Controls on diel soil CO_2 flux across moisture gradients in a polar desert

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Abstract: The McMurdo Dry Valleys of Antarctica are a climate-sensitive ecosystem, where future projected climate warming will increase liquid water availability to release soil biology from physical limitations and alter ecosystem processes. For example, many studies have shown that CO_2 flux, an important aspect of the carbon cycle, is controlled by temperature and moisture, which often overwhelm biotic contributions in desert ecosystems. However, these studies used either single-point measurements during peak times of biological activity or diel cycles at individual locations. Here, we present diel cycles of CO_2 flux from a range of soil moisture conditions and a variety of locations and habitats to determine how diel cycles of CO_2 flux vary across gradients of wet-to-dry soil and whether the water source influences the diel cycle of moist soil. Soil temperature, water content and microbial biomass significantly influenced CO_2 flux. Soil temperature explained most of the variation. Soil CO_2 flux moderately increased with microbial biomass, demonstrating a sometimes small but significant role of biological fluxes. Our results show that over gradients of soil moisture, both geochemical and biological fluxes contribute to soil CO_2 flux, and physical factors must be considered when estimating biological CO_2 flux in systems with low microbial biomass.

Introduction

The McMurdo Dry Valleys of Antarctica are a climate-sensitive ecosystem, where past climates have left ecological legacies affecting contemporary soil functioning (Moorhead *et al.* 1999), and where projected climate warming (Chapman & Walsh 2007, Steig *et al.* 2009, Walsh 2009) will alter precipitation and promote melting of ice reserves to increase liquid water availability to the soil ecosystem. These changes in temperature and moisture should stimulate soil biological activity to alter ecosystem processes such as biogeochemical cycling. A key process is soil CO_2 flux, given its potential as a greenhouse gas to act as either a positive feedback (via temperature-induced increases in respiration) or a negative feedback (via temperature-induced increases in soil carbon storage) of climate change (Oechel *et al.* 1993, Bokhorst *et al.* 2007, Allison *et al.* 2010). Many studies have shown that soil CO_2 flux is sensitive to changing soil moisture and temperature in a variety of ecosystems (e.g. Ball *et al.* 2009, Matías *et al.* 2012, Schindlbacher *et al.* 2012).

Studies of the diel cycle of CO_2 flux in the Dry Valleys show positive fluxes (net release of CO_2) in the daytime hours when air temperatures often exceed 0°C and lower, often negative fluxes (uptake of CO_2), during the colder evening hours or during periods when air temperatures

are declining (e.g. Ball *et al.* 2009). Though daylight is continuous during the summer, the uptake of CO_2 by soil is probably not the result of autotrophy, given the lack of vascular plants and limited primary production capacity of soil algae and microbes across most of the Dry Valley landscape (Adams *et al.* 2006). The negative uptake is probably the result of the dissolution of atmospheric CO_2 in soil water as temperatures decrease, and under these conditions, geochemical uptake of CO_2 can exceed biological release (Ball *et al.* 2009, Shanhun *et al.* 2012, Risk *et al.* 2013). Thus, physical factors, particularly temperature and moisture, have a dominant influence on both geochemical and biological contributions to soil CO_2 flux in the Dry Valleys. Increased temperature and moisture can stimulate biological respiration, but increased temperature may reduce geochemical dissolution of CO_2 in soil water (Parsons *et al.* 2004, Ball *et al.* 2009). Similar patterns of CO_2 flux controlled by dissolution and temperature have been observed in hot desert soils (Ma *et al.* 2013). Therefore, climate change, both warmer temperatures and increased liquid water availability, will influence soil CO_2 flux.

The response of soil CO_2 flux to changes in physical conditions is not predictable with accuracy. For example, increases in moisture will interact with soil conditions to influence CO_2 flux, either positively or negatively, because
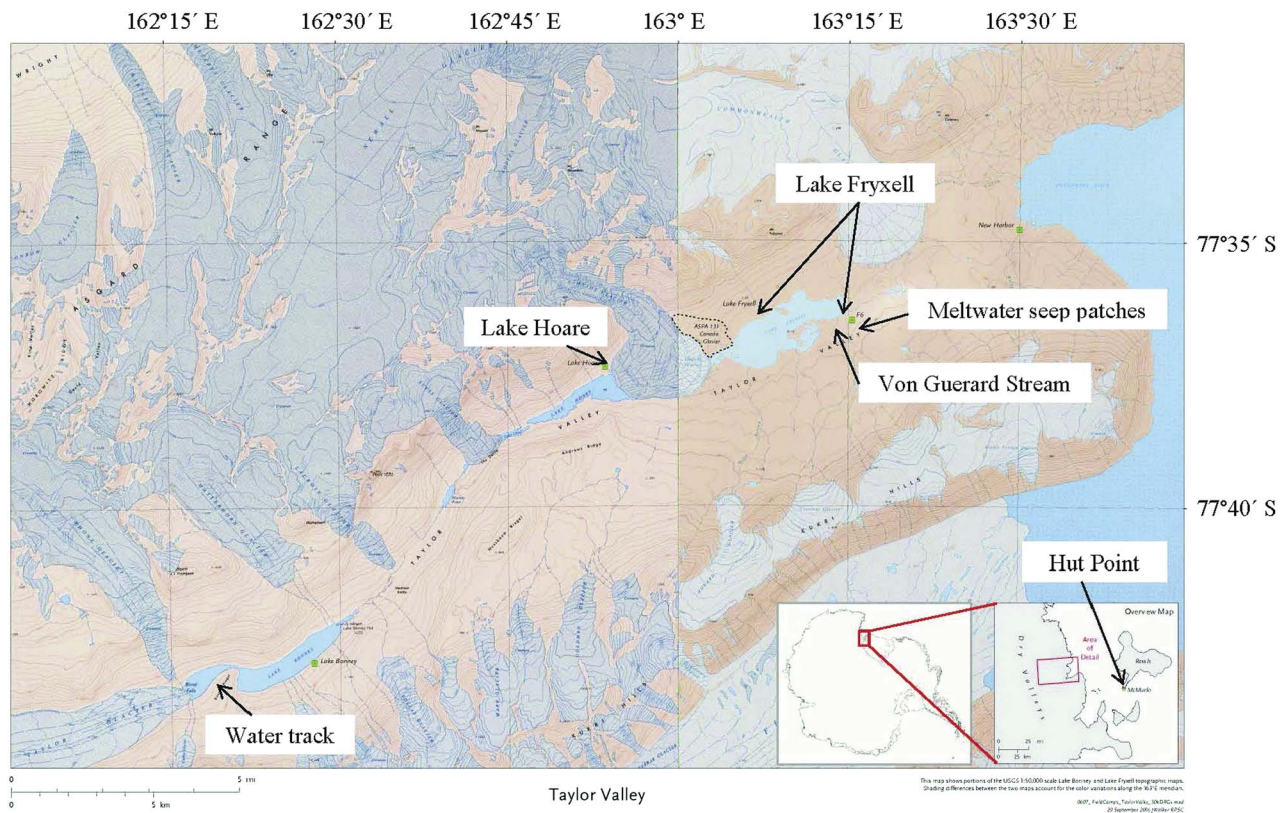
Fig. 1. Locations in Taylor Valley and on Ross Island, Antarctica, where diel cycles of CO_2 flux were measured in a variety of soils wetted by different water sources and in surrounding dry soil.

different sources of meltwater contribute to non-uniform influences on soil biology and geochemistry (Ball *et al.* 2011). An increase in glacial melt may increase the load of the re-occurring ephemeral surface streams and alter the wetted margins of lakes into which they drain, thus extending the wetted hyporheic sediments. These newly wetted soils derived from surface waters may differ in physical and chemical characteristics from newly wetted areas formed by subsurface flow of water, such as water tracks and seep patches. During periodic discrete warm summer pulse events over the past decade, water tracks (re-occurring downslope drainages of subsurface meltwater) carry greater loads of water, sometimes even developing surface flow and wetlands. Additionally, smaller-scale seep patches (amorphous patches of subsurface meltwater that have wicked moisture to the surface via capillary action) become more abundant across the landscape during these events (Levy *et al.* 2011, Ball & Virginia 2012, Nielsen *et al.* 2012). Increased stream flow may enhance biological productivity already abundant there, but saline meltwater from water tracks and seep patches may negatively influence biological activity (Ball & Virginia 2012). It is important to understand how these various sources and qualities of meltwater will influence CO_2 flux and the impacts of future warming on the Dry Valley carbon cycle.

Previous research in the McMurdo Dry Valleys has demonstrated the physical (temperature and moisture) and biotic influences on soil respiration in the field using single-point measurements during peak times of biological activity, as well as from diel cycles at individual locations (e.g. Burkins *et al.* 2001, Parsons *et al.* 2004, Elberling *et al.* 2006, Ball *et al.* 2009). Here, we present diel cycles of CO_2 flux from a variety of moisture gradients, representing several different sources of water and also dry soil habitats from a variety of locations. The following questions were addressed: i) How do diel cycles of CO_2 flux differ between wetted and dry soil? ii) Does the source of water influence the diel cycle of CO_2 flux from wet soil? iii) What are the relative influences of temperature, moisture and microbial biomass in controlling CO_2 flux over diel cycles?

Methods

Site description

The study was conducted in the McMurdo Dry Valleys (Taylor Valley), southern Victoria Land, Antarctica, and on Ross Island (Fig. 1). Field measurements of diel CO_2 flux were made at multiple locations over five summers, including dry soil and soil wetted from a variety of water sources: lake, stream, water track and meltwater seeps.

Over the entire area, soils are poorly developed and coarse (typically 95–99% sand in the <2 mm fine fraction), dry (largely <1–5% moisture), high in salt content and pH, and low in organic matter (typically 0.1–0.3 mg organic C g soil^{-1}) (Campbell & Claridge 1987, Campbell *et al.* 1997, Burkins *et al.* 2000). Two lake gradients, one stream gradient and three meltwater seep patches were sampled in the Fryxell basin, where CO$_2$ flux from both wet soils and dry soils outside the influence of the water source were measured. Soils here are Typic Haploturbels occurring on Ross Sea drift (late-Quaternary, 9–28 ka) that contain ice-cemented permafrost and are strongly cryoturbated (Hall & Denton 2000, Bockheim & McLeod 2008), with a shallow active layer (10–70 cm; Bockheim *et al.* 2007). One large-scale water track (Wormherder Creek), which also receives stream-like overland flow during discrete warm summers, was sampled in the Bonney basin (Nielsen *et al.* 2012). These soils are Typic Anhyorthels occurring on Taylor III drift (mid-Quaternary, 250–340 ka) in areas of dry permafrost (Higgins *et al.* 2000, Bockheim *et al.* 2008). The CO$_2$ flux from dry soil was measured in the Hoare basin, which are also Typic Anhyorthels. Additionally, dry soil outside Taylor Valley was measured at Hut Point on Ross Island near McMurdo Station, where soils are Typic Haploturbels (Bockheim & McLeod 2008).

Field measurements

Soil CO$_2$ flux was measured in the field using a battery powered automated LI-COR 8100 system (LI-COR Biosciences, Lincoln, Nebraska, USA), which allows for unattended measurement at designated intervals across diel cycles. At each site, a 20 cm PVC collar was placed *c.* 10 cm into the ground at least one hour prior to measurement. Previous tests have shown that 1 hour is sufficient time for these low biomass soils to recover from the disturbance of inserting the collar. The height of the collar aboveground (offset) was measured for calculation of volume of the headspace in each PVC ring. An automated long-term respiration chamber was placed beside the collar to record soil CO$_2$ flux every 20 minutes for *c.* 24 hours. Every 20 minutes, the machine automatically placed and sealed the chamber over the collar and recorded CO$_2$ flux for 60 seconds after a 10 second deadband. The raw data for each individual measurement were reviewed, and those visually determined to have high noise were removed from analysis (typically 1–2 measurements out of *c.* 70 over a 24 hour period). The flux measured using a linear fit was recorded, as is recommended by LI-COR for low flux levels. Standard error on flux measurements was on average 0.002–0.003% of the slope of the linear fit, and ranged from 0.001 to 0.004%. When possible, attached soil temperature (thermistor) and moisture (Theta meter,

Delta T Devices, Cambridge, UK) probes were inserted *c.* 10 cm into the soil just outside the collar to record these soil properties along with CO$_2$ flux; however, working probes were not always available. After the 24 hours of measurement, soil within the collar was collected to a depth of 10 cm for measurement of microbial biomass, but only if the sample could be returned to the lab at McMurdo Station in a timely manner. Microbial carbon was measured using the chloroform fumigation extraction technique with a 1:2 ratio of soil and 0.5 M K$_2$SO$_4$ (Horwath & Paul 1994). Approximately 35 g of soil from each sample was extracted in 70 ml of 0.5 M K$_2$SO$_4$. Extracts were shaken at 200 rpm for 30 minutes, centrifuged at $25\,000 \times$ g, then poured through 0.45 µm nylon filters and acidified with 3 ml 6N HCl. A duplicate 35 g subsample was placed in a vacuum desiccator and fumigated with ethanol-free chloroform for 120 hours. After fumigation, soils were extracted as described above. All extracts were frozen prior to analysis on a Shimadzu TOC analyzer for dissolved organic carbon.

Data analysis

Data were analysed in R (R Foundation, v2.15.1). First, data from all sampling locations were combined and a three-way analysis of covariance (ANCOVA) was conducted to determine how soil water content (SWC), soil temperature, microbial biomass carbon, and their interactions influence soil CO$_2$ flux. The proportion of the variation explained by each main effect or interaction was calculated by dividing the sum of squares for that effect/interaction by the total sum of squares. Additionally, a Pearson's product moment correlation coefficient was calculated for each main effect to determine whether a linear relationship exists with CO$_2$ flux. Regression analysis determined the nature of the linear relationships (for the diel cycles at each sampling location see Appendix A found at http://dx.doi.org/10.1017/S0954102015000255). Given that the CO$_2$ flux data did not show an exponential relationship with soil temperature, the trend lines from these linear regressions were used to describe the relationships instead of calculating Q$_{10}$ values. Finally, regression tree analysis was performed using the rpart package in R. Regression trees describe the relationship between a response variable (CO$_2$ flux) and multiple predictor variables of a range of data types by progressively splitting the data into dichotomous branches (Logan 2010, Kelsey *et al.* 2012). Temperature, SWC and microbial biomass were used as continuous predictor variables to explain CO$_2$ flux. To avoid overfitting, the tree was pruned to a maximum of three branches (or four levels).

To further explore the effect of different water sources, wet sites were categorized into lake, stream and subsurface meltwater (seeps and water track), and an analysis of variance (ANOVA) was used to determine the effect of water source on CO$_2$ flux and microbial biomass.

Table I. Pearson's product moment correlation coefficients and associated P-values assessing the potential linear relationship between key factors and soil CO_2 flux.

Factor	Pearson coefficient	P-value
Soil temperature	0.416 ± 0.068	< 0.001
Change in soil temperature	0.074 ± 0.049	0.012
Soil water content	-0.090 ± 0.063	0.006
Microbial biomass carbon	0.227 ± 0.070	< 0.001

Post-hoc Tukey tests were used to determine the nature of significant effects of water source.

Results

Overall, the 17 diel cycles of CO_2 flux that were measured showed the greatest positive CO_2 fluxes during the warmest hours of the day (often reaching as high as $0.2\,\mu\text{mol}\ CO_2\ \text{m}^{-2}\ \text{s}^{-1}$) and low, usually negative fluxes during the evening hours when temperatures were cooler (often reaching as low as $-0.1\,\mu\text{mol}\ CO_2\ \text{m}^{-2}\ \text{s}^{-1}$; Appendix A). Soil CO_2 flux tended to mirror rather than lag behind temperature changes. Given the different
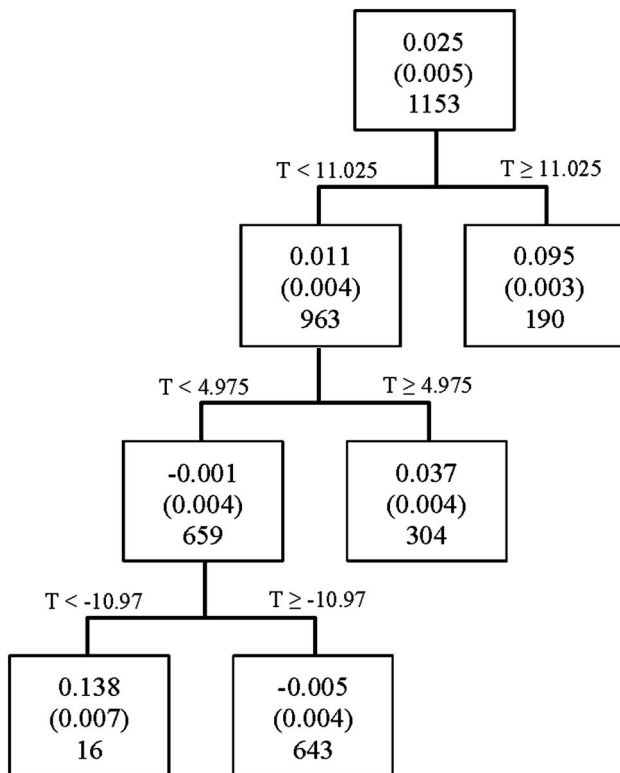

Fig. 2. Results of the regression tree analysis predicting soil CO_2 flux with soil temperature. Boxes list the mean CO_2 flux ($\mu\text{mol}\ CO_2\ \text{m}^{-2}\ \text{s}^{-1}$) with standard deviation in parentheses, followed by the number of observations. The lines between boxes show the thresholds of soil temperature (°C) specified by the regression tree analysis that dichotomize the data.
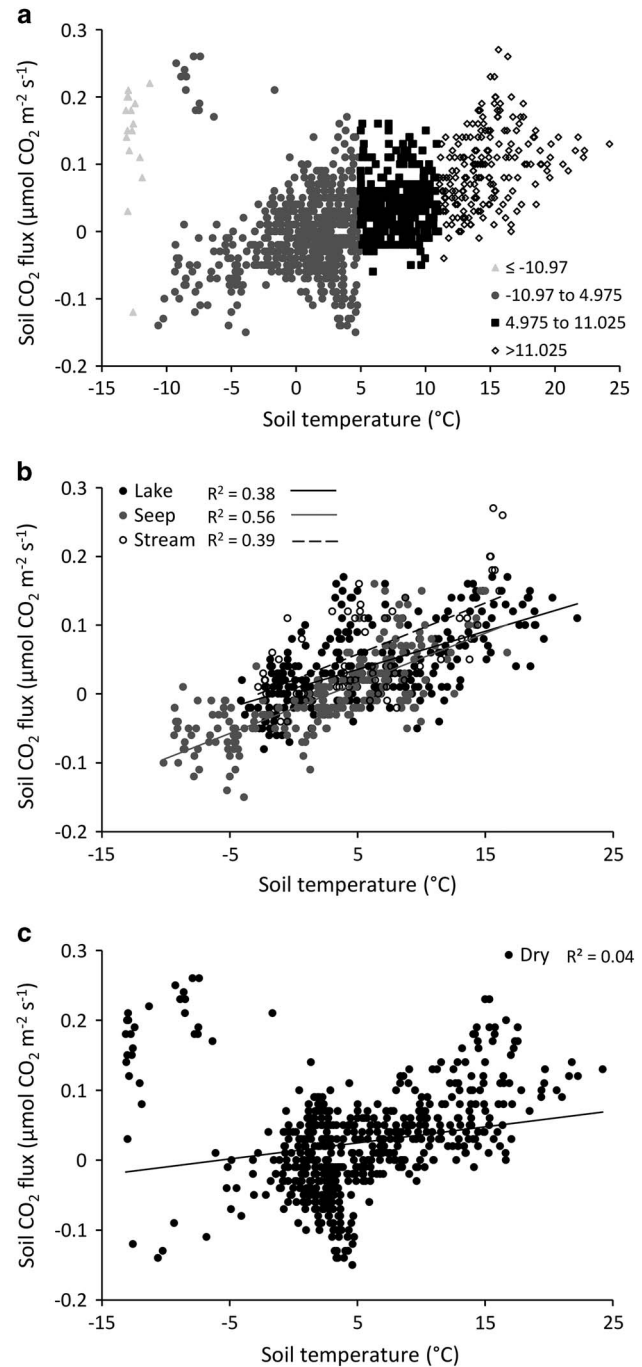

Fig. 3. Relationship between CO_2 flux and soil temperature **a.** across all of the sampling locations, depicting the dichotomies in soil temperature designated by the regression tree analysis, as well as the same data divided into **b.** the three different water sources sampled and **c.** dry soil with a linear trend line and associated R^2 value.

weather conditions over each diel cycle, it is difficult to directly compare the diel cycles along moisture gradients and across sources of water; therefore, statistical analyses were used to investigate the patterns and identify interactions.
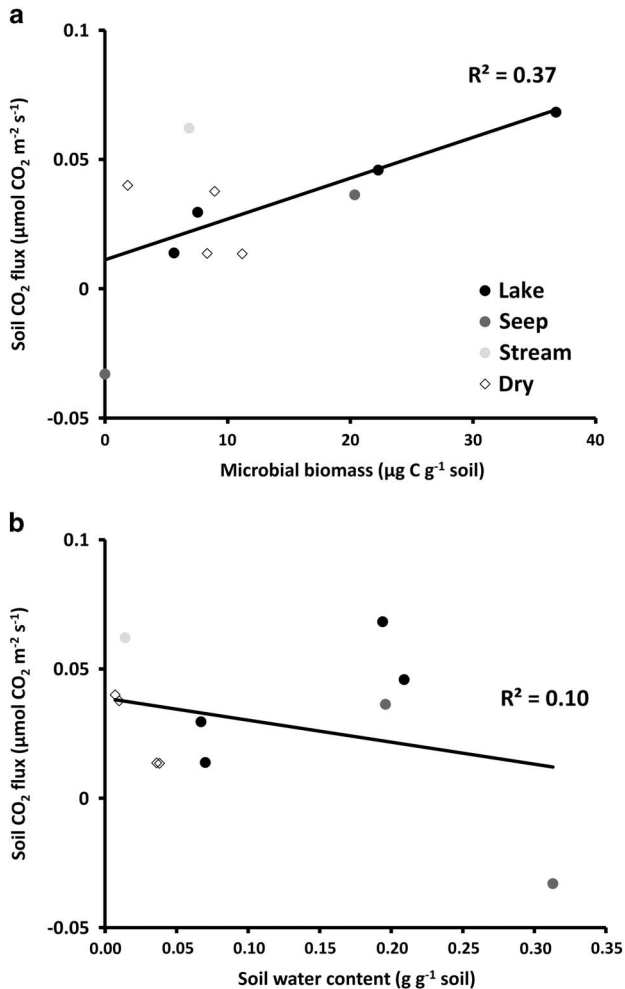
Fig. 4. Relationship between average CO_2 flux over a 24 hour cycle and **a.** microbial biomass, and **b.** maximum soil moisture across all of the sampling locations of various water sources, including the calculated linear trend line and associated R^2 value.

When considering all of the data across sampling locations, soil temperature, moisture and microbial biomass interact to influence soil CO_2 flux ($F_{1,720} = 9.70$, $P = 0.002$). Soil temperature alone explained 48% of the variability in CO_2 flux, while moisture, microbial biomass and the interactions explained between < 1% and 4%, respectively. Soil temperature also has the highest Pearson coefficient (Table I) and is the only factor that determines the branch splits in the regression tree analysis (Fig. 2). If the tree is not limited to three branches, SWC and microbial biomass become factors, though temperature is still dominant (data not shown). As would be expected, soil temperature is positively related to soil CO_2 flux. However, the CO_2 flux sensitivity to soil temperature differed among the temperature ranges separated by the regression tree analysis (Fig. 3a). The linear regression trend lines show the steepest slope at the highest temperatures

(m = 0.007 at T > 11.025°C), followed by the lower temperatures (m = 0.005 at -10.97 > T < 4.975°C), with a weak correlation at intermediate temperatures (m = 0.002 at 4.975 > T < 11.025°C) and also at the lowest temperatures (m = −0.002 at T ≤ -10.97°C), though variability is high. Further, CO_2 flux from wet soils seems to be more temperature sensitive than flux from dry soils (Fig. 3b & c). However, the weak correlation between temperature and CO_2 flux in dry soils is largely due to the fluxes in one particular location, in the dry soils outside seep patch 1, where at extremely cold temperatures a large positive CO_2 flux was observed (Appendix A found at http://dx.doi.org/ 10.1017/S0954102015000255). When data from that single site are removed, the trend line has a slope comparable to wet soils with an $R^2 = 0.35$.

After temperature, microbial biomass has the next strongest linear relationship with CO_2 flux (Table I), such that CO_2 flux tends to increase with increasing microbial biomass; however, it is a moderate relationship largely driven by the influence of wet soils (Fig. 4a). Microbial biomass is influenced by an interaction between soil temperature and moisture ($F_{1,724} = 37.78$, $P < 0.001$). The SWC alone explained 25% of the variability in biomass, and its influence differs with water source ($F_{3,724} = 89.66$, $P < 0.001$). Microbial biomass is greatest in areas wetted by lakes, but the biomass relationship with CO_2 flux is variable, as two lake sites and the stream site have equivalent biomass:flux ratios that are comparable to the dry soils. Seep patches also vary in biomass, with high biomass at one patch and the other patch below detection (Fig. 4a).

Soil CO_2 flux was weakly correlated with SWC (Table I, Fig. 4b), with the highest maximum fluxes during a diel cycle from the stream hyporheic zone and dry soil (Appendix A). If the seep with the highest SWC is removed from the regression, the relationship becomes slightly positive. The source of water had a significant influence on CO_2 flux ($F_{3,572} = 57.14$, $P < 0.001$), and significantly interacted with soil temperature, SWC and microbial biomass ($F_{2,596} = 4.31$, $P = 0.014$). A post-hoc Tukey test revealed that dry locations differed from all wet locations, and subsurface sources of water (seeps and the water track) had significantly more low level CO_2 fluxes than both the soil wetted by surface water and dry soil (Appendix A). However, the three water sources did not differ greatly in their sensitivity to soil temperature, given that the regressions of CO_2 flux and temperature yield trend lines with roughly equivalent slopes (Fig. 3b).

Discussion

As expected, soil temperature and microbial biomass had a positive relationship with soil CO_2 flux, but CO_2 flux was only weakly correlated with SWC. Of the measured variables, soil temperature had the largest influence, given

that it explained most of the variation in CO_2 flux. Increasing temperature can both decrease the solubility of CO_2 in water according to Henry's Law, as well as stimulate biological respiration. Further, high fluxes at very cold temperatures may occur via CO_2 exclusion from freezing of the soil solution, as is seen at the lowest temperatures in Fig. 3a. Many other studies have found a similarly dominant role of soil temperature in determining McMurdo Dry Valley soil CO_2 flux (Parsons *et al.* 2004, Ball *et al.* 2009, Shanhun *et al.* 2012) and greater temperature sensitivity of soil CO_2 flux in polar deserts than hot deserts (Cable *et al.* 2010). Notably, a time lag in CO_2 flux with changes in temperature was not identified. This relationship observed in some studies makes temperature sensitivity of soil CO_2 flux challenging to detect (Phillips *et al.* 2011).

Previous studies have suggested that much of measured CO_2 fluxes from Dry Valley soils are abiotic, with low or negligible biological contributions (Shanhun *et al.* 2012). We observed that microbial biomass has a small but significant influence on soil CO_2 flux, demonstrating the contribution of biological fluxes. This result suggests that biological contributions are not always as low as other studies suggest. The method used to assess microbial biomass measures both active and dormant microbes, and it is possible that CO_2 flux would be more significantly related to measures of active biomass rather than total biomass. Additionally, it is possible that microbes could become substrate limited in these carbon limited soils during the warmest and most metabolically active period of the day (e.g. Hartley *et al.* 2008). This would limit the microbial contribution to what would otherwise be a more noticeable correlation. Regardless, since the average CO_2 flux was positive for most sites (Fig. 3a & b) we conclude that there is a biological contribution, assuming the net geochemical fluxes are zero over a diel cycle (i.e. when there are no strong directional changes in soil temperature on this short timescale).

Temperature, moisture and microbial biomass are only able to explain slightly more than half of the variability in the measured CO_2 fluxes. Other factors, including the influence of salinity on soil osmotic potential and pH, also influence soil CO_2 flux (Ball & Virginia 2012, Mavi *et al.* 2012, Shanhun *et al.* 2012), which were not measured here. The type of subsurface meltwater and whether there is significant horizontal flow and redistribution of salts, i.e. seep patches versus water tracks, will influence soil salinity. High levels of soil salinity can decrease habitat suitability for biota and reduce biotic CO_2 flux (depending upon the relative magnitude of changes in SWC and the osmotic potential of the soil solution (Ball & Virginia 2012)). It is also possible that temperature would explain more of the variation in CO_2 fluxes if temperature had been measured across the depths from which soil CO_2 flux is generated (Graf *et al.* 2008), in itself an unknown.

A comparatively weak correlation of SWC with CO_2 flux was found. Shanhun *et al.* (2012) also found CO_2 flux to be insensitive to SWC in high pH soils, which are prevalent in the Dry Valleys. A possible explanation for the weak contribution of SWC in explaining CO_2 flux is that we sampled across several distinct water sources. The seeps have some of the highest SWC levels, but also lower CO_2 fluxes. This finding may reflect in part the low microbial biomass in one of the seeps, as well as the increased capacity for CO_2 dissolution in the wetter soils, together resulting in low CO_2 flux. Conversely, an increase in soil moisture along lake and stream edges or in dry soil tends to increase CO_2 flux because background levels of microbial biomass and organic carbon are higher (Ball & Virginia 2014). Dry Valley lakes are the most biologically productive landscape feature in this ecosystem and changes in the SWC and chemistry of their margins would be expected to elicit changes in CO_2 flux (Zeglin *et al.* 2009).

Overall, the dominant importance of temperature and a small but significant contribution associated with microbial biomass suggests future warming will influence CO_2 flux by altering the relative importance of geochemical and biological contributions to CO_2 flux. It is difficult to predict the direct role of changing SWC on CO_2 flux as the valleys warm and greater hydrological connectivity is likely between soils, streams and lakes. The high spatial variation in our results is typical of other Dry Valley studies of biota and biogeochemical processes (Barrett *et al.* 2004). Modelling the response of the Dry Valley CO_2 flux to climate warming will require greater understanding of the distribution and diversity of soil biota, the interactions of SWC and salinity under warming, and the altered hydrological landscape as more surface area appears as seeps, water tracks and wetted margins along streams and lakes.

Author contribution

Planning by BAB and RAV; data collection and analysis by BAB; manuscript preparation by BAB and RAV.

Supplemental material

A supplemental appendix will be found at http://dx.doi.org/10.1017/S0954102015000255.

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