking the quadrat or by sampling cores and sieving them. It is unclear how these two approaches differ and how the results from each are used. *The macrofaunal data has been removed.*

Line 224-237: This section is very unclear. Actually I don't know what was done. Is it really necessary to go into this kind of detail? The fauna data are not used for much. *The macrofaunal data has been removed.*

Line 245-248: Delete these lines. They repeat what is stated just above.” ; *we deleted these sentences*

Comments from referee/author's response: Results

Line 264-266: Please correct the units as described by me above. I still don't believe a CO₂ uptake by the tidal flats in darkness.; *Please see the comment above regarding the units used.*

Line 269: Table 2 is not the correct table to refer to here.; *changed accordingly*

Line 275-284: Scale down this description of fauna – and scale up your description of CO₂ fluxes above. The study focuses on emissions and not fauna.; *the fauna have been removed*

Line 285-315: These lines are just a long list of correlations. Please rewrite this in a meaningful way and include all correlation values in a table. Is the first value in all parentheses r²? This is not mentioned.; *the result section was modified*

Line 316-319: This biofilm effect is not true. It is simply because carbon fixation by benthic microalgae is missing after removing the upper 2 mm of the sediment.; *Please refer to the comments earlier in regards to the impact of pre-shading the sediment.*

Comments from referee/author's response: Discussion

Line 321-322: Again, the units are wrong. Line 322-323: This is a contradiction. First it is stated that the results are within the range of those previously reported, then they are suddenly higher than

previously reported!!!! What about the results obtained by Alongi and/or Kristensen. They are not mentioned.” ; *we revised this section*

Changes to manuscript discussion:

Dark sediment CO₂ efflux in intact Avicennia marina forests across its distribution range in New Zealand (1.95 ± 0.53 μmol m⁻² s⁻¹ which equals 168.4 ± 45.8 mmol CO₂ m⁻² d⁻¹) is similar to values reported for intact Avicennia marina forests in other temperate (New Zealand, Australia; Lovelock (2008), Lovelock et al. (2014), Livesley and Andrusiak (2012)) and tropical locations (New Caledonia; Leopold et al. (2013); Leopold et al. (2015)) (Table 2). In contrast, our values are higher than the global estimates of sediment CO₂ efflux from intact mangrove forests including a number of other tropical mangrove species (0.71 ± 0.65 μmol m⁻² s⁻¹ (Bouillon et al., 2008); 0.80 ± 0.09 μmol m⁻² s⁻¹ (Alongi, 2014)) (Table 2). Higher sediment CO₂ efflux observed within our study may partly be explained by the inclusion of crab burrows and short pneumatophores within flux measurements. The omission of crab burrows and pneumatophores has previously been proposed as a potential explanation of why global estimates may be underestimated (Bouillon et al., 2008). Crab burrows have been shown to increase CO₂ efflux by increasing the surface area for sediment-air exchange of CO₂ (Kristensen et al., 2008) and enhancing carbon decomposition processes (Pülmanns et al., 2014). Pneumatophores have been associated with increased CO₂ emissions by efficient translocation of CO₂ exchange from deeper sediments (Bouillon et al., 2008; Kristensen et al., 2008).

Line 323: Change to “. . . tropical mangrove forests. . .” , *changed accordingly*

Line 333-334: It seems that everything is affecting CO₂ emission. The list mentioned covers almost everything. *The manuscript has been modified.*

Line 337: Now the unit becomes even more strange “m² s⁻¹” .” , *units were corrected (μmol m⁻² s⁻¹).*

Line 344-349: These lines are nonsense. The efflux in darkness is not driven by autotrophic communities, but rather the heterotrophic degraders. These lines must be deleted. ; *we re-wrote this section.*

Line 355-356: How can sediment characteristics play any role? Please clarify.

The manuscript has been modified to include the following:

High clay which was found at these sites may have also contributed to the accumulation of sediment carbon which has been shown to be associated with higher CO₂ efflux in tropical mangrove forests (Chen et al., 2012; Chen et al., 2010; Chen et al., 2014; Leopold et al., 2013).

Line 358-363: I still don't believe the biofilm story. However, the sites that are referred to here have apparently dense algal mats. They will then be assimilating CO₂ long time after darkening. So, the studies cited here must have the same flaw as the present study. ; *Please refer to the comments earlier in regards to the impact of pre-shading the sediment.*

Line 373-375: Did you consider the burrows as chimneys of CO₂ release as found in other studies. Also pneumatophores act as conduits for CO₂ transported from deep in the sediment.

We have looked into the relationship between crab burrow/pneumatophore abundance and CO₂ efflux, but were not able to draw any significant conclusions from the dataset, likely due to other site characteristics confounding expected relationships. We have expanded on this as a potential explanation for the increased flux we observed.

Line 393-395: I don't understand this sentence. *This section has been revised*

Changes to manuscript:

Higher sediment carbon concentrations have been measured in older mangrove forests, growing further inland compared to younger mangrove forests, growing at the expanding seaward edge (Lovelock et al., 2010). This may also be related to the protection offered by seaward mangroves, enabling greater accumulation of carbon enriched mangrove detritus within the centre of the stand (Yang et al., 2013).

Line 396-397: This effect must be short-term.

Changes to manuscript:

Increased sediment CO₂ efflux has been observed within intact mangrove forest following disturbance of the top 30 cm of the sediment, however the effect was transitory, returning to pre disturbed levels within two days (Lovelock et al., 2011).

Line 407- 411: I don't believe in this adjustment.; *The manuscript has been modified and the CO₂prop calculation removed.*

Line 434: We have not heard that crab burrows were counted. These burrows are important conduits for CO₂ release.; *Crab burrows were counted at each site but not within individual chamber incubations. As no significant relationship between crab burrow abundance and CO₂ efflux was observed we have removed crab burrow abundance data from the manuscript. However, we have expanded on the importance of crab burrows within our discussion.*

Line 424-440: There is no explanation for the uptake of CO₂ in tidal flats. Again, I believe that it is a flaw. The correlations can therefore not be fully trusted; *The tidal flat data has been removed from the*

manuscript.. Please see above for further information on the additional testing conducted on CO₂ efflux data.

Line 442-446: This statement supports my argument for continued assimilation of CO₂ by microalgae right after darkening. These biofilms are important for the benthic primary production in the light, but they are part of the heterotrophic community during night (hours after sunset). *Please refer to the comments earlier in regards to the impact of pre-shading the sediment.*

Line 447-449: No, such polymeric surface film cannot be a strong barrier. This has been shown by others. *This statement has been modified.*

Changes to manuscript: Other studies have suggested that the biofilm may also act as a barrier to the flow of CO₂ from deeper sediment, which when removed results in a rapid increase in CO₂ efflux (Leopold et al., 2015; Leopold et al., 2013).

Line 450-452: Such aeration will not result in instant oxidation by microorganisms. Furthermore, labile organic fractions are degraded at the same speed irrespective of the presence of oxygen. It is degradation of refractory organic matter that is speeded up by the presence of oxygen.

This sentence has been removed

Table 1: The chlorophyll and phaeophytin units are weird. They must be wrong.

This was an oversight. The manuscript has been modified to include the correct unit ($\mu\text{g}^{-1} \text{g}^{-1}$ sediment)

Thank you for your valuable suggestions on this manuscript.

References cited:

Alfaro, A. C.: Benthic macro-invertebrate community composition within a mangrove/seagrass estuary in northern New Zealand, *Estuar. Coast Shelf Sci.*, 66, 97-110, 2006.

Alongi, D. M.: Carbon Cycling and Storage in Mangrove Forests, *Annu. Rev. Marine. Sci.*, 6, 195-219, 2014.

Alongi, D. M.: *The energetics of mangrove forests*, Springer, 2009.

Boschker, H. T. S., Vasquez-Cardenas, D., Bolhuis, H., Moerdijk-Poortvliet, T. W. C., and Moodley, L.: Chemoautotrophic carbon fixation rates and active bacterial communities in intertidal marine sediments, *PLoS ONE*, 9, 1-12, 2014.

Bouillon, S., Borges, A. V., Castañeda-Moya, E., Diele, K., Dittmar, T., Duke, N. C., Kristensen, E., Lee, S. Y., Marchand, C., Middelburg, J. J., Rivera-Monroy, V. H., Smith Iii, T. J., and Twilley, R. R.: Mangrove production and carbon sinks: A revision of global budget estimates, *Global Biogeochem. Cy.*, 22, 2008.

Burns, B. R. and Ogden, J.: The demography of the temperate mangrove *Avicennia marina* at its southern limit in New Zealand, *Aust. J. Ecol.*, 10, 125-133, 1985.

Chanda, A., Akhand, A., Manna, S., Dutta, S., Das, I., Hazra, S., Rao, K. H., and Dadhwal, V. K.: Measuring daytime CO₂ fluxes from the inter-tidal mangrove soils of Indian Sundarbans, *Environ Earth Sci*, 72, 417-427, 2014.

Chen, G. C., Tam, N. F. Y., and Ye, Y.: Spatial and seasonal variations of atmospheric N₂O and CO₂ fluxes from a subtropical mangrove swamp and their relationships with soil characteristics, *Soil Biol. Biochem.*, 48, 175-181, 2012.

Chen, G. C., Tam, N. F. Y., and Ye, Y.: Summer fluxes of atmospheric greenhouse gases N₂O, CH₄ and CO₂ from mangrove soil in South China, *Sci. Total Environ.*, 408, 2761-2767, 2010.

Chen, G. C., Ulumuddin, Y. I., Pramudji, S., Chen, S. Y., Chen, B., Ye, Y., Ou, D. Y., Ma, Z. Y., Huang, H., and Wang, J. K.: Rich soil carbon and nitrogen but low atmospheric greenhouse gas fluxes from North Sulawesi mangrove swamps in Indonesia, *Sci. Total Environ.*, 487, 91-96, 2014.

Krauss, K. and Whitbeck, J.: Soil greenhouse gas fluxes during wetland forest retreat along the lower Savannah river, Georgia (USA), *Wetlands*, 32, 73-81, 2012.

Kristensen, E.: Organic matter diagenesis at the oxic/anoxic interface in coastal marine sediments, with emphasis on the role of burrowing animals, *Hydrobiologia*, 426, 1-24, 2000.

Kristensen, E. and Alongi, D. M.: Control by fiddler crabs (*Uca vocans*) and plant roots (*Avicennia marina*) on carbon, iron, and sulfur biogeochemistry in mangrove sediment, *Limnol. Oceanog.*, 51, 1557-1571, 2006.

Kristensen, E., Bouillon, S., Dittmar, T., and Marchand, C.: Organic carbon dynamics in mangrove ecosystems: A review, *Aquat. Bot.*, 89, 201-219, 2008.

Lenk, S., Arnds, J., Zerjatke, K., Musat, N., Amann, R., and Mußmann, M.: Novel groups of Gammaproteobacteria catalyse sulfur oxidation and carbon fixation in a coastal, intertidal sediment, *Environ. Microbiol.*, 13, 758-774, 2011.

- Leopold, A., Marchand, C., Deborde, J., and Allenbach, M.: Temporal variability of CO₂ fluxes at the sediment-air interface in mangroves (New Caledonia), *Sci. Total Environ.*, 502, 617-626, 2015.
- Leopold, A., Marchand, C., Deborde, J., Chaduteau, C., and Allenbach, M.: Influence of mangrove zonation on CO₂ fluxes at the sediment-air interface (New Caledonia), *Geoderma*, 202-203, 62-70, 2013.
- Livesley, S. J. and Andrusiak, S. M.: Temperate mangrove and salt marsh sediments are a small methane and nitrous oxide source but important carbon store, *Estuarine, Coastal and Shelf Science*, 97, 19-27, 2012.
- Lovelock, C. E.: Soil respiration and belowground carbon allocation in mangrove forests, *Ecosystems*, 11, 342-354, 2008.
- Lovelock, C. E., Feller, I. C., Reef, R., and Ruess, R. W.: Variable effects of nutrient enrichment on soil respiration in mangrove forests, *Plant Soil*, 379, 135-148, 2014.
- Lovelock, C. E., Sorrell, B. K., Hancock, N., Hua, Q., and Swales, A.: Mangrove forest and soil development on a rapidly accreting shore in New Zealand, *Ecosystems*, 13, 437-451, 2010.
- Lundquist, C. J., Morrissey, D. J., Gladstone-Gallagher, R. V., and Swales, A.: Managing mangrove habitat expansion in New Zealand. In: *Mangrove Ecosystems of Asia*, Faridah-Hanum, I., Latiff, A., Hakeem, K. R., and Ozturk, M. (Eds.), Springer New York, 2014.
- Ma, J., Wang, Z.-Y., Stevenson, B. A., Zheng, X.-J., and Li, Y.: An inorganic CO₂ diffusion and dissolution process explains negative CO₂ fluxes in saline/alkaline soils, *Scientific Reports*, 3, 2025, 2013.
- Morrissey, D. J., Swales, A., Dittmann, S., Morrison, M., Lovelock, C., and Beard, C.: The ecology and management of temperate mangroves. In: *Oceanogr. Mar. Biol., Oceanography and Marine Biology - An Annual Review*, CRC Press, 2010.
- Oakes, J. M. and Eyre, B. D.: Transformation and fate of microphytobenthos carbon in subtropical, intertidal sediments: potential for long-term carbon retention revealed by ¹³C-labeling, *Biogeosciences*, 11, 1927-1940, 2014.
- Saintilan, N. and Williams, R. J.: Mangrove transgression into saltmarsh environments in south-east Australia, *Global Ecol. Biogeogr.*, 8, 117-124, 1999.
- Saintilan, N., Wilson, N. C., Rogers, K., Rajkaran, A., and Krauss, K. W.: Mangrove expansion and salt marsh decline at mangrove poleward limits, *Glob. Change Biol.*, 20, 147-157, 2014.
- Santoro, A. L., Bastviken, D., Gudas, C., Tranvik, L., and Enrich-Prast, A.: Dark carbon fixation: An important process in lake sediments, *PLoS ONE*, 8, e65813, 2013.
- Stokes, D. J.: The physical and ecological impacts of mangrove expansion and mangrove removal: Tauranga Harbour, New Zealand, PhD Thesis. University of Waikato, 2010. 2010.
- Stokes, D. J., Healy, T. R., and Cooke, P. J.: Surface elevation changes and sediment characteristics of intertidal surfaces undergoing mangrove expansion and mangrove removal, Waikaraka Estuary, Tauranga Harbour, New Zealand, *International Journal of Ecology and Development*, 12, 88-106, 2009.

Swales, A., Bentley, S. J., Lovelock, C., and Bell, R. G.: Sediment processes and mangrove-habitat expansion on a rapidly-prograding Muddy Coast, New Zealand, *Coastal Sediments*, doi: 10.1061/40926(239)111, 2007. 2007.

Thomsen, U. and Kristensen, E.: Dynamics of sigma CO₂ in a surficial sandy marine sediment: the role of chemoautotrophy, *Aquat. Microb. Ecol.*, 12, 165-176, 1997.

Yang, J., Gao, J., Cheung, A., Liu, B., Schwendenmann, L., and Costello, M. J.: Vegetation and sediment characteristics in an expanding mangrove forest in New Zealand, *Estuar. Coast Shelf S.*, 134, 11-18, 2013.