We thank both reviewers for their comments. They were thoughtful and contained many good suggestions that have improved the manuscript. Below we sorted comments from both reviewers into major categories and describe the changes we made based on the comments.

SELF CONTAINMENT

METHODS SECTION SHOULD BE IMPROVED. THERE IS A REFERENCE TO A PREVIOUS STUDY WITH FURTHER DETAILS; HOWEVER THERE ARE SOME KEY QUESTIONS THAT SHOULD BE EXPLAINED IN THE DOCUEMNT: I) I UNDERSTAND THAT THERE ARE A TOTAL OF 20 PLOTS (5 PER TREATMENT). IS IT CORRECT?

The Reviewer is correct that there are 20 plots, five replicates of each treatment. We reworded this section of the methods to make this more clear and tried to describe all relevant information in all cases where we referenced other studies.

I THINK THAT, IN ORDER TO UNDERSTAND THIS MANUSCRIPT PROPERLY, READERS HAVE TO GO TO TOO MANY OTHER RELATED WORKS (REED ET AL. 2012; DARROUZET-NARDI ET AL. 2015; FERRENBERG ET AL. 2017; TUCKER ET AL 2017. . ...) - This is a fair criticism. We worked to make this manuscript more “self-contained” in numerous places throughout the manuscript

MOREOVER, I WOULD LIKE TO EMPHASIZE THE POTENTIAL EFFECT OC AND ESPECIALLY SOIL LABILE ORGANIC MATTER ON SOIL RESPIRATION. LARGE EFFORT HAS BEEN MADE TO EXPLAIN THE POTENTIAL EFFECT OF ROOTS RESPIRATION HOWEVER I RECOMMENDED TALKING ABOUT SOIL RESPIRATION (INCLUDING ROOTS, MICROBIAL, AND OTHER HETEROTROPHS) AND THE RELATIONSHIP BETWEEN SOIL C POOLS AND RAIN OR WATER PULSES (SEE LOPEZ-BALLESTEROS ET AL., 2016).

We appreciate this comment and agree that partitioning sources (e.g., heterotrophic consumption of OC vs. root respiration) is important in understanding the mechanisms that drive CO_2 exchange with the atmosphere, both now and into the future. With that in mind, the Lopez-Ballesteros et al. 2016 is a very nice exploration of the different components of CO_2 efflux. Here we cannot perfectly partition the sources of flux – our goal with this study was to carefully quantify soil CO_2 flux with different climates using a manipulative experiment – and thus the mix of eddy covariance, ANPP assessment, and soil chambers as performed by Lopez-Ballesteros et al. 2016 was outside of our experiment’s scope. The case we are making here is that, though we are aware of all these sources, the data we have suggest roots are playing a large role in regulating soil flux as observed at the surface. One mistake we made in constructing this argument was referring readers to the appendix in our previous paper (Darrouzet-Nardi et al. Biogeochemistry 2015), where this issue was discussed in detail, including calculations of the size of the organic matter pool and whether it was a plausible source (it is). Instead we have now laid out this logic in this manuscript as well. We didn't want to repeat too much of our previous paper’s analysis from there, but we erred too far on the side of redirecting to other papers, which the other review commented on as well. We have largely rewritten this section (discussion section 4.3) to be a more complete and self-contained discussion. Hopefully this will allow a more balanced discussion of sources in this paper to address this critique.

L152: WHAT ABOUT INORGANIC C FLUXES? THEY ARE NOT INCLUDED IN THE THEORETICAL BALANCE OF NSE.

We did some further reading on this and decided we in fact cannot rule inorganic C fluxes out as playing a role so we have included a paragraph on the issue.

L250-270: AUTHORS EXPLAIN THAT THEY FOUND HIGHER C LOSSES IN THE INITIAL PHASE OF THE WARMING EXPERIMENT, BUT THAT THIS EFFECT WAS REVERSED IN THE LONG TERM. THIS IS INTERESTING, AND IT SEEMS TO ME THAT TWO POSSIBLE EXPLANATIONS ARE GIVEN FOR THIS (I) REDUCED SOIL C AVAILABILITY, WHICH SEEMS TO BE SOMETHING LIKE A NEGATIVE BIOTIC IMPACT DUE TO A LEGACY OF HIGH C LOSS IN THE SOIL AND (II) AN EFFECT OF LAMPS DRYING THE SOIL. I DO NOT KNOW IF AUTHORS ARE GIVING MORE WEIGHT TO ONE OR ANOTHER TO EXPLAIN THE RESULTS, BUT AFTER READING WITH INTEREST THE TUCKER ET AL. 2017 PAPER QUOTED, A CLEAR QUESTION ARISES: ARE THE HEATING LAMPS AFFECTING THE T AND MOISTURE OF THE FIRST MILIMITERS OF SOIL UNDERNEATH THE CRUSTS? (IF SO, C FLUXES WOULD BE AFFECTED ALSO FOLLOWING TUCKER ET AL.). IF THE ANSWER IS YES, A SECOND ONE WOULD BE, IS THIS CREATING ANY EXPERIMENTAL BIAS OR THE SAME EFFECT COULD BE EXPECTED OVER THE UPPER MM OF SOIL UNDER A GENERAL RAISE OF T BETWEEN 2-4◦ AS THE ONE ASSAYED? I WOULD WELCOME A BIT OF DEBATE ABOUT THIS

We agree that this is one of the crucial details in interpreting these data and we did try to address the point more completely in the revision. Our basic argument was that we in fact do not see obvious moisture differences among treatments (the supplemental figure provides some information on this). However, the Tucker paper implies that our current measurement may have been missing the surface moisture dynamics. In addition, it is to be expected that the change in community composition of the crusts will play some role. So we think both likely play a role and unfortunately from this study, we can't totally disentangle which is more important. The inclusion of the biocrust cover data helps to inform on this matter as well. As for any anomalous heating effects on the surface of the soil creating a bias, we are not aware of such an effect and believe that the heating simulates within reason what future conditions may be like in these ecosystems.

ADDED DATA AND ANALYSIS

Add biocrust composition data

-*WERE BIOCRUST COMMUNITY COMPOSITION, BIOMASS AND COVERAGE OF ALL PLOTS COMPARABLE AT THE BEGINNING OF THE EXPERIMENT?.*

-*BIOCRUST COVERAGE INFORMATION IN THE CONTROL PLOTS AND TREATMENTS. IS THIS INFORMATION PROVIDED IN OTHER RESEARCH WORKS? IT SHOULD BE STATED SOMEWHERE,*

-L287-288 WHAT ABOUT THE EVOLUTION OF BIOCRUST COVER AT THIS EXPERIMENT IN CONTROL AND EXPERIMENTAL PLOTS, LET ME KNOW PLEASE IF I AM MISSING ANY POINT HERE. IF IT IS NECESSARY TO GO TO OTHER PUBLISHED PAPER TO SEE THIS DATA (OR SIMILAR), AUTHORS SHOULD AT LEAST EXPLAIN IT CLEARLY. I WOULD SUGGEST TO ADD A TABLE OR FIGURE TO SUMMARIZE THIS INFORMATION.

-BESIDES, I THINK THAT THE NSE CONCEPT IS INTERESTING AND USEFUL FOR UNDERSTANDING RELEVANCE OF BIOCRUSTS OVER SOIL C FLUXES, BUT IN ORDER TO HAVE A COMPLETE UNDERSTANDING OF THE CONTRIBUTION I THINK THAT SOME DATA ABOUT BIOCRUST COVERAGE SHOULD BE PROVIDED. WHICH % OF THE SOIL SURFACE ENCLOSED BY THE CHAMBER IS COVERED BY BSC AT EACH OF THE TREATMENTS AT THE BEGINNING OF THE EXPERIMENT? AND AT THE END? WE KNOW THAT VASCULAR PLANTS ARE EXCLUDED FROM THE SURFACE, BUT WE DO NOT KNOW ANY THRESHOLD OF BSC COVER IN THE PLOTS CHOSEN.

We added a figure in which we show these data and discussed them throughout the manuscript. This has improved the manuscript and we thank the reviewers for the suggestion.

INTRODUCTION COULD BE BETTER STRUCTURED BY: I) BETTER DESCRIPTION OF BIOCRUST COMMUNITIES

We added some biocrust species cover info in the introduction.

Add a control plot to figure 2

FIG 2: IT COULD BE INTERESTING TO SHOW A CONTROL PLOT AS FIGURE 2.B.

We added this as suggested.

Assemble climate data for whole study period

-MAYBE 9 YEARS ARE NOT ENOUGH FOR THE ANALYSIS OF A NATURAL (NON-INDUCED BY THE TREATMENT) CLIMATIC TREND. BUT I WOULD LIKE TO SEE AN EXPLORATORY ANALYSIS OF CURRENT CLIMATE TREND (AT LEAST DURING THE STUDY PERIOD). THIS COULD HELP TO IDENTIFY ANY TREND IN TEMPERATURE OR PRECIPITATION THAT COULD ACT IN A SYNERGISTIC MANNER WITH EXPERIMENTAL TREATMENTS.

-MORE DETAILED INFORMATION ABOUT THE MACROCLIMATE AND THE MICROCLIMATE OF THE RESEARCH AREA BETWEEN 2006-2014 (TABLE 1 AND SUPPORTING INFORMATION ABOUT SOIL MOISTURE ARE NOT ENOUGH UNDER MY POINT OF VIEW FOR A WORK OF THIS DIMENSION)

We added substantially more climate information to the figures and results.

"WATER WAS ADDED IN 1.2 MM EVENTS MANUALLY WITH BACKPACK SPRAYERS AND WAS APPLIED 40 TIMES FROM MAY 31-SEP 20, 2006 AND 36 TIMES FROM JUNE 14-SEP 20 IN 2007, WITH AN AVERAGE TIME BETWEEN WATERING OF 2.8 DAYS (TABLE 1)"

ACCORDING TO THIS SENTENCE, WATER WAS ADDED IN 2006 AND 2007. HOWEVER AS YOU EXPLAIN WATERING WAS STOPPED IN 2012. EVEN TAKEN IN TO ACCOUNT THAT 2008-2009-2010-2011 WERE NOT INCLUDED IN THIS ANALYSIS, THIS INFORMATION SHOULD BE INCLUDED AS IT IS EXPECTED TO AFFECT NEE MEASUREMENTS AT 2013 AND 2014. DID YOU EXPECT THAT THIS COULD HAVE SOME EFFECT ON RESPIRATION PATTERNS OBSERVED ON 2013-2014.

We included information on the watering for the years that we left out.

Add extra statistical comparisons among time periods (Compare expected change in temp/moisture based on correlations through time with what we saw)

-AN EVALUATION OF THE EFFECT OF THE PASS OF THE TIME OVER THE SAME PLOTS (E.G COMPARISONS IN C FLUXES AND BIOCRUSTS COVERS IN CONTROLS IN 2006 WITH THE SAME CONTROL PLOT IN 2014).

-L 306-309. ADD INFORMATION ON CHANGES IN NSE IN CONTROLS UNDER NATURAL ENVIRONMENTAL CONDITIONS OVER THE COURSE OF THE STUDY. SHALL WE EXPECT A SIMILAR OR DIFFERENT SHIFT IN TREATMENTS?

We added a supplementary table showing effect sizes for change within treatments over time and discussed it in the results.

DESCRIPTION OF STATISTICS

Improve description of statistics

WAS THE SIZE EFFECT OF EARLY WARMING, WATERING, AND COMBINED TREATMENTS ON NSE CALCULATED FROM THE RANDOM FOREST MODELS? IT IS NOT CLEAR IN THE CLEAR IN THE CURRENT FORM.

The random forest models were only used for gap filling. The effect sizes were calculated using subtraction (treatment - control) and the uncertainty around those differences were calculated using a confidence intervals. We did a couple of things here. First, we include switched to a more straightforward technique used to calculate the confidence intervals (mixed effects models). Changes to the results were negligible but the analyses are more reproducible and standard. We also worked to make it more clear which techniques (random forest vs. mixed effects models) were associated with which parts of data processing and analysis.

I UNDERSTAND THAT AUTHORS HAVE USED STATISTICAL METHODOLOGIES TO EXTRAPOLATE MISSING DATA INSIDE THE DATA SET TOGETHER WITH OTHER METHODOLOGY TO CALCULATE THE TD COMPARING CONTROLS AND TREATMENTS. I FEEL CURIOUS ABOUT THE FACT OF NOT HAVING STATISTICAL COMPARISON BETWEEN TREATMENTS AND CONTROLS (E.G, IF THE EFFECT OF THE CHANGE IN THE FLUX IN ONE PARTICULAR YEAR IN THE WARMING TREATMENT (OR IN ANY OTHER TREATMENT) IS STATISCALLY SIGNIFICANT COMPARED WITH THE CONTROL)

-FIG 3, PLEASE EXPLAIN A BIT MORE HOW WERE CUMULATIVE NSE CALCULATED. IS IT POSSIBLE TO INCLUDE SOME STATS ABOUT THE DIFFERENCES IN NSE CREATED BY THE TREATMENTS?

There is a statistical comparison but we focus on effect sizes instead of statistical "significance." The cited Nakagawa and Cuthill paper provides a good justification for this approach. We calculate uncertainty surrounding *td* using confidence intervals. Though we have explicitly avoided using the null hypothesis statistical testing (NHST) paradigm, we note that as a heuristic, confidence intervals that do not contain 0 would be marked as "significant" in NHST. Thus, confidence intervals provide more complete information as compared to what a p-value would provide: they constrain effect size with bounds instead of only telling us the probability that that bounds on the effect size contain zero. Tukey (1991) "Philosophy of multiple comparisons" provides another strong and concise argument on why significance testing is too black and white. As an example, both the -11.8 [-21.7, 0.4] and the -1.2 [20.3, -15.1] would technically be "not significant" but these are different results that warrant different interpretations. The first implies a much greater likelihood that the effect is in the direction of less C flux in the control and could well be of substantial quantity whereas the second implies poor constraint and lack of good information on the effect size due to high variability among chambers. It could be high, low, or negligible, with greater sample size needed for better constraints.

Make sure reason for watering is included

L131: WHY DID THE AUTHORS CHOOSE THE PERIOD END OF MAY/BEGINNING OF JUNE TO MID-SEPTEMBER FOR THE WETTING OF THE PLOTS? ARE CLIMATE CHANGE PREDICTIONS IN THE AREA GOING TOWARDS HIGHER PRECIPITATION DURING THAT PERIOD OF THE YEAR? I THINK THAT THE REASON SHOULD BE INCLUDED IN THE METHODOLOGY

The reason is that this was based on predictions of greater precipitation frequency during the monsoon season. We have added this reasoning into the manuscript.

Technical details on chamber measurement

L145: WHICH IS THE FREQUENCY OF GAS EXCHANGE MEASUREMENTS INSIDE THE CHAMBER DURING THE 3 MINUTES PERIOD THAT IT GETS CLOSED? HOW IS THE FLUX EXACTLY CALCULATED AT EACH MEASURING POINT?

We added these technical details.

Patterns of longer-term climate change effects on CO_2 efflux from biocrusted soils differ from those observed in the short-term

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Abstract. Biological soil crusts (biocrusts) are predicted to be sensitive to the increased temperature and altered precipitation associated with climate change. We assessed the effects of these factors on soil carbon dioxide (CO_2) balance in biocrusted soils using a sequence of manipulations over a nine-year period. We warmed biocrusted soils by 2 and, later, by 4 °C to better capture updated forecasts of future temperature~~, as well as altered monsoon-season precipitation~~ at a site on the Colorado Plateau, USA~~.~~. We also watered soils to alter monsoon-season precipitation amount and frequency, and had plots that received both warming and altered precipitation treatments. Within treatment plots, we used 20 automated flux chambers to monitor net soil exchange (NSE) of CO_2 hourly, first in 2006-2007 and then again in 2013-2014, for a total of 39 months. Net CO_2 efflux from biocrusted soils in the warming treatment increased a year after the experiment began (2006-2007). However, after 9 years and even greater warming (4 °C), results were more mixed, with a reversal of the increase in 2013 (i.e., controls showed higher net CO_2 efflux than treatment plots) and with similarly high rates in all treatments during 2014, a wet year. Over the longer-term, we saw evidence of reduced photosynthetic capacity of the biocrusts in response to both the temperature and altered precipitation treatments. Patterns in biocrusted soil CO_2 exchange under experimentally altered climate suggest that (1) warming ~~effects~~ stimulation of CO_2 efflux was ~~were~~ diminished later in the experiment, even in the face of ~~larger~~ greater warming and (2) ~~likely drivers of the~~ treatment effects on CO_2 flux patterns were likely driven by changes in biocrust species composition and by changes in root respiration due to vascular plant responses.

1 Introduction

Soils with active biological soil crust (biocrust) communities are essential components of dryland ecosystems worldwide and are also one of the most sensitive components of drylands to climate change (Ferrenberg et al., 2017; Reed et al., 2016). Given the vast and growing global extent of dryland regions (Safriel et al., 2005; Prăvălie, 2016), the response of biocrusts to major global change phenomena, such as climate change, may be an important aspect of the overall response of ~~Earth's~~ Earth’s ecosystems. In particular, due to the potential for dryland feedbacks to future climate (Poulter et al., 2014; Ahlström et al., 2015; Rutherford et al., 2017), a key parameter to consider as dryland ecosystems warm is ~~their~~ carbon (C) balance, specifically carbon exchange of biocrusted soils. Dryland soils are characterized by low soil organic matter that is negatively correlated with aridity across many drylands (Delgado-Baquerizo et al., 2013) and there is an association between C loss and the phenomenon of desertification (Lal, 2004). Drylands can also show large year-to-year variation in C fluxes that are relevant for explaining global-scale fluxes (Ahlström et al., 2015; Poulter et al., 2014; Biederman et al., 2017). ~~Thus, improving our understanding of dryland C cycle responses to change matters at the global scale. At the organism scale, the viability of biocrusts is linked directly to their ability to maintain a positive C balance among hydration-desiccation cycles (Grote et al., 2010; Coe et al., 2012; Oliver et al., 2005).~~ At the ecosystem scale, ~~soils in drylands with~~ biocrusted soils within drylands~~s~~ are often ~~large~~substantial contributors to both C uptake (Elbert et al., 2012) and ~~overall~~ ecosystem respiration (Castillo-Monroy et al., 2011). At the organism scale, the viability of biocrust~~s~~ is linked to their ability to maintain a positive C balance among hydration-desiccation cycles (Grote et al., 2010; Coe et al., 2012; Oliver et al., 2005). ~~that contribute substantially to C uptake (Elbert et al., 2012)~~~~Though~~ Despite the importance of C ~~cycling~~ balance ~~is central~~ to understanding biocrust function and ~~although~~dryland ecosystem feedbacks to global change~~s~~ ~~soils in drylands with biocrusts are often large contributors to overall ecosystem respiration (Castillo-Monroy et al., 2011) that contribute substantially to C uptake (Elbert et al., 2012)~~, few studies have addressed how ~~it~~biocrust soil CO_2 fluxes will respond to changing temperature and precipitation ~~biocrust contributions to ecosystem CO_2 exchange~~in biocrusted soils ~~remain incompletely understood~~.

Carbon balance in biocrusted soils includes not only the activities of the biocrusts themselves, but also the activities of subsurface vascular plant roots and soil heterotrophic microbes. Considering biocrusted soils together with the function of adjacent vascular plants is important given that there is increasing evidence for ~~strong ~~biotic connections, possibly mediated by fungi, between these functional groups (Green et al., 2008) and for linkages in plant-soil C cycle responses to warming. For example, at another~~a~~ site on the Colorado Plateau~~ near the site for this study~~, measurements of plant photosynthesis, coupled with spot measurements of soil respiration under plant canopies, showed plant photosynthet~~s~~ic rates~~sphotosynthesis~~ ~~was ~~were tightly coupled to soil respiration rates, with both showing reduced fluxes in response to warming during the spring when plants are most active (Wertin et al., 2017). While these patterns could be the result of independent climate controls, such as temperature and moisture, on each individual flux, vascular plant C allocation to roots and heterotrophs belowground~~,~~ ~~and/and/~~or biotic connections between biocrust organisms and vascular plants could also help explain~~,~~ ~~they highlight the potential for strong~~the coupling between above- and belowground CO_2 fluxes~~, regardless of the mechanisms~~.

In addition to affecting soil C balance through direct physiological means, warming has been shown to have substantial effects on biocrust species composition, including macroscopic components such as moss and lichens (Ferrenberg et al., 2015; Escolar et al., 2012; Maestre et al., 2015) and microbial communities ~~ycommunity composition ~~(Steven et al., 2015; Johnson et al., 2012). Climate models predict rapidly rising temperatures for already hot and moisture-limited dryland regions, including the site of our study in the southwestern United States (Stocker, 2014; Jardine et al., 2013). Forecasts of future precipitation patterns are less certain, but overall drier conditions with changes in precipitation event size and frequency are likely (Seager et al., 2007). Climate models predict increases in dryland annual average temperature of up to 4 °C by the end of the 21st century, as well as significant alterations to the amount and timing of rainfall (Christensen et al., 2007). For example, the Intergovernmental Panel on Climate Change (IPCC) A1B scenario suggests a decrease in precipitation amount of 5-10% for the southwestern U.S., as well as significant changes to the timing and magnitude of precipitation (D'Odorico and Bhattachan, 2012). Across many ecosystems, including drylands, both plant C uptake and soil respiration ~~are often~~show an optimum, ~~in which they ~~such that rates are positively correlated with increased temperatures and moisture (Wu et al., 2011)~~, although~~ until a point at which high temperatures (often accompanied with drying) begin suppressing both ~~temperature can also have a negative relationship with~~ photosynthesis (e.g., Wertin et al., 2015) and ~~with~~ soil respiration ~~when increased temperatures relates to rapid drying~~ (Tucker and Reed, 2016). Drought also tends to reduce vascular plant production and respiration, with greater sensitivity in drier areas (Knapp et al., 2015). In soils overlain by biocrusts (hereafter, biocrusted soils) specifically, temperature and moisture are key physiological parameters for C flux (Grote et al., 2010; Darrouzet-Nardi et al., 2015) and, although few, the warming experiments that do exist suggest that biocrusted soils will have higher net CO$_2$ efflux with a warming climate (Darrouzet-Nardi et al., 2015; Maestre et al., 2013). There is evidence for a limit to this association though, with very high temperatures leading to reduced biotic activity, including microbial respiration, in biocrusted soils (Tucker and Reed, 2016).

To improve our understanding of dryland C flux responses to global change, we used a warming by watering manipulation experiment on the Colorado Plateau established in 2005. When the study began, we explored the hypothesis that warming would increase net losses of CO$_2$ from ~~biocrusted~~ soils covered with late successional biocrusts (~50% moss, ~30% lichen cover) via detrimental impacts on biocrust physiology caused by warming~~.~~. At the same time we wanted to explore how altered precipitation could directly affect biocrust soil CO$_2$ exchange and/or interact with the effects of increased temperatures. These early results supported the basic hypothesis concerning the warming-only treatment, showing that warming led to increased CO$_2$ loss after 1-2 years, with the largest differences during periods in which soils were wet enough to support substantial biocrust photosynthesis (Darrouzet-Nardi et al., 2015). ~~We~~ Crucially, we also found that the increased frequency of small frequent precipitation events negatively affected biocrusts: the treatment caused the death of a major biocrust component, the moss *Syntrichia caninervis* (Coe et al., 2012; Reed et al., 2012; Zelikova et al., 2012). This finding represented a ~~major~~substantial alteration to the system and led to a second phase of the experiment. In this phase, we ceased the watering treatment that had caused moss death and increased the warming treatment from 2° to 4° to see if greater warming would negatively impact biocrusts. We found that the greater warming did in fact reduce ~~biocrust~~moss and lichen cover as well, though not as rapidly as the watering treatment (Ferrenberg et al., 2015). ~~The new work described here~~Here we ~~aims~~ report the C balance response to these multiple phases of the experiment~~to~~. Our main goals were to:~~:~~ (1) determine if the increased net soil CO$_2$ loss observed after a year of warming ~~years~~ was maintained after 8 years, and (2) to assess how the altered precipitation patterns affected net soil CO_2 exchange ~~at both~~during the early phase when mosses were dying and, then ~~and the~~ later, after mosses were lost and the increased watering had ceased~~ time points~~.

2 Materials and Methods

2.1 Site Description

The study was located in a semiarid ecosystem on the Colorado Plateau (36.675 N, -109.416 W; elevation = 1310 m; mean annual temperature = 13 °C, mean annual precipitation = 269 mm; WRCC 2014) that supports multiple species of grasses and shrubs. Soils are Rizno series Aridisols and the dominant plants include *Achnatherum hymenoides, Pleuraphis jamesii, Atriplex confertifolia,* and *Bromus tectorum.* Biocrust communities are dominated by the cyanobacterium *Microcoleus vaginatus*, the moss *Syntrichia caninervis*, and the cyanolichens *Collema tenax* and *Collema coccophorum*. The site is on a moderate hillslope (~10~~%~~%) surrounded by steep gullies that make it hard to access for livestock, which may explain its relict biocrust and plant composition that includes late successional crusts with well-developed communities of native grasses and shrubs, similar to sites found in Canyonlands National Park (Belnap and Phillips, 2001). ~~For a more detailed description of the site including co-located experiments, see Wertin et al. (2015).~~ Rainfall during the study period was distributed around the mean (Table 1, Fig. S1), with several slightly above average years including the first and last year of the experiment (2006: 294 mm; 2014: 304 mm), and one year with substantial drought (2012: 122 mm). Rainfall and temperatures went up and down across years, with no notable directional shift over the 9-year course of the study. Long-term records from a nearby weather station in Moab, UT show that mean annual temperatures have been increasing (21.3 °C for 1900-1924 vs. 22.9 °C for 1991-2016, a difference of 1.5 °C). Precipitation trends since 1925 do not show a clear trend (Fig. S2).

2.2 Warming and watering treatments

The experiment contained 20 plots with 5 replicates (*n* = 5) for each of 4 treatments: ~~five blocks of four treatments each:~~ *control*, *warmed*, *watered*, and *combined* (~~(~~warmed + watered~~)~~) ~~for a total of 20~~. Plots were 2 × 2.5 m ~~plots~~in size. Each plot contained ~~, each of which contained~~ ~~an~~one automated CO_2 chamber (described below). The warming treatment began in October

2005 in plots fitted with 800 W infrared radiant (IR) heat lamps (Kalglo Model MRM-2408) mounted at a height of 1.3 m. Control plots had dummy lamps that do not provide heat. The heating treatment was regulated by altering the voltage supplied to each lamp. While some drying of soil moisture from the lamps may have occurred, we saw little evidence for this phenomenon in soil moisture values, with drying after precipitation events occurring at similar rates in all treatments (Fig. S3). A previously published analysis also reported no easily detectable moisture effects from the infrared lamps in either this experiment or a similar co-located experiment despite soil moisture probes at 2, 5, and 10 cm- throughout all plots (Wertin et al., 2015). However, we cannot rule out very shallow surface moisture effects, which could be important (Tucker et al., 2017).

-The target temperature increase was ambient soil temperature +2 °C from 2005-2008, at which point a second lamp was added to each plot and the warming treatment was increased to +4 °C where it remained through the end of the automated chamber sampling in September of 2014. The treatment temperatures were increased from 2 to 4 °C above ambient in order to better match changing predictions of future temperature by 2100 (Christensen et al., 2007). To simulate predictions of increased frequency of small precipitation events (Weltzin et al., 2003; Christensen et al., 2007), ~~W~~water was added in 1.2 mm events manually with backpack sprayers and was applied 40 times from May 31-Sep 20, 2006 and 36 times from June 14-Sep 20 in 2007, with an average time between watering of 2.8 days (~4x natural frequency; Table 1). ~~(Christensen et al., 2007)~~ The amount of water varied by year because watering did not occur on days when natural rainfall occurred. Watering was stopped in 2012 because the late successional biocrust community had been eliminated after the first year and was showing no further change through time (Reed et al., 2012; Ferrenberg et al., 2015). ~~There were intermittent automated chamber measurements in 2012, the last year of watering, crossed with the higher warming level, providing enough data for analyses of daily patterns, though not enough to assess seasonal total rates.~~

2.3 Net soil exchange measurements with automated chambers

Carbon dioxide fluxes were assessed with automated CO_2 flux chambers, described in detail in Darrouzet-Nardi et al. (2015). The chambers ~~are~~ were placed within the soil ~~(details below) and,~~ ~~are~~ open at the bottom and have ~~closed systems in which~~ clear lids at the top ~~, allowing~~

~~sunlight and hence photosynthesis by biocrust organisms,~~ that are closed once per hour for 3 min~~utes~~ to assess net CO_2 flux~~,~~. The chambers allow in~~ing~~ sunlight and hence allow photosynthesis by biocrust organisms.~~.~~ Fluxes of CO_2 during that time are calculated as the rate of change in CO_2 concentrations during the 3 min~~nute~~ period. During that 3 min period, CO_2 was recorded every 2 s and averaged every 10 s. Aberrant points were down-weighted with a smoothing function ('supsmu' implemented in MATLAB; Friedman, 1984), allowing a robust calculation of slope for a given 3-minute interval (Bowling et al., 2011). The chambers were 30 cm tall × 38 cm inner diameter, covering a soil surface area of 0.11 m^2. Chambers were installed to a depth of 27 cm in the soil, leaving ~3 cm of the chamber protruding above the soil surface. The chambers were placed in plot locations containing biocrusts but no vascular plants. Values from these chambers were reported as net soil exchange (NSE) of CO_2. The concept of NSE is defined in Darrouzet-Nardi et al. (2015) to include biocrust photosynthesis as the sole form of CO_2 uptake (i.e., because the chambers do not include vascular plants) along with CO_2 losses via respiration from biocrusts, other soil microbes, ~~and~~ plant roots, and any abiotic soil sources. While it would have been ideal to operate the chambers year round for the entire course of the experiment, it was beyond the operational capacity of the project to do so and there are times when the systems were not operational. The chambers have more frequent malfunctions during the winter due to weather conditions, so those months are least represented. There were intermittent automated chamber measurements in 2012, the last year of watering, crossed with the higher warming level, providing enough data for analyses of daily patterns, though not enough to assess seasonal total rates.

Biocrust community composition of the autochambers was measured at the initiation of the experiment in 2005 and again in 2017. ~~Photos of the biocrust communities were taken at multiple times between 2005 and 2017.~~ Assessment of the biocrust community was performed using a frame that covered the autochamber area in which the cover of thirty-one individual 25.8 cm^2 squares as estimated for all biocrust species. The total cover of each species was summed from the individual quadrats and the quadrats covered 800 cm^2 of the chambers' 1100 cm^2 area.

2.4 Imputation and statistical analysis

Hourly data from the automated chambers were collected from January 1, 2006 - September 20, 2007, February 19 - November 17, 2013, and February 14 - November 17, 2014, for a total of

28,058 time points for each of the 20 chambers. Of these time points, 29~~%~~% of the data were missing, primarily due to technical issues with the chambers. To allow calculations of cumulative NSE, data were imputed following the same procedure as in our previous work (Darrouzet-Nardi et al., 2015). Data were assembled into a data frame containing columns for (i) each of the 20 chambers; (ii) environmental data including soil and air temperature, soil moisture, 24-hour rainfall totals, photosynthetically active radiation (PAR); and (iii) six days of time-shifted fluxes (before and after each measurement; i.e., -72 h, -48 h, -24 h, +24 h, +48 h, +72h) for one chamber from each treatment, soil temperature, and soil moisture. Lagged values were added due to their ability to greatly improve prediction of missing time points, particularly for short time intervals such as those caused by, for example, several hours of power outage at the site. One data frame was created for each of the three continuous recording periods: 2006-2007, 2013, and 2014 and each was imputed separately. Imputation was performed using the missForest algorithm, which iteratively fills missing data in all columns of a data frame using predictions based on random forest models (Stekhoven and Buhlmann, 2012; Breiman, 2001).

After imputing the hourly values, cumulative fluxes were calculated by summing NSE over seven-month periods (~~,~~February 19 - September 19~~,~~) for each year (2006, 2007, 2013, and 2014). This seven-month period ~~which~~ was selected due to availability of data in all four analysis years. The total number of cumulative fluxes evaluated was 80 (4 years × 4 treatments × 5 replicates). We also ~~distinguished~~made separate cumulative estimates of time periods in which we observed active photosynthesis, defining these periods as days during which the NSE values were -0.2 μmol CO_2 m^{-2} s^{-1} or lower, with more negative numbers showing higher net photosynthesis. These periods ~~were selected as subsets of the seven-month periods, varying in duration by the number of days with active photosynthesis, which~~ typically correspond ~~s~~ to times with sufficient precipitation to activate biocrusts.

The effect of the ~~early~~ *warmed~~ing~~*, ~~*watering*~~*watered*, and *combined* treatments on cumulative NSE values were evaluated by ~~evaluating~~ ~~assessing~~calculating the size of the differences between each treatment and the control ~~effect size of these treatments on each variable of interest~~ (Nakagawa and Cuthill, 2007; Cumming, 2013). ~~Treatment differences, which we notate as t_d, were assessed as treatment - control with 95% confidence intervals estimated~~Treatment differences, which we notate as t_d, were ~~assessed~~ calculated as treatment ~~-~~– control (paired by block) with 95% confidence intervals estimated using mixed effects linear models for each year with treatment as a fixed effect and block as random effect (Pinheiro and Bates, 2000).~~ by bootstrapping, with $n = 5$ in all cases (Carpenter and Bithell, 2000).~~ Analyses were facilitated by a custom-made R package "treateffect", available at https://github.com/anthonydn/treateffect. The data used for these analyses are available at https://doi.org/10.6084/m9.figshare.6347741.v1. Finally, to evaluate differences over time, differences between 2006 data for each treatment and each subsequent year were calculated, also using mixed effects models.~~.(Efron, 1987) Analyses were facilitated by a custom-made R package treateffect, available at https://github.com/anthonydn/treateffect. The data used for these analyses are available at https://github.com/anthonydn/warmed_biocrusts_nine_years. Using the imputed data, treatment differences were assessed both on individual hourly measurements and on cumulative NSE through time. The cumulative measurements were done on a seven-month period, February 19 - September 19, which was selected due to availability of data in all four analysis years. We also distinguished time periods in which we observed active photosynthesis, defining these periods as days during which the NSE values were -0.2 μmol CO_2 m^{-2} s^{-1} or lower, with more negative numbers showing higher net photosynthesis. These periods were selected as subsets of the seven-month periods, varying in duration by the number of days with active photosynthesis, which typically corresponds to times with sufficient precipitation to activate biocrusts.~~

3 Results

Biocrust cover within the soil collars used by the automated chambers was relatively similar in all treatments at the beginning of the experiment, with an average of 49% moss and 31% lichen in each treatment (Fig. 1). Between 2005 and 2017, these percentages fell in all treatments including the controls, eventually being replaced primarily by lightly-pigmented cyanobacterial crusts, probably *Microcoleus vaginatus* (Gundlapally and Garcia-Pichel, 2006). Lichen went to <3% in all treatments. Mosses were more variable, remaining at 25% in controls, but falling to 7% in warmed plots and to 0% in both watering plots. Cyanobacteria cover started at 0% in all chambers and rose to 50-90%.

Seasonal time courses of NSE showed similar patterns among years and treatments, with peaks in NSE in the spring associated with peak vascular plant activity, and peaks in both ~~photosynthesis and respiration~~negative and positive NSE associated with rain events (Fig. ~~1a~~2a).

In the early time period (1-2 years after treatments began), the supplemental 1.2 mm watering treatment caused large “puffs” of CO_2 when water was added. By the final year of watering (2012), the size of these puffs was substantially smaller and after watering ceased (2014), they did not occur even with natural rainfall events (Fig. ~~2~~3).

~~was at the beginning of the experiment ly-pigmented, probably *Microcoleus vaginatus*~~

In the early time period (2006-2007), i~~I~~nterannual comparisons of cumulative Feb. 19 - Sep. 19 (seven-month) ~~C~~CO_2 fluxes were consistent with the hypothesized ~~effects~~ trend of the warming and watering treatments increasing CO_2 flux to the atmosphere~~in the early time period (2006-2007),~~. ~~but showed varying results in the later time period (2013-2014).~~ In the early time period, shortly after the establishment of the treatments, we observed higher NSE (greater movement of CO_2 from soil to the atmosphere) in both watered and combined treatment plots, with less evidence of difference in the warming only treatment (Fig. ~~3a~~4a; Table 2). Fluxes were similar between 2006 and 2007 (Table S1).

In the later time period (2013-2014), the treatments showed varying results. In 2013, after the watering treatment had ceased, we observed ~~the opposite trend~~a reversal of the~~opposite trend~~treatment trend from the early period, with lower CO_2 efflux from soils in all three treatments (Fig~~ 3a~~. ~~3a~~4a; Table 2). This trend was particularly visible in the months of May and June (Fig. ~~1a~~2a,b). However, in the following year, 2014, a wet year with high spring rainfall (Table 1, Fig. ~~1a~~2a), all plots showed the highest CO_2 efflux observed in the experiment~~.~~ (e.g., 36.2 [21.7, 52.9] μmol m^{-2} s^{-1} higher compared to 2006 in control plots; Table S1). While no obvious treatment effects were observed, treatment effect sizes were relatively poorly constrained due to the higher variation that year (Table 2).

Interannual comparisons of cumulative CO_2 fluxes during periods of active photosynthesis showed higher photosynthesis in all treatments during the early measurement period (e.g., 2006 warmed t_d = 4.1 [-0.1, 8.2]~~4.05 [0.91, 7.48]~~; Fig. ~~3b~~4b; Table 2). In the later period (8-9 years after treatments began), subsequent to the cessation of watering, warmed plots still showed elevated CO_2 losses during periods of active photosynthesis but this difference was smaller than in the earlier measurements (e.g., 2013 warmed t_d = 1.3 [-0.5, 3.1]~~1.32 [-0.13, 3.03]~~; Fig. ~~3b~~4b; Table 2). In contrast, watered plots that were not warmed were similar to control plots.

In examining the daily cycles in the hourly data, further detail on the nature of the treatment effects was observed. After one year, watered treatments in which mosses had died showed strong reductions in CO_2 uptake capacity during wet-up events, but warmed treatments still showed a similar maximum uptake capacity relative to controls (e.g., minimum NSE on October 15, 2006 control = -0.93 ± 0.19 μmol m^2 s^{-1}; warmed = -0.89 ± 0.11, watered = -0.35 ± 0.06, combined = -0.2 ± 0.08; Fig. ~~4a~~5a). However, after 8 years of treatment, clear differences were present in the CO_2 flux dynamics in response to natural rainfall events (Fig. 5~~4~~b). Biocrusted soils in control plots still exhibited substantial net uptake of CO_2 (e.g., minimum NSE on August 14, control = -0.68 ± 0.12 μmol m^2 s^{-1}), whereas the other treatments showed less uptake relative to the control, with a similar trend visible on August 23rd.

4 Discussion

4.1 Early period: 2 °C warming × watering (2006-2007)

The increase in CO_2 effluxes in the watered treatments during the early period (Fig. 34, Table 2) were likely driven by both the loss of photosynthetic ~~mosses~~ biocrust organisms~~s~~ during that time (Reed et al., 2012), as well as increased soil respiration from soil heterotrophs. Moss death may have contributed to net soil C loss via (i) eliminating CO_2 uptake from this important biocrust CO_2-fixer (Reed et al., 2012; Coe et al., 2012); and (ii) decomposition of dead mosses. Elevated soil respiration with warming and watering is broadly consistent with the results of similar experiments across many ecosystems (Wu et al., 2011; Rustad et al., 2001), dryland sites specifically (Nielsen and Ball, 2015; López-Ballesteros et al., 2016; Patrick et al., 2007; Thomey et al., 2011), and previously documented effects in biocrusted soils at this site and others (Darrouzet-Nardi et al., 2015; Maestre et al., 2013; Escolar et al., 2015). In the warmed treatment, elevated NSE was not as evident in 2006 as in the watered and combined treatments, and this is consistent with the biocrust community changes. While moss died off quickly in the watered plots, mosses in the warmed plots ~~the negative effects of temperature~~ took longer to ~~emerge~~ show negative effects ~~(Ferrenberg et al.~~(Ferrenberg et al., 2017)~~(Ferrenberg et al. 2017)~~. Indeed, increased CO_2 efflux with warming was clearer in the following year (2007) and moss cover was substantially reduced by 2010 (Ferrenberg et al., 2015). Such rapid species composition changes have been repeatedly implicated as drivers of system change in drylands, even with seemingly subtle changes in climate (Wu et al., 2012; Collins et al., 2010).

4.2 Late period: 9 years warming (2-4 °C) × legacy watering (2013-2014)

During the later period (2013) when warming had been increased to +4 °C (in 2009) and watering had ceased (effectively making the treatments: control, +4 °C, legacy watering, and +4 °C × legacy watering), several differences in treatment effects emerged in comparison to the early measurement period (2006-2007). First, the trend in the 2013 seven-month cumulative CO_2 fluxes (Fig. 34, Table 2) were reversed from those of the early measurement period (2006-2007), with the control plots having the highest NSE and all other treatments showing lower CO_2 efflux. The reversal of the NSE trend in the +4 °C and +4 °C × legacy watering treatments is likely due in large part to changes in biocrust community composition, with mosses largely eliminated in relation to the control plots where about half of the mosses were retained (Fig. ~~X~~1).~~.~~ The climate treatment-induced transition from late- to early-successional biocrusts (Ferrenberg et al., 2015) greatly reduces the potential for biocrusts to uptake atmospheric CO_2 (e.g., Housman et al., 2006).~~.~~ Further, vascular plant photosynthesis in multiple species was reduced with warming, which would be expected to reduce plant allocation of C belowground (Wertin et al., 2017). A number of warming experiments in more mesic systems that do not have photosynthetic soils have shown an initial warming-induced increase in soil CO_2 respiratory loss followed by subsequent declines in warmed plots; in these situations, reduced soil C availability for heterotrophic respiration and changes to heterotroph C use efficiency are often suggested to play a role (Bradford et al., 2008; Bradford, 2013; Tucker et al., 2013). Such effects would also be consistent with drying from the infrared heat lamps, a mechanism that was supported in a Wyoming grassland experiment (Pendall et al., 2013). Our soil moisture data showed little evidence of such drying effects (~~Supplemental~~ Fig. ~~1~~S3). However, with a minimum moisture probe depth of 2 cm, we may have missed moisture effects relevant only to the top several millimeters of soil, an area of current active investigation at the site: more recent results suggest that surface moisture (0-2 mm) can be a potent predictor of soil C fluxes on these biocrusted soils (Tucker et al., 2017). The reduction in CO_2 efflux with warming was also seen in a nearby set of plots in 2011, in which soil respiration was measured at individual time points with non-automated chambers (Wertin et al., 2017). In that study, the reduction with warming was observed three years after +2 °C warming treatment was implemented. The dark respiration measurements were made in the spring (at peak plant activity) and it was at the same point in the season (see Fig. 12) that we saw the strongest seasonal driver for the seven-month cumulative data. In sum, although our NSE data don’t allow us to ~~we can’t~~ disentangle the driving mechanisms~~se~~~~with our current data~~, changes in (i) biocrust composition, (ii) nearby plant activity, and (iii) possibly surface moisture could all have contributed to the reversal in the effect of the warming treatment in the late period of the study. -Regardless of the cause, these data suggest large, sustained changes to dryland soil C cycling at our site in response to climate change treatments.

We also observed reduced NSE values in the 2012-2013 sampling period ~~during the late period~~ in ~~the~~ plots that were previously watered plots ~~in comparison~~compared to the control plots, suggesting some legacy treatment effects. This was likely linked to loss of mosses, cyanobacteria, or changes in vascular plant physiology. For example, at a European site, biocrusted soil microsites ~~in Spain~~ were shown to be a dominant source of midday soil respiration (Castillo-Monroy et al., 2011). Furthermore,~~,~~ ~~and~~ reductions in the autotrophic biomass seen with the climate treatments ~~(Ferrenberg et al., 2017; Reed et al., 2016)~~ could reduce respiration rates (Ferrenberg et al., 2017; Reed et al., 2016)~~s~~. Plants accustomed to the extra water may also have responded negatively to its absence, causing reduced physiological activity and hence lower root respiration, an effect that has been documented in drought simulation experiments (Talmon et al., 2011). Soil heterotrophs can also show legacy effects of their species composition in response to changes in precipitation regime (Kaisermann et al., 2017). Water retention may also have been reduced due to the decline in biocrust cover, an effect for which there is some evidence, particularly in semiarid ecosystems like our study site (Belnap, 2006; Chamizo et al., 2012). Mosses have unique adaptations allowing them to absorb high fractions of precipitation without loss to splash and evaporation (Pan et al., 2016), a process that would be lessened in the climate manipulation plots due to moss death. In addition to effects on soil moisture, changes in biocrust community composition can have significant effects on soil nutrient availability (Reed et al., 2012) and nutrient availability can be tightly coupled with soil respiration rates (Reed et al., 2011). Although the NSE data do not allow us to ~~disentangle~~ determine which gross C fluxes caused the opposing treatment effects between the early (2006-2007) and late (2012-2013) measurement periods, ~~it~~ the observation of a reversal like this is important ~~to see such a reversal as~~because ~~a sustained~~if the ~~increase in~~ larger CO_2 loss had been sustained, it would have ~~the~~ indicated the potential for large feedbacks to increasing atmospheric CO_2 concentrations.

Interestingly, the CO_2 loss reversal observed in 2013 did not continue in 2014, likely due to the higher rainfall, particularly during spring. In 2014, we saw high NSE in all plots in the seven-month cumulative data, with no significant differences among treatments. Accompanying the higher precipitation in 2014 – which occurred in a series of large rain events in April and May – perennial plants were noticeably greener and there was a ~~large ~~flush of annual plants (data not shown).~~.~~ During wet conditions, warmed plots ~~showed ~~had higher NSE values, which could have been due to higher root respiration or higher subsoil microbial activity, potentially linked to root turnover or rhizodeposition (Jones et al., 2004). These results from the later period of the experiment (2013-2014) underscore that taking a long-term perspective (i.e., nearly a decade of warming) may be necessary for understanding climate change effects, particularly those that maintain interactions with species composition changes. Further, these data suggest more complexity in soil CO_2 efflux controls, such that some systems may not manifest a simple transition from temperature-induced increases in soil CO_2 loss to temperature-induced decreases at later stages of warming. The interannual variations in the magnitude of NSE fit with results from other drylands that show high interannual variation in net ecosystem exchange (NEE) as measured with eddy flux towers (Biederman et al., 2017). At least one other longer-term manipulation in a dryland has also observed early stimulation of plant growth with warming that then lessened over time, with longer-term effects driven by changes in species composition (Wu et al., 2012). The finding that decadal-~~-~~scale studies can have mixed and context-dependent effects not visible at the annual scale (Nielsen and Ball, 2015) is exemplified in our study by the reversal in effects seen in 2013, followed by the swamping out of those effects in a subsequent wet year.

4.3 ~~Plant versus biocrust signal~~Source of CO_2 efflux~~ in NSE~~

Observed NSE fluxes were almost always net positive (C loss to atmosphere), indicating that soil profile C losses are greatly outpacing biocrust photosynthetic uptake (Fig. 12). This necessitates a non-biocrust C source as biocrusts cannot persist with consistently negative C balance (e.g., Coe et al. 2012). The CO_2 efflux data also support these non-biocrust sources. For example, t~~T~~hough we did lose biocrusts, even in control plots, C losses continued even in plots where the larger biocrust constituents were gone (e.g., watered plots in 2014). Besides biocrust organisms, there are three other potential sources of CO_2 efflux: soil heterotrophs, vascular plant roots, and pedogenic carbonates (Darrouzet-Nardi et al., 2015). All three are possible~~y~~ ~~substantial~~ contributors and further work ~~would~~is ~~be~~ needed to partition their contributions.

We would expect the biocrusts themselves to have the biggest impact on NSE when soils are wet and biocrusts are active. During such time periods, we saw treatment effects that were distinct from the seven-month totals (Fig 2b), which could be interpreted as evidence of a biocrust signal that did not follow the general vascular plant trends of spring activity. Indeed, several pieces of evidence point directly to a biocrust signal. First, in the later time period (2013-2014), the reduction in minimum daily NSE during precipitation events (Fig. 5) ~~s~~suggests that loss of biocrust ~~production~~CO_2 uptake contributed to higher net C loss from these soils. In particular, the *combined* treatment lost a large proportion of its capacity to assimilate C, as well as much of the biocrust biomass. Second, the decline in the size of the “puffs” of CO_2 that were associated with the 1.2 mm watering treatments are likely driven by declines in biocrust activity (Fig. 3), as these small watering events primarily affect the surface of the soil. In our previous work (Darrouzet-Nardi et al., 2015), we saw evidence of these puffs in control plots without supplemental watering, though they were presumably not frequent enough to kill the mosses under natural conditions, a situation that could be altered if precipitation is altered in the future (Reed et al., 2012; Coe et al., 2012).

Heterotrophic respiration could also be a substantial contributor to the CO_2 effluxes we observed. The ~~SOM~~soil ~~organic~~CO_2 efflux was observed rapidly after each rain pulse (natural or experimental), which could indicate soil heterotrophic respiration since plant photosynthesis may take longer to become activated (López-Ballesteros et al., 2016). The soil organic C pool in these soils includes ~300 g C m^{-2} in the 0-2 cm biocrust layer, which would be depleted rapidly if it were the sole C source. However,~~,~~ ~~but~~ the sub-biocrust 2-10 cm layer has ~430 g m^{-2} and soils are on average 50 cm deep at the site, suggesting that the total sub-crust soil C is >1500 g C m^{-2} (~~Roybal, Whitney, and Reed, *unpublished data*~~data not shown). With a C pool of that magnitude, depletion of ~~SOM~~soil organic matter C stocks could be substantial contributors to the C losses we observed. However, if losses on the order of 62 g C m^{-2} (the amount lost in control plots during 2006)~~,~~ were to continue, these stocks would be completely depleted (which normally does not occur in soils) in ~25 years, suggesting another source is also extremely likely.~~(López-Ballesteros et al., 2016)~~

Root respiration is a contributor we consider highly likely. (Emmerich, 2003; Stevenson and Verburg, 2006; Schlesinger, 2017)~~Although we cannot partition the treatment effects we observed in NSE among vascular plants, biocrusts, or other soil sources, several aspects of the data provide compelling evidence of a strong root respiration signal. First, d~~During excavations of the chambers in 2017, root biomass was observed inside the chambers, making a root signal ~~highly~~ plausible. ~~Second, p~~Previously published measurements from a nearby site that did not have a well-developed biocrust community showed~~show~~ tightly coupled measurements of plant photosynthesis with soil respiration directly beneath plant canopies (Wertin et al., 2015) while~~.~~ correlations between soil C concentration and soil respiration were much weaker (Wertin et al., 2018). ~~Third~~Furthermore, the seasonal ~~respiration~~ NSE trends are broadly consistent with a plant photosynthetic signal, particularly the peak in fluxes during the spring growing season, which coincides with plant uptake as indicated by negative NEE seen using eddy flux towers (Darrouzet-Nardi et al., 2015; Bowling et al., 2010). ~~Fourth, t~~The interannual trends presented in this study are ~~as well~~also ~~strongly~~ consistent with a plant signal~~ (Wertin et al., 2015; Bowling et al., 2010)~~:~~.~~ f~~F~~or example, ~~our~~ the wettest year, 2014, was the year in which the highest CO_2 efflux rates were observed, a phenomenon that was likely driven by both increased activity in perennials and the flush of annual plants observed in that year. ~~Finally, the autochamber data suggest soil profile C losses are greatly outpacing biocrust photosynthetic uptake (Fig. 1), strongly suggesting a non-biocrust C source. This is more likely to be root respiration over the other possibilities such as long-term soil or biocrust C loss and pedogenic carbonates, which don't match the timing of C loss and which would have trouble accounting for the magnitude of C loss observed (see Appendix 2 in Darrouzet-Nardi et al., 2015).~~ Finally, not only is a strong plant signal likely in these NSE measurements, but the interpretation of the treatment differences, particularly the unexpected finding of a reversal in the seven-month cumulative fluxes discussed above, is clearer in light of a plant signal. We believe that by 2013, reductions in plant productivity could have resulted in reduced root respiration in the non-control plots.

Finally, pedogenic carbonates can contribute to CO_2 efflux and we cannot rule out their contribution in this study (Emmerich, 2003; Stevenson and Verburg, 2006). Some studies suggest that CO_2 efflux during dry periods is likely to be from inorganic sources (Emmerich, 2003). Others make the case that the timing of CO_2 efflux from $CaCO_3$ would be more likely to overlap with the times when plants were active and calcite could be dissolved in conjunction with a source of acidity such as acid deposition, root exudation, or nitrification (Tamir et al., 2011). Either way, long-term loss of CO_2 from dissolved calcite from our site cannot be ruled out and a~~. A~~ field investigation of the isotopic composition of released CO_2 would be particularly valuable in assessing inorganic contributions.

4.4 Conclusions

Both warming and watering with the associated moss death initially led to higher CO_2 losses in our experimental plots. After the cessation of watering, the patterns in the C balances were reversed in an average moisture year (2013), with the climate manipulation plots of all treatments showing lowered soil CO_2 loss relative to controls. These data are in line with warming experiments from a range of climates suggesting warming-induced increases in soil CO_2 are not a long-term phenomenon, at least within these experimental frameworks.~~.~~ Moreover, in a subsequent wet year (2014), CO_2 fluxes were uniformly high among treatments. When focusing just on periods of active biocrust photosynthesis, after 8 years, biocrust photosynthetic performance was much weaker in both warmed and legacy watered ~~and warmed~~ treatments relative to the control plots despite biocrust changes in control plots as well. These results suggest that the community composition changes that are highly likely in dryland plants (Collins et al., 2010; Wu et al., 2011) and biocrusts (Ferrenberg et al., 2017; Johnson et al., 2012) as a response to global change are likely to affect C balances even if effects are not consistent year to year. Our results show how community shifts, such as the loss of a major photosynthetic component like mosses, will contribute to an altered C balance of these biocrusted soils. Finally, our results underscore a strong role for biocrust, ~~as well as plant~~root, and possibly soil heterotrophic and ~~and~~ inorganic signals in NSE, suggesting that further study of the balance of plant assimilation and root/rhizosphere respiration of C, as well as patterns in biocrust C, in response to climate change will be an important determinant of future C fluxes in drylands.

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Year	Moab MAT (°C)	Moab MAP (mm)	Study site MAT (°C)	Study site MAP (mm)	Spring precipitation (mm)	Supplemental water (mm)	First watering date	Last watering date	Number of watering days
2006	22.6 (2)	208 (0)	21.4 (0)	294 (0)	22	48	May 31	Sep 20	40
2007	22.9 (8)	191 (4)	22.1 (0)	223 (0)	68	42	Jun 14	Sep 20	36
2008	21.8 (4)	138 (0)	22.6 (0)	200 (0)	62	44.4	Jun 17	Sep 23	43
2009	21.9 (1)	126 (0)	20.8 (1)	189 (0)	57	27.8	Jun 10	Sep 04	32
2010	21.4 (0)	204 (0)	20.0 (13)	286 (13)	51	48	Jun 09	Sep 29	40
2011	21.7 (0)	161 (0)	20.0 (1)	199 (0)	71	42	Jun 13	Sep 19	36
2012	23.6 (1)	92 (1)	22.1 (85)	122 (84)	9	54	Jun 04	Oct 05	45
2013	20.7 (2)	183 (2)	19.3 (36)	253 (32)	43	0	May 31	Sep 20	0
2014	22.8 (0)	208 (0)	21.5 (1)	304 (0)	73	0	Jun 14	Sep 20	0

Table 1. MAT = mean annual temperature. Values are shown for the nearby Moab site (see Fig. S2 for long-term record) as well as for the instruments at our study site. Values in parentheses indicate the number of days of missing data for the given year. ~~Annual rainfall totals (Rainfall)~~MAP = mean annual precipitation and spring ~~rainfall~~ precipitation totals were~~as~~ determined by a rain gauge at the ~~research~~ study site. Detailed timing of temperature and precipitation over the study period are shown in Fig. S1. Supplemental water was only added to the watering and combined treatments and was not added on days when natural precipitation occurred. Spring rainfall is from day of year 80-173 and is the time of peak plant growth.

Year	Comparison	*Seven-month periods* t_d (g C m^{-2})	*Active photosynthesis periods* t_d (g C m^{-2})
2006	Warmed - Control	5.1 [-9.7, 19.9]	4.1 [-0.1, 8.2]
2006	Watered - Control	14.6 [-0.2, 29.4]	5 [0.8, 9.1]
2006	Combined - Control	9.8 [-5.1, 24.6]	7.6 [3.5, 11.8]
2007	Warmed - Control	6.1 [-6.7, 18.7]	2 [0.6, 3.5]
2007	Watered - Control	10.9 [-1.8, 23.6]	1.5 [0, 2.9]
2007	Combined - Control	8.33 [-4.4, 21.0]	2.6 [1.2, 4.1]
2013	Warmed - Control	-10.7 [-27.7, 6.2]	1.3 [-0.5, 3.1]
2013	Watered - Control	-15.3 [-32.2, 1.6]	-0.1 [-1.8, 1.7]
2013	Combined - Control	-11.8 [-28.7, 5.2]	0.9 [-0.9, 2.7]
2014	Warmed - Control	-1.2 [-30.6, 28.1]	2.9 [-1.1, 7]
2014	Watered - Control	-4.0 [-33.3, 25.3]	0.4 [-3.7, 4.4]
2014	Combined - Control	-6.2 [-35.5, 23.1]	1.6 [-2.4, 5.6]

Table 2. Effect sizes of our treatments are shown as mean differences in NSE between treatments and controls with 95% ~~bootstrap~~ confidence intervals (t_d). Values were calculated as the control plot rate subtracted from the rate in the treatment plot, with positive values indicating higher NSE values in the treatment plot relative to the control and vice versa. Analyses correspond to the NSE data shown in Fig~~ 3.~~ ~~3~~4. Note that all underlying fluxes are positive (source to atmosphere), but here the *differences* between treatments are shown.

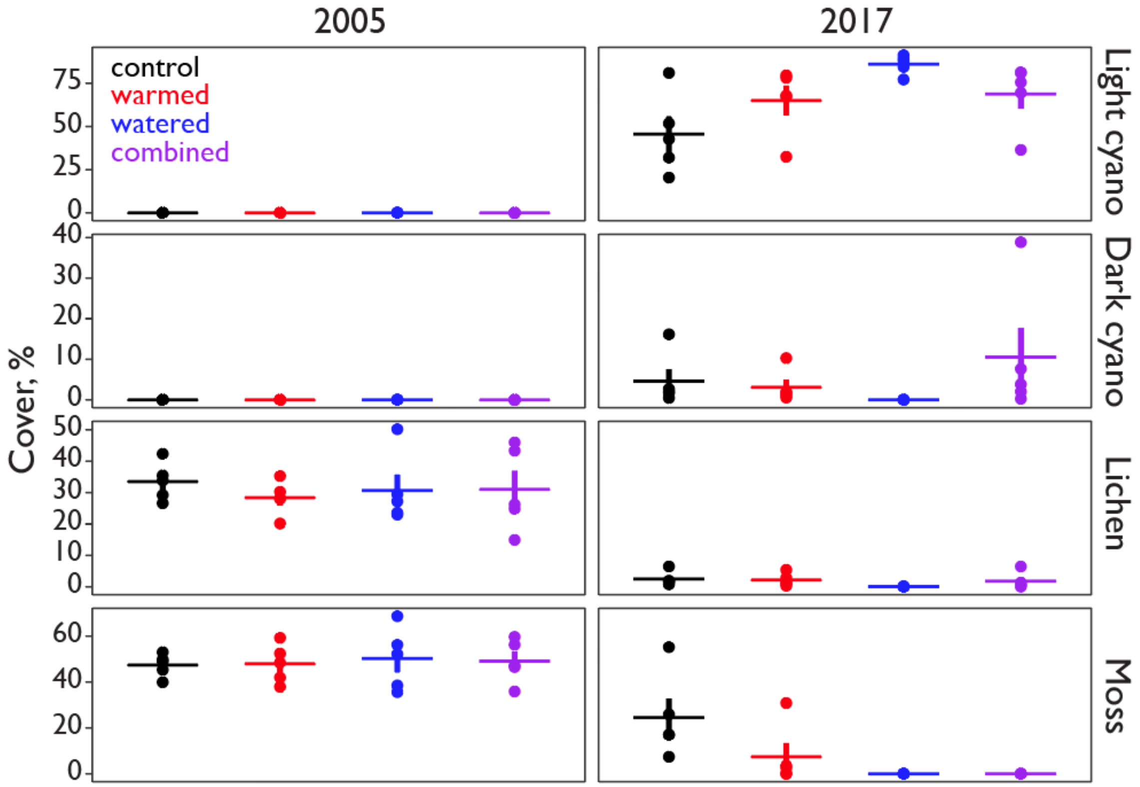


Fig. 1. Cover (%) of major biocrust constituents inside of the automated CO_2 flux chambers representative of the early and later periods of the study.

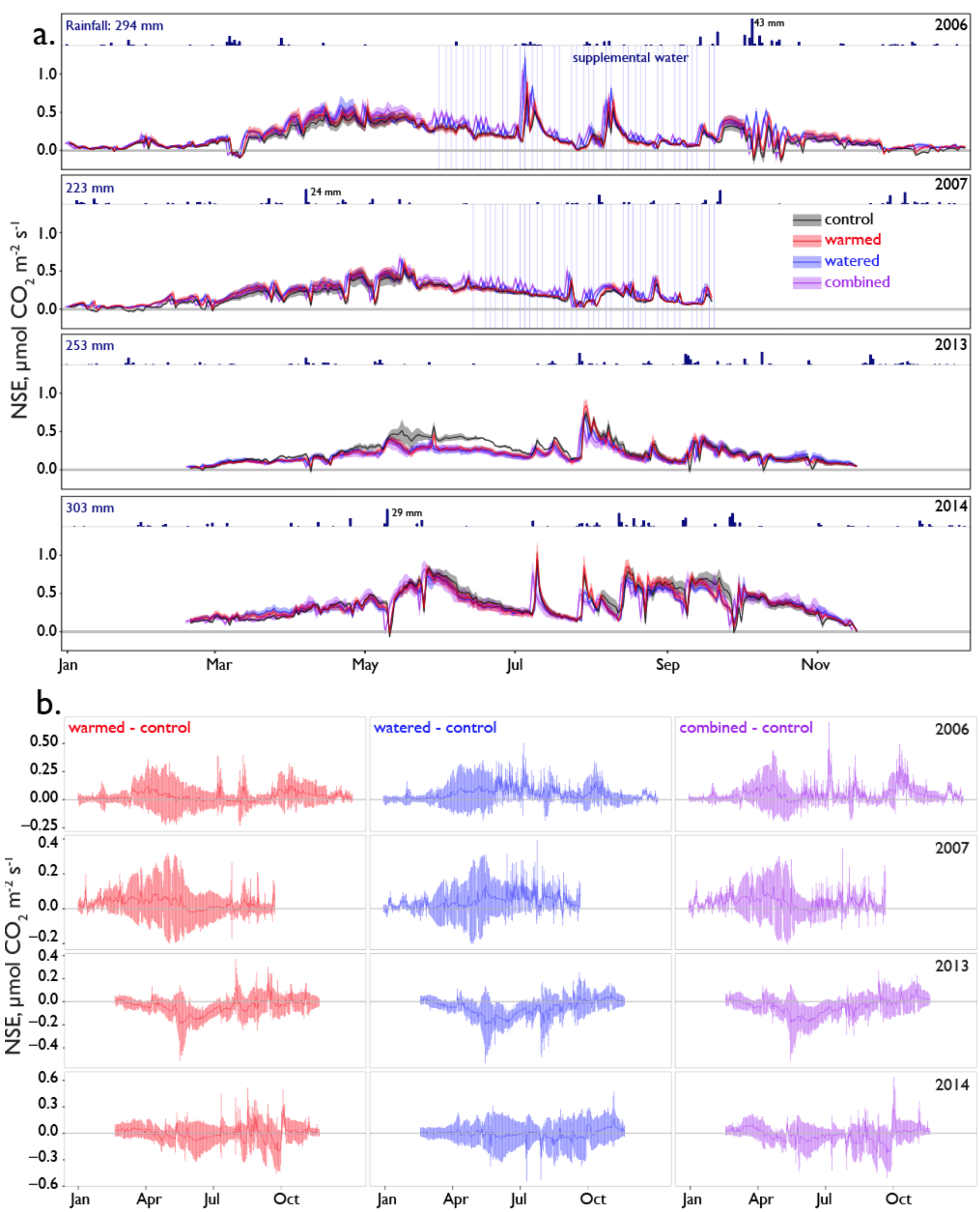


Fig. ~~1~~2. a. 24-hour average net soil exchange (NSE) of CO_2 through all treatments and years. Dates of supplemental watering applications are shown as vertical blue lines. Ribbons indicate ± 1 SE. Precipitation is shown above each year's data, with annual totals shown on the left and the size of several of the largest events noted for scale. Means for each treatment are shown with different colors representing different treatments (control = black, warmed = red, altered monsoonal precipitation [watered] = blue, warmed × watered [combined] = purple). Positive NSE rates depict respiratory losses that were greater than CO_2 uptake and negative NSE rates depict C fixation rates that outpaced respiratory losses. b. Differences between treatments and control (t_d) are shown as solid lines ± 95% CI calculated for each daily average shown with shading. Values were calculated by subtracting the control rates from the treatment (red = warmed – control; blue = altered monsoonal precipitation [watered] – control; purple = warmed × watered [combined] – control).

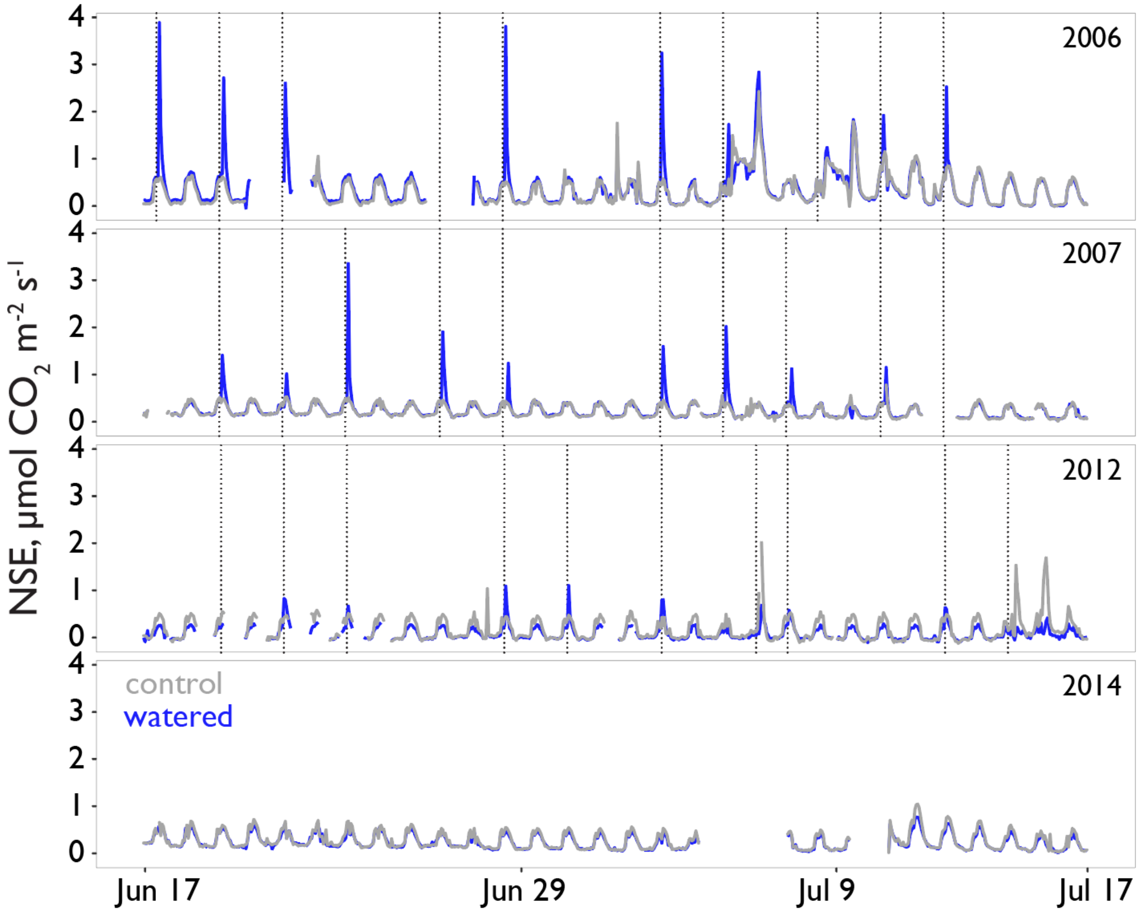
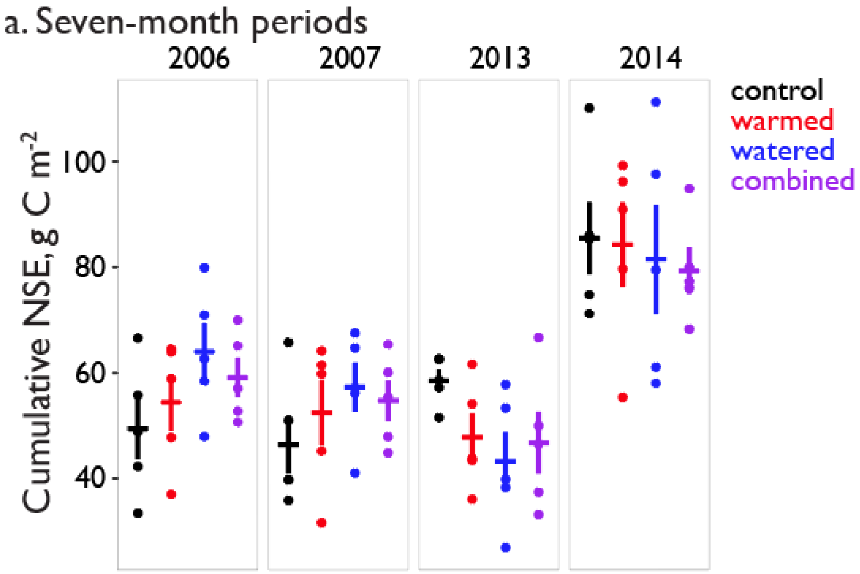


Fig. ~~2~~3. Interannual comparison of “puffs” of CO$_2$ from ~~a~~ single automated flux chambers (watering treatment, block 2 in blue and comparable control chambers in gray) observed in response to mid-summer experimental watering treatments. Time resolution is hourly. Plots were experimentally watered from 2005-2012, with no watering in the final panel (2014). Timing of the watering treatments ~~are~~ is shown by the vertical dotted lines. The puffs shown here are CO$_2$ fluxes at or above ~1 µmol CO$_2$ m^{2} s^{-1} and these occurred in response to active watering treatments.



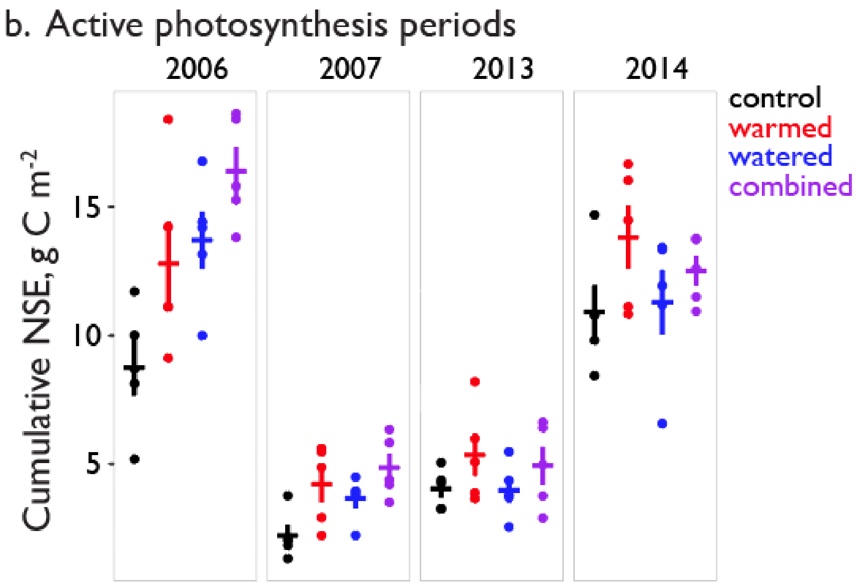


Fig. ~~3~~4. (a). Seven-month cumulative CO_2 fluxes during 4 measurement years: 2006, 2007, 2013, and 2014 for the period of February 19 - September 18, a period chosen due to availability of data in all measurement years. (b) Cumulative CO_2 flux during periods with active photosynthesis (defined as days during which NSE was < -0.2 µmol CO_2 m^{-2} s^{-1} or lower, largely corresponding with wet periods). Though selection was made on this daily minimum, numbers are positive because 24 hour totals during these periods were still largely net sources of CO_2 to the atmosphere despite active photosynthesis during peak hours. Dots indicate values from individual automated chambers and horizontal and vertical bars indicate mean ± SE. For effect sizes associated with each treatment, see Table 2.

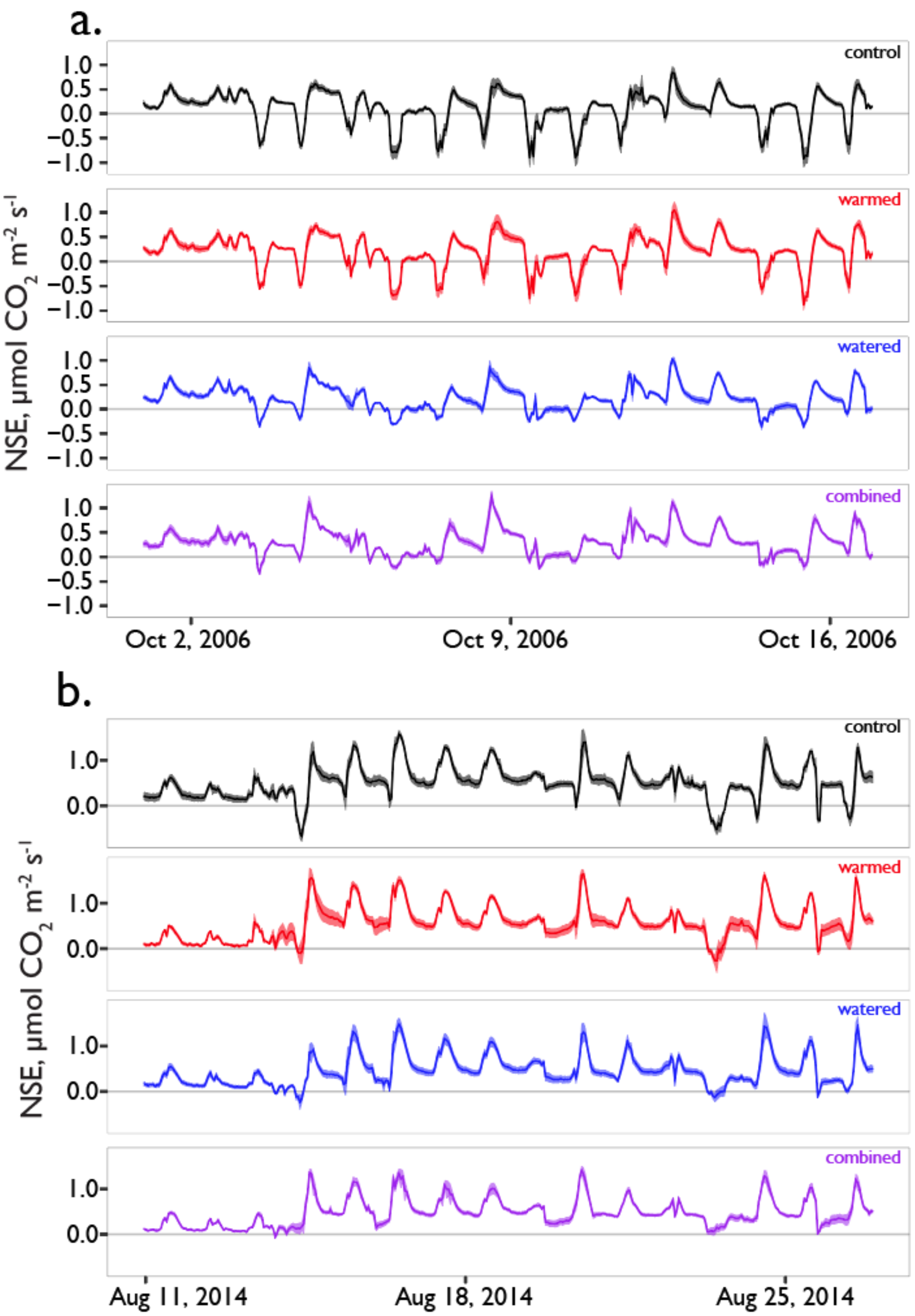


Fig. ~~4~~5. Examples of hourly CO_2 flux patterns during rain events (a) early in the experiment and (b) in the final season of measurement. Solid lines are the mean and ribbons indicate ± 1 SE. See Fig. 1a for rainfall patterns at these times.