



1 **Patterns of longer-term climate change effects on CO₂ efflux from biocrusted soils differ**
2 **from those observed in the short-term**

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10 **Abstract.** Biological soil crusts (biocrusts) are predicted to be sensitive to the increased
11 temperature and altered precipitation associated with climate change. We assessed the effects of
12 these factors on soil carbon dioxide (CO₂) balance in biocrusted soils using a sequence of
13 manipulations over a nine-year period. We warmed biocrusted soils by 2 and, later, by 4 °C to
14 better capture updated forecasts of future temperature, as well as altered monsoon-season
15 precipitation at a site on the Colorado Plateau, USA. Within treatment plots, we used 20
16 automated flux chambers to monitor net soil exchange (NSE) of CO₂ hourly, first in 2006-2007
17 and then again in 2013-2014, for a total of 39 months. Net CO₂ efflux from biocrusted soils in
18 the warming treatment increased a year after the experiment began (2006-2007). However, after
19 9 years and even greater warming (4 °C), results were more mixed, with a reversal of the
20 increase in 2013 (i.e., controls showed higher net CO₂ efflux than treatment plots) and with
21 similarly high rates in all treatments during 2014, a wet year. Over the longer-term, we saw
22 evidence of reduced photosynthetic capacity of the biocrusts in response to both the temperature
23 and altered precipitation treatments. Patterns in biocrusted soil CO₂ exchange under
24 experimentally altered climate suggest that (1) warming effects were diminished later in the
25 experiment, even in the face of larger warming and (2) likely drivers of the treatment effects
26 were changes in biocrust species composition and changes in root respiration due to vascular
27 plant responses.



28 **1 Introduction**

29 Soils with active biological soil crust (biocrust) communities are essential components of
30 dryland ecosystems worldwide and are also one of the most sensitive components of drylands to
31 climate change (Ferrenberg et al., 2017; Reed et al., 2016). Given the vast and growing global
32 extent of dryland regions (Safriel et al., 2005; Prävǎlie, 2016), the response of biocrusts to major
33 global change phenomena, such as climate change, may be an important aspect of the overall
34 response of Earth's ecosystems. In particular, due to the potential for dryland feedbacks to future
35 climate (Poulter et al., 2014; Ahlström et al., 2015; Rutherford et al., 2017), a key parameter to
36 consider as dryland ecosystems warm is their carbon (C) balance, specifically carbon exchange
37 of biocrusted soils. Dryland soils are characterized by low soil organic matter that is negatively
38 correlated with aridity across many drylands (Delgado-Baquerizo et al., 2013) and there is an
39 association between C loss and the phenomenon of desertification (Lal, 2004). Drylands can also
40 show large year-to-year variation in C fluxes that are relevant for explaining global fluxes
41 (Ahlström et al., 2015; Poulter et al., 2014; Biederman et al., 2017). Thus, improving our
42 understanding of dryland C cycle responses to change matters at the global scale. At the
43 organism scale, the viability of biocrusts is linked directly to their ability to maintain a positive C
44 balance among hydration-desiccation cycles (Grote et al., 2010; Coe et al., 2012; Oliver et al.,
45 2005). Though C cycling is central to understanding biocrust function and although soils in
46 drylands with biocrusts are often large contributors to overall ecosystem respiration (Castillo-
47 Monroy et al., 2011) that contribute substantially to C uptake (Elbert et al., 2012), biocrust
48 contributions to ecosystem CO₂ exchange remain incompletely understood.

49 Carbon balance in biocrusted soils includes not only the activities of the biocrusts
50 themselves, but also the activities of subsurface vascular plant roots and soil microbes.
51 Considering biocrusted soils together with the function of adjacent vascular plants is important
52 given that there is increasing evidence for strong biotic connections, possibly mediated by fungi,
53 between these functional groups (Green et al., 2008) and for linkages in plant-soil C cycle
54 responses to warming. For example, at a site on the Colorado Plateau near the site for this study,
55 measurements of plant photosynthesis, coupled with spot measurements of soil respiration under
56 plant canopies, showed plant photosynthesis was tightly coupled to soil respiration, with both
57 showing reduced fluxes in response to warming during the spring when plants are most active
58 (Wertin et al., 2017). While these patterns could be the result of independent climate controls on



59 each individual flux, vascular plant C allocation to roots and heterotrophs belowground, and/or
60 biotic connections between biocrust organisms and vascular plants, they highlight the potential
61 for strong coupling between above- and belowground CO₂ fluxes, regardless of the mechanisms.

62 In addition to affecting soil C balance through direct physiological means, warming has been
63 shown to have substantial effects on biocrust species composition, including macroscopic
64 components such as moss and lichens (Ferrenberg et al., 2015; Escolar et al., 2012; Maestre et
65 al., 2015) and microbial community composition (Steven et al., 2015; Johnson et al., 2012).
66 Climate models predict rapidly rising temperatures for already hot and moisture-limited dryland
67 regions, including the site of our study in the southwestern United States (Stocker, 2014; Jardine
68 et al., 2013). Forecasts of future precipitation patterns are less certain, but overall drier
69 conditions with changes in precipitation event size and frequency are likely (Seager et al., 2007).
70 Across many ecosystems, including drylands, both plant C uptake and soil respiration are often
71 positively correlated with increased temperatures and moisture (Wu et al., 2011), although
72 temperature can also have a negative relationship with photosynthesis (e.g., Wertin et al., 2015)
73 and with soil respiration when increased temperatures relates to rapid drying (Tucker and Reed,
74 2016). Drought also tends to reduce vascular plant production and respiration, with greater
75 sensitivity in drier areas (Knapp et al., 2015). In soils overlain by biocrusts (hereafter, biocrusted
76 soils) specifically, temperature and moisture are key physiological parameters for C flux (Grote
77 et al., 2010; Darrouzet-Nardi et al., 2015) and, although few, the warming experiments that do
78 exist suggest that biocrusted soils will have higher net CO₂ efflux with a warming climate
79 (Darrouzet-Nardi et al., 2015; Maestre et al., 2013). There is evidence for a limit to this
80 association though, with very high temperatures leading to reduced biotic activity, including
81 microbial respiration, in biocrusted soils (Tucker and Reed, 2016).

82 To improve our understanding of dryland C flux responses to global change, we used a
83 warming by watering manipulation experiment on the Colorado Plateau established in 2005.
84 When the study began, we explored the hypothesis that warming would increase net losses of
85 CO₂ from biocrusted soils via detrimental impacts on biocrust physiology caused by warming. At
86 the same time we wanted to explore how altered precipitation could directly affect biocrust soil
87 CO₂ exchange and/or interact with the effects of increased temperatures. These early results
88 supported the basic hypothesis concerning the warming-only treatment, showing that warming
89 led to increased CO₂ loss after 1-2 years, with the largest differences during periods in which



90 soils were wet enough to support substantial biocrust photosynthesis (Darrouzet-Nardi et al.,
91 2015). We also found that the increased frequency of small frequent precipitation events
92 negatively affected biocrusts: the treatment caused the death of a major biocrust component, the
93 moss *Syntrichia caninervis* (Coe et al., 2012; Reed et al., 2012; Zelikova et al., 2012). The new
94 work described here aims to: (1) determine if the increased net soil CO₂ loss observed after a
95 year of warming years was maintained after 8 years, and (2) to assess how the altered
96 precipitation patterns affected net soil CO₂ exchange at both the early and the later time points.

97

98 **2 Materials and Methods**

99

100 **2.1 Site Description**

101 The study was located in a semiarid system on the Colorado Plateau (36.675 N, -109.416 W;
102 elevation = 1310 m; mean annual temperature = 13 °C, mean annual precipitation = 269 mm;
103 WRCC 2014) that supports multiple grasses and shrubs. Soils are Rizno series Aridisols and the
104 dominant plants include *Achnatherum hymenoides*, *Pleuraphis jamesii*, *Atriplex confertifolia*,
105 and *Bromus tectorum*. Biocrust communities are dominated by the cyanobacterium *Microcoleus*
106 *vaginatus*, the moss *Syntrichia caninervis*, and the cyanolichens *Collema tenax* and *Collema*
107 *coccophorum*. The site is on a moderate hillslope (~10%) surrounded by steep gullies that make
108 it hard to access for livestock, which may explain its relict biocrust and plant composition that
109 includes late successional crusts with well-developed communities of native grasses and shrubs,
110 similar to sites found in Canyonlands National Park (Belnap and Phillips, 2001). For a more
111 detailed description of the site including co-located experiments, see Wertin et al. (2015).

112 Rainfall during the study period was distributed around the mean (Table 1), with several slightly
113 above average years including the first and last year of the experiment (2006: 294 mm; 2014:
114 304 mm), and one year with substantial drought (2012: 122 mm).

115

116 **2.2 Warming and watering treatments**

117 The experiment contained five blocks of four treatments each: control, warmed, watered, and
118 combined (warmed + watered) for a total of 20 2 × 2.5 m plots, each of which contained an
119 automated CO₂ chamber (described below). The warming treatment began in October 2005 in
120 plots fitted with 800 W infrared radiant (IR) heat lamps (Kalglo Model MRM-2408) mounted at



121 a height of 1.3 m. Control plots had dummy lamps that do not provide heat. The heating
122 treatment was regulated by altering the voltage supplied to each lamp. While some drying of soil
123 moisture from the lamps may have occurred, we saw little evidence for this phenomenon in soil
124 moisture values, with drying after precipitation events occurring at similar rates in all treatments
125 (Figure S1; see also Wertin et al., 2015). The target temperature increase was ambient soil
126 temperature +2 °C from 2005-2008, at which point a second lamp was added to each plot and the
127 warming treatment was increased to +4 °C where it remained through the end of the automated
128 chamber sampling in September of 2014. The treatment temperatures were increased from 2 to 4
129 °C above ambient in order to better match changing predictions of future temperature by 2100.
130 Water was added in 1.2 mm events manually with backpack sprayers and was applied 40 times
131 from May 31-Sep 20, 2006 and 36 times from June 14-Sep 20 in 2007, with an average time
132 between watering of 2.8 days (Table 1). The amount of water varied by year because watering
133 did not occur on days when natural rainfall occurred. Watering was stopped in 2012 because the
134 late successional biocrust community had been eliminated after the first year and was showing
135 no further change through time (Reed et al., 2012; Ferrenberg et al., 2015). There were
136 intermittent automated chamber measurements in 2012, the last year of watering, crossed with
137 the higher warming level, providing enough data for analyses of daily patterns, though not
138 enough to assess seasonal total rates.

139

140 **2.3 Net soil exchange measurements with automated chambers**

141 Carbon dioxide fluxes were assessed with automated CO₂ flux chambers, described in detail
142 in Darrouzet-Nardi et al. (2015). The chambers are closed systems in which clear lids, allowing
143 sunlight and hence photosynthesis by biocrust organisms, are closed once per hour for 3 minutes.
144 Fluxes of CO₂ during that time are calculated as the rate of change in CO₂ concentrations during
145 the 3 minute period. The chambers were 30 cm tall × 38 cm inner diameter, covering a soil
146 surface area of 0.11 m². Chambers were installed to a depth of 27 cm in the soil, leaving ~3 cm
147 of the chamber protruding above the soil surface. The chambers were placed in plot locations
148 containing biocrusts but no vascular plants. Values from these chambers were reported as net soil
149 exchange (NSE) of CO₂. The concept of NSE is defined in Darrouzet-Nardi et al. (2015) to
150 include biocrust photosynthesis as the sole form of CO₂ uptake (i.e., because the chambers do not
151 include vascular plants) along with CO₂ losses via respiration from biocrusts, other soil



152 microbes, and plant roots. While it would have been ideal to operate the chambers year round for
153 the entire course of the experiment, it was beyond the operational capacity of the project to do so
154 and there are times when the systems were not operational. The chambers have more frequent
155 malfunctions during the winter due to weather conditions, so those months are least represented.
156

157 **2.4 Imputation and statistical analysis**

158 Hourly data from the automated chambers were collected from January 1, 2006 - September
159 20, 2007, February 19 - November 17, 2013, and February 14 - November 17, 2014, for a total of
160 28,058 time points for each of the 20 chambers. Of these time points, 29% of the data were
161 missing, primarily due to technical issues with the chambers. To allow calculations of
162 cumulative NSE, data were imputed following the same procedure as in our previous work
163 (Darrouzet-Nardi et al., 2015). Data were assembled into a data frame containing columns for (i)
164 each of the 20 chambers; (ii) environmental data including soil and air temperature, soil
165 moisture, 24-hour rainfall totals, photosynthetically active radiation (PAR); and (iii) six days of
166 time-shifted fluxes (before and after each measurement; i.e., -72 h, -48 h, -24 h, +24 h, +48 h,
167 +72h) for one chamber from each treatment, soil temperature, and soil moisture. Lagged values
168 were added due to their ability to greatly improve prediction of missing time points, particularly
169 for short time intervals such as those caused by, for example, several hours of power outage at
170 the site. One data frame was created for each of the three continuous recording periods: 2006-
171 2007, 2013, and 2014 and each was imputed separately. Imputation was performed using the
172 missForest algorithm, which iteratively fills missing data in all columns of a data frame using
173 predictions based on random forest models (Stekhoven and Buhlmann, 2012; Breiman, 2001).

174 The effect of the early warming, watering, and combined treatments on NSE were evaluated
175 by evaluating the effect size of these treatments on each variable of interest (Nakagawa and
176 Cuthill, 2007; Cumming, 2013). Treatment differences, which we notate as t_d , were assessed as
177 treatment - control with 95% confidence intervals estimated by bootstrapping, with $n = 5$ in all
178 cases (Carpenter and Bithell, 2000). Analyses were facilitated by a custom-made R package
179 `treateffect`, available at <https://github.com/anthonydn/treateffect>. The data used for these analyses
180 are available at https://github.com/anthonydn/warmed_biocrusts_nine_years. Using the imputed
181 data, treatment differences were assessed both on individual hourly measurements and on
182 cumulative NSE through time. The cumulative measurements were done on a seven-month



183 period, February 19 - September 19, which was selected due to availability of data in all four
184 analysis years. We also distinguished time periods in which we observed active photosynthesis,
185 defining these periods as days during which the NSE values were $-0.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ or lower,
186 with more negative numbers showing higher net photosynthesis. These periods were selected as
187 subsets of the seven-month periods, varying in duration by the number of days with active
188 photosynthesis, which typically corresponds to times with sufficient precipitation to activate
189 biocrusts.

190

191 **3 Results**

192 Seasonal time courses of NSE showed similar patterns among years and treatments, with
193 peaks in NSE in the spring associated with peak vascular plant activity, and peaks in both
194 photosynthesis and respiration associated with rain events (Fig. 1a). In the early time period (1-2
195 years after treatments began), the supplemental 1.2 mm watering treatment caused large “puffs”
196 of CO_2 when water was added. By the final year of watering (2012), the size of these puffs was
197 substantially smaller and after watering ceased (2014), they did not occur even with natural
198 rainfall events (Fig. 2).

199 Interannual comparisons of cumulative Feb. 19 - Sep. 19 (seven-month) C fluxes were
200 consistent with the hypothesized effects in the early time period (2006-2007), but showed
201 varying results in the later time period (2013-2014). In the early time period, shortly after the
202 establishment of the treatments, we observed higher NSE (greater movement of CO_2 from soil to
203 the atmosphere) in both watered and combined treatment plots, with less evidence of difference
204 in the warming only treatment (Fig. 3a; Table 2). In 2013, after the watering treatment had
205 ceased, we observed the opposite trend, with lower CO_2 efflux from soils in all three treatments
206 (Fig 3a; Table 2). This trend was particularly visible in the months of May and June (Fig. 1a,b).
207 However, in the following year, 2014, a wet year with high spring rainfall (Table 1, Fig. 1a), all
208 plots showed the highest CO_2 efflux observed in the experiment. While no obvious treatment
209 effects were observed, treatment effect sizes were relatively poorly constrained due to the higher
210 variation that year (Table 2).

211 Interannual comparisons of cumulative CO_2 fluxes during periods of active photosynthesis
212 showed higher photosynthesis in all treatments during the early measurement period (e.g., 2006
213 warmed $t_d = 4.05$ [0.91, 7.48]; Fig. 3b; Table 2). In the later period (8-9 years after treatments



214 began), subsequent to the cessation of watering, warmed plots still showed elevated CO₂ losses
215 during periods of active photosynthesis but this difference was smaller than in the earlier
216 measurements (e.g., 2013 warmed $t_d = 1.32 [-0.13, 3.03]$; Fig. 3b; Table 2). In contrast, watered
217 plots that were not warmed were similar to control plots.

218 In examining the daily cycles in the hourly data, further detail on the nature of the treatment
219 effects was observed. After one year, watered treatments in which mosses had died showed
220 strong reductions in CO₂ uptake capacity during wet-up events, but warmed treatments still
221 showed a similar maximum uptake capacity relative to controls (e.g., minimum NSE on October
222 15, 2006 control = $-0.93 \pm 0.19 \mu\text{mol m}^2 \text{s}^{-1}$; warmed = -0.89 ± 0.11 , watered = -0.35 ± 0.06 ,
223 combined = -0.2 ± 0.08 ; Fig. 4a). However, after 8 years of treatment, clear differences were
224 present in the CO₂ flux dynamics in response to natural rainfall events (Fig. 4b). Biocrusted soils
225 in control plots still exhibited substantial net uptake of CO₂ (e.g., minimum NSE on August 14,
226 control = $-0.68 \pm 0.12 \mu\text{mol m}^2 \text{s}^{-1}$), whereas the other treatments showed less uptake relative to
227 the control, with a similar trend visible on August 23rd.

228

229 **4 Discussion**

230

231 **4.1 Early period: 2 °C warming × watering (2006-2007)**

232 The increase in CO₂ effluxes in the watered treatments during the early period were likely
233 driven by both the loss of photosynthetic mosses during that time (Reed et al., 2012), as well as
234 increased soil respiration from soil heterotrophs. Moss death may have contributed to net soil C
235 loss via (i) eliminating CO₂ uptake from this important biocrust CO₂-fixer (Reed et al., 2012;
236 Coe et al., 2012); and (ii) decomposition of dead mosses. Elevated soil respiration with warming
237 and watering is broadly consistent with the results of similar experiments across many
238 ecosystems (Wu et al., 2011; Rustad et al., 2001), dryland sites specifically (Nielsen and Ball,
239 2015; Patrick et al., 2007; Thomey et al., 2011), and previously documented effects in biocrusted
240 soils at this site and others (Darrouzet-Nardi et al., 2015; Maestre et al., 2013; Escolar et al.,
241 2015). In the warmed treatment, elevated NSE was not as evident in 2006 as in the watered and
242 combined treatments, and this is consistent with the biocrust community changes. While moss
243 died off quickly in the watered plots, the negative effects of temperature took longer to emerge
244 (Ferrenberg et al. 2017). Indeed, increased CO₂ efflux with warming was clearer in the following



245 year (2007) and moss cover was substantially reduced by 2010 (Ferrenberg et al., 2015). Such
246 rapid species composition changes have been repeatedly implicated as drivers of system change
247 in drylands, even with seemingly subtle changes in climate (Wu et al., 2012; Collins et al., 2010).
248

249 **4.2 Late period: 9 years warming (2-4 °C) × legacy watering (2013-2014)**

250 During the later period (2013) when warming had been increased to +4 °C (in 2009) and
251 watering had ceased (effectively making the treatments: control, +4 °C, legacy watering, and +4
252 °C × legacy watering), several differences in treatment effects emerged in comparison to the
253 early measurement period (2006-2007). First, the trend in the 2013 seven-month cumulative CO₂
254 fluxes were reversed from those of the early measurement period (2006-2007), with the control
255 plots having the highest NSE and all other treatments showing lower CO₂ efflux. The reversal of
256 the NSE trend in the +4 °C and +4 °C × legacy watering treatments is likely due in large part to
257 changes in biocrust community composition. The climate treatment-induced transition from late-
258 to early-successional biocrusts (Ferrenberg et al., 2015) greatly reduces the potential for
259 biocrusts to uptake atmospheric CO₂ (e.g., Housman et al., 2006). Further, vascular plant
260 photosynthesis in multiple species was reduced with warming, which would be expected to
261 reduce plant allocation of C belowground. A number of warming experiments in more mesic
262 systems that do not have photosynthetic soils have shown an initial increase in soil CO₂
263 respiratory loss followed by subsequent declines in warmed plots; in these situations, reduced
264 soil C availability for heterotrophic respiration and changes to heterotroph C use efficiency are
265 often suggested to play a role (Bradford et al., 2008; Bradford, 2013; Tucker et al., 2013). Such
266 effects would also be consistent with drying from the infrared heat lamps, a mechanism that was
267 supported in a Wyoming grassland experiment (Pendall et al., 2013). Our soil moisture data
268 showed little evidence of such drying effects (Supplemental Fig. 1). However, with a minimum
269 moisture probe depth of 2 cm, we may have missed moisture effects relevant only to the top
270 several millimeters of soil, an area of current active investigation at the site (Tucker et al., 2017).
271 The reduction in CO₂ efflux with warming was also seen in a nearby set of plots in 2011, in
272 which soil respiration was measured at individual time points with non-automated chambers
273 (Wertin et al., 2017). In that study, the reduction with warming was observed three years after +2
274 °C warming treatment was implemented. The dark respiration measurements were made in the



275 spring (at peak plant activity) and it was at the same point in the season that we saw the strongest
276 seasonal driver for the seven-month cumulative data.

277 We also observed reduced NSE values during the late period in the previously watered plots
278 in comparison to the control plots, suggesting some legacy treatment effects. This was likely
279 linked to loss of mosses, cyanobacteria, or changes in vascular plant physiology. For example,
280 biocrusted soil microsites in Spain were shown to be a dominant source of midday soil
281 respiration (Castillo-Monroy et al., 2011), and reductions in the autotrophic biomass seen with
282 the climate treatments (Ferrenberg et al., 2017; Reed et al., 2016) could reduce respiration rates.
283 Plants accustomed to the extra water may also have responded negatively to its absence, causing
284 reduced physiological activity and hence lower root respiration, an effect that has been
285 documented in drought simulation experiments (Talmon et al., 2011). Soil heterotrophs can also
286 show legacy effects of their species composition in response to changes in precipitation regime
287 (Kaisermann et al., 2017). Water retention may also have been reduced due to decline in biocrust
288 cover, an effect for which there is some evidence, particularly in semiarid ecosystems like our
289 study site (Belnap, 2006; Chamizo et al., 2012). Mosses have unique adaptations allowing them
290 to absorb high fractions of precipitation without loss to splash and evaporation (Pan et al., 2016),
291 a process that would be lessened in the climate manipulation plots due to moss death. In addition
292 to effects on soil moisture, changes in biocrust community composition can have significant
293 effects on soil nutrient availability (Reed et al., 2012) and nutrient availability can be tightly
294 coupled with soil respiration rates (Reed et al., 2011). Although the NSE data do not allow us to
295 disentangle which gross C fluxes caused the opposing treatment effects between the early (2006-
296 2007) and late (2012-2013) measurement periods, it is important to see such a reversal as a
297 sustained increase in larger CO₂ loss would have the potential for large feedbacks to increasing
298 atmospheric CO₂ concentrations.

299 Interestingly, the CO₂ loss reversal observed in 2013 did not continue in 2014, likely due to
300 the higher rainfall, particularly during spring. In 2014, we saw high NSE in all plots in the seven-
301 month cumulative data, with no significant differences among treatments. Accompanying the
302 higher precipitation in 2014 – which occurred in a series of large rain events in April and May –
303 perennial plants were noticeably greener and there was a large flush of annual plants. During wet
304 conditions, warmed plots showed higher NSE values, which could have been due to higher root
305 respiration or higher subsoil microbial activity, potentially linked to root turnover or



306 rhizodeposition (Jones et al., 2004). These results from the later period of the experiment (2013-
307 2014) underscore that taking a long-term perspective (i.e., nearly a decade of warming) may be
308 necessary for understanding climate change effects, particularly those that maintain interactions
309 with species composition changes. Further, these data suggest more complexity in soil CO₂
310 efflux controls, such that some systems may not manifest a simple transition from temperature-
311 induced increases in soil CO₂ loss to temperature-induced decreases at later stages of warming.
312 The interannual variations in the magnitude of NSE fit with results from other drylands that
313 show high interannual variation in net ecosystem exchange (NEE) as measured with eddy flux
314 towers (Biederman et al., 2017). At least one other longer-term manipulation in a dryland has
315 also observed early stimulation of plant growth with warming that then lessened over time, with
316 longer-term effects driven by changes in species composition (Wu et al., 2012). The finding that
317 decadal scale studies can have mixed and context-dependent effects not visible at the annual
318 scale (Nielsen and Ball, 2015) is exemplified in our study by the reversal in effects seen in 2013,
319 followed by the swamping out of those effects in a subsequent wet year.

320

321 **4.3 Plant versus biocrust signal in NSE**

322 Although we cannot partition the treatment effects we observed in NSE among vascular
323 plants, biocrusts, or other soil sources, several aspects of the data provide compelling evidence of
324 a strong root respiration signal. First, during excavations of the chambers in 2017, root biomass
325 was observed inside the chambers, making a root signal highly plausible. Second, previously
326 published measurements from a nearby site that did not have a well-developed biocrust
327 community show tightly coupled measurements of plant photosynthesis with soil respiration
328 directly beneath plant canopies (Wertin et al., 2015). Third, the seasonal respiration trends are
329 broadly consistent with a plant photosynthetic signal, particularly the peak in fluxes during the
330 spring growing season (Darrouzet-Nardi et al., 2015). Fourth, the interannual trends presented in
331 this study are strongly consistent with a plant signal (Wertin et al., 2015; Bowling et al., 2010).
332 For example our wettest year, 2014, was the year in which the highest CO₂ efflux rates were
333 observed, a phenomenon that was likely driven by both increased activity in perennials and the
334 flush of annual plants observed in that year. Finally, the autochamber data suggest soil profile C
335 losses are greatly outpacing biocrust photosynthetic uptake (Fig. 1), strongly suggesting a non-
336 biocrust C source. This is more likely to be root respiration over the other possibilities such as



337 long-term soil or biocrust C loss and pedogenic carbonates, which don't match the timing of C
338 loss and which would have trouble accounting for the magnitude of C loss observed (see
339 Appendix 2 in Darrouzet-Nardi et al., 2015). Finally, not only is a strong plant signal likely in
340 these NSE measurements, but the interpretation of the treatment differences, particularly the
341 unexpected finding of a reversal in the seven-month cumulative fluxes discussed above, is
342 clearer in light of a plant signal.

343 We would expect biocrusts to have the biggest impact on NSE when soils are wet and
344 biocrusts are active. During such time periods, we saw treatment effects that were distinct from
345 the seven-month totals, which could be interpreted as evidence of a biocrust signal that did not
346 follow the general vascular plant trends of spring activity. Indeed, several pieces of evidence
347 point directly to a biocrust signal. First, in the later time period (2013-2014), the reduction in
348 minimum daily NSE during precipitation events suggest that loss of biocrust production
349 contributed to higher net C loss from these soils. In particular, the combined warming and
350 watering treatment lost a large proportion of its capacity to assimilate C, as well as much of the
351 biocrust biomass. Second, the decline in the size of the "puffs" of CO₂ that were associated with
352 the 1.2 mm watering treatments are likely driven by declines in biocrust activity (Fig. 2), as these
353 small watering events primarily affect the surface of the soil. In our previous work (Darrouzet-
354 Nardi et al., 2015), we saw evidence of these puffs in control plots without supplemental
355 watering, though they were presumably not frequent enough to kill the mosses under natural
356 conditions, a situation that could be altered if precipitation is altered in the future (Reed et al.,
357 2012; Coe et al., 2012). Clearly, both root respiration and biocrusts are contributing to the NSE
358 signal, and although we cannot disentangle these gross fluxes, they must be both considered in
359 understanding the total soil contribution to C fluxes in the face of the warming and watering
360 treatments. Future work disentangling the gross fluxes would complement the long-term patterns
361 described here.

362

363 4.4 Conclusions

364 Both warming and watering with the associated moss death initially led to higher CO₂ losses
365 in our experimental plots. After the cessation of watering, the patterns in the C balances were
366 reversed in an average moisture year (2013), with the climate manipulation plots of all
367 treatments showing lowered soil CO₂ loss relative to controls. These data are in line with



368 warming experiments from a range of climates suggesting warming-induced increases in soil
369 CO₂ are not a long-term phenomenon. Moreover, in a subsequent wet year (2014), CO₂ fluxes
370 were uniformly high among treatments. When focusing just on periods of active biocrust
371 photosynthesis, after 8 years biocrust photosynthetic performance was much weaker in both
372 legacy watered and warmed treatments relative to the control plots. These results suggest that the
373 community composition changes that are highly likely in dryland plants (Collins et al., 2010; Wu
374 et al., 2011) and biocrusts (Ferrenberg et al., 2017; Johnson et al., 2012) as a response to global
375 change are likely to affect C balances even if effects are not consistent year to year. Our results
376 show how community shifts, such as the loss of a major photosynthetic component like mosses,
377 will contribute to an altered C balance of these biocrusted soils. Finally, our results underscore a
378 strong role for biocrust as well as plant signals in NSE, suggesting that further study of the
379 balance of plant assimilation and root/rhizosphere respiration of C, as well as patterns in biocrust
380 C, in response to climate change will be an important determinant of future C fluxes in drylands.
381

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383 work. All authors performed the experiment, with E.E.G. leading design and construction of the
384 automated chambers and data management. A.D.N analyzed the data and led manuscript writing,
385 and all authors contributed to the writing.

386

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394

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396

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595

Year	Rainfall (mm)	Spring rainfall (mm)	Supplemental water (mm)
2006	294	22	48
2007	223	68	42
2008	200	62	44.4
2009	189	57	27.8
2010	286	51	48
2011	199	71	42
2012	122	9	54
2013	253	43	0
2014	304	73	0

596

597 Table 1. Annual rainfall totals (Rainfall) and spring rainfall totals as determined by a rain gauge
598 at the research site. Supplemental water was only added to the watering and combined treatments
599 and was not added on days when natural precipitation occurred. Spring rainfall is from day of
600 year 80-173 and is the time of peak plant growth.
601

*Seven-month periods*

Year	Comparison	t_d ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
2006	Warmed - Control	5.1 [-9, 17.7]
2006	Watered - Control	14.6 [1.2, 28.6]
2006	Combined - Control	9.8 [-2.2, 21.6]
2007	Warmed - Control	6 [-9.4, 19.3]
2007	Watered - Control	10.9 [-2.4, 23]
2007	Combined - Control	8.3 [-2.7, 19.6]
2013	Warmed - Control	-10.7 [-19.3, -2]
2013	Watered - Control	-15.3 [-25.5, -4.8]
2013	Combined - Control	-11.8 [-21.7, 0.4]
2014	Warmed - Control	-1.2 [-20.3, 15.1]
2014	Watered - Control	-4 [-25.6, 17.2]
2014	Combined - Control	-6.2 [-21.6, 7.3]

Active photosynthesis periods

Year	Comparison	t_d ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
2006	Warmed - Control	4.1 [1, 7.7]
2006	Watered - Control	5 [2.2, 7.7]
2006	Combined - Control	7.6 [5.3, 10.2]
2007	Warmed - Control	2 [0.6, 3.4]
2007	Watered - Control	1.5 [0.3, 2.3]
2007	Combined - Control	2.6 [1.5, 3.8]
2013	Warmed - Control	1.3 [-0.2, 2.9]
2013	Watered - Control	-0.1 [-1.1, 1]
2013	Combined - Control	0.9 [-0.6, 2.3]
2014	Warmed - Control	2.9 [0, 5.5]
2014	Watered - Control	0.4 [-2.8, 2.9]
2014	Combined - Control	1.6 [-0.5, 3.5]

602

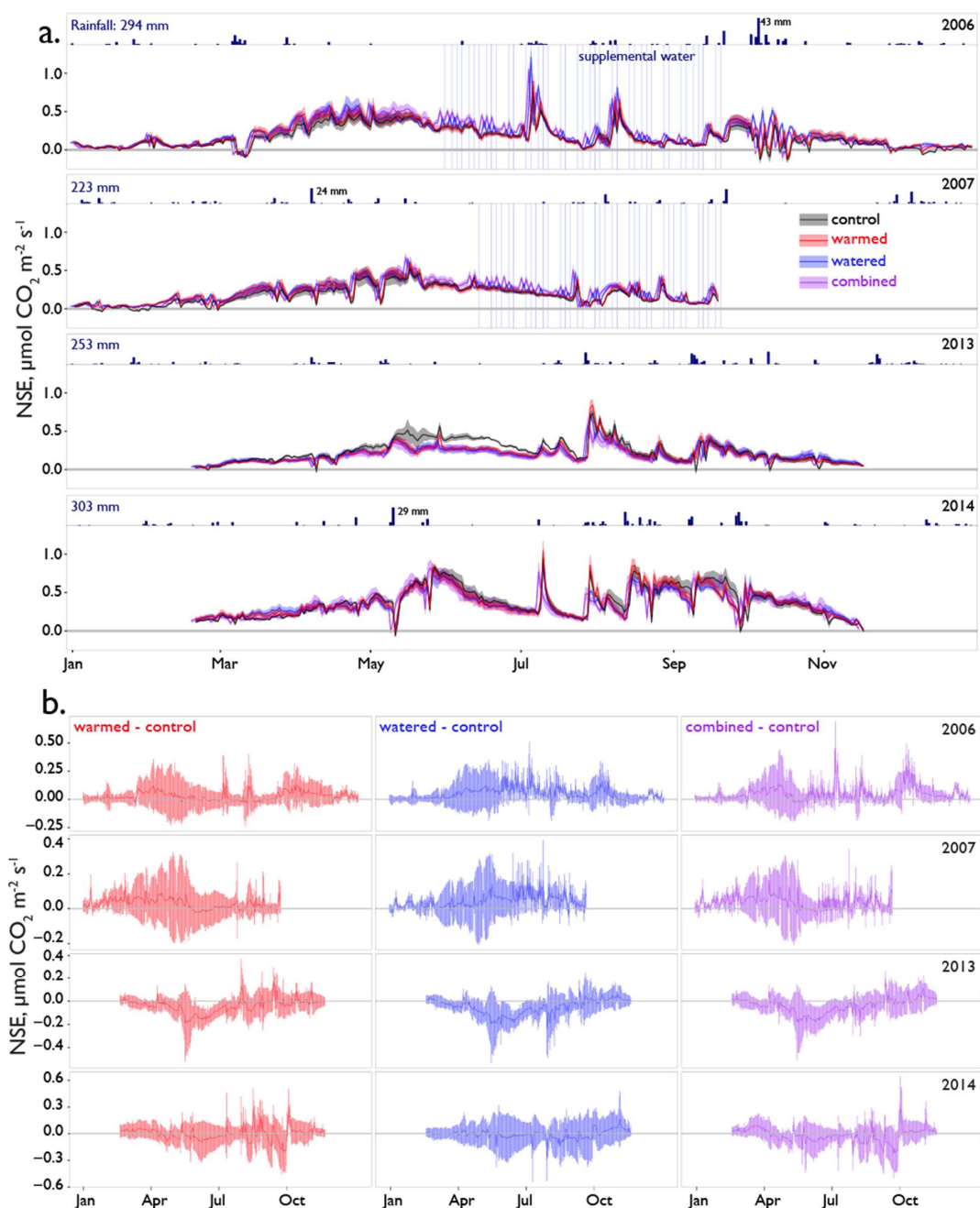
603 Table 2. Effect sizes of our treatments are shown as mean differences in NSE between treatments

604 and controls with 95% bootstrap confidence intervals (t_d). Values were calculated as the control

605 plot rate subtracted from the rate in the treatment plot. Analyses correspond to the data shown in

606 Fig 3.

607



608

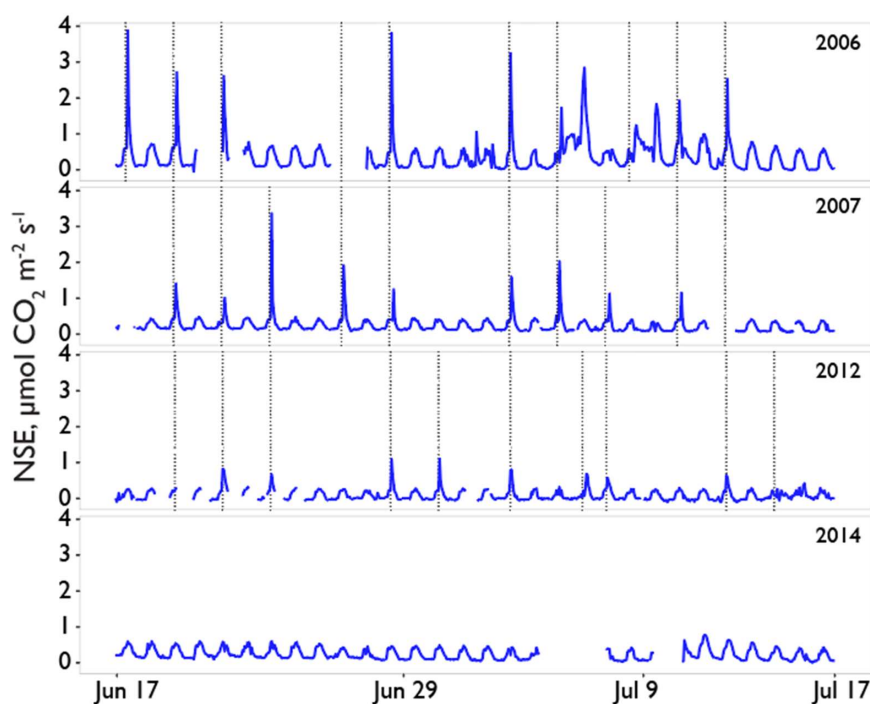
609 Fig. 1. a. 24-hour average net soil exchange (NSE) of CO₂ through all treatments and years.

610 Dates of supplemental watering applications are shown as vertical blue lines. Ribbons indicate ±

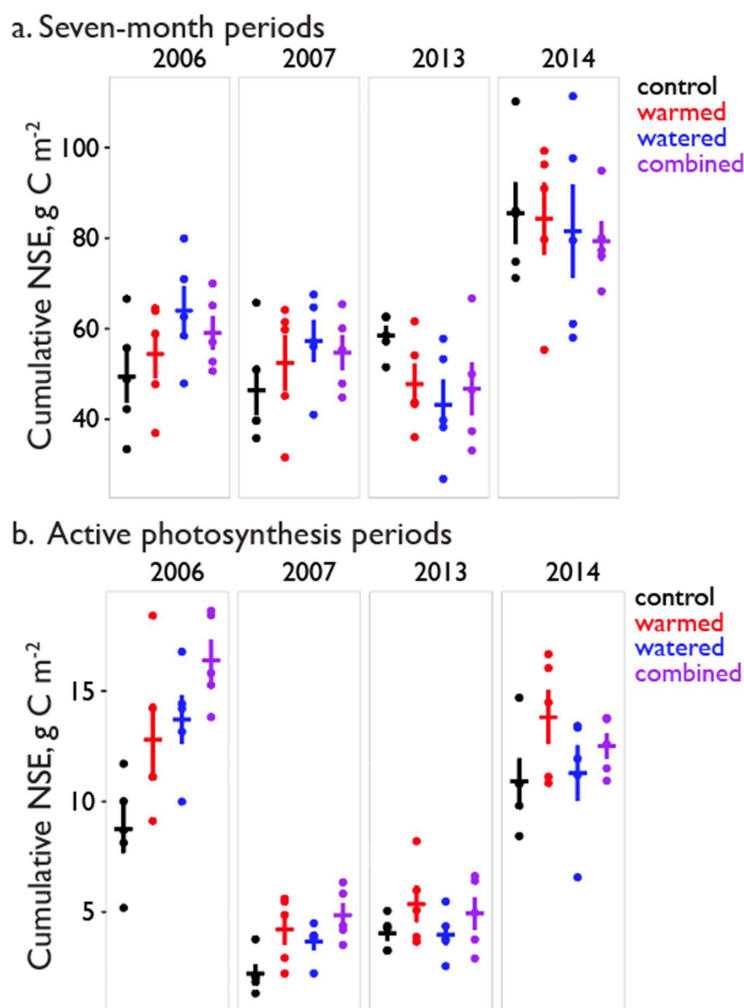
611 1 SE. Precipitation is shown above each year's data, with annual totals shown on the left and the



612 size of several of the largest events noted for scale. Means for each treatment are shown with
613 different colors representing different treatments (control = black, warmed = red, altered
614 monsoonal precipitation [watered] = blue, warmed × watered [combined] = purple). Positive
615 NSE rates depict respiratory losses that were greater than CO₂ uptake and negative NSE rates
616 depict C fixation rates that outpaced respiratory losses. b. Differences between treatments and
617 control (t_d) are shown as solid lines ± 95% CI calculated for each daily average shown with
618 shading. Values were calculated by subtracting the control rates from the treatment (red =
619 warmed – control; blue = altered monsoonal precipitation [watered] – control; purple = warmed
620 × watered [combined] – control).
621

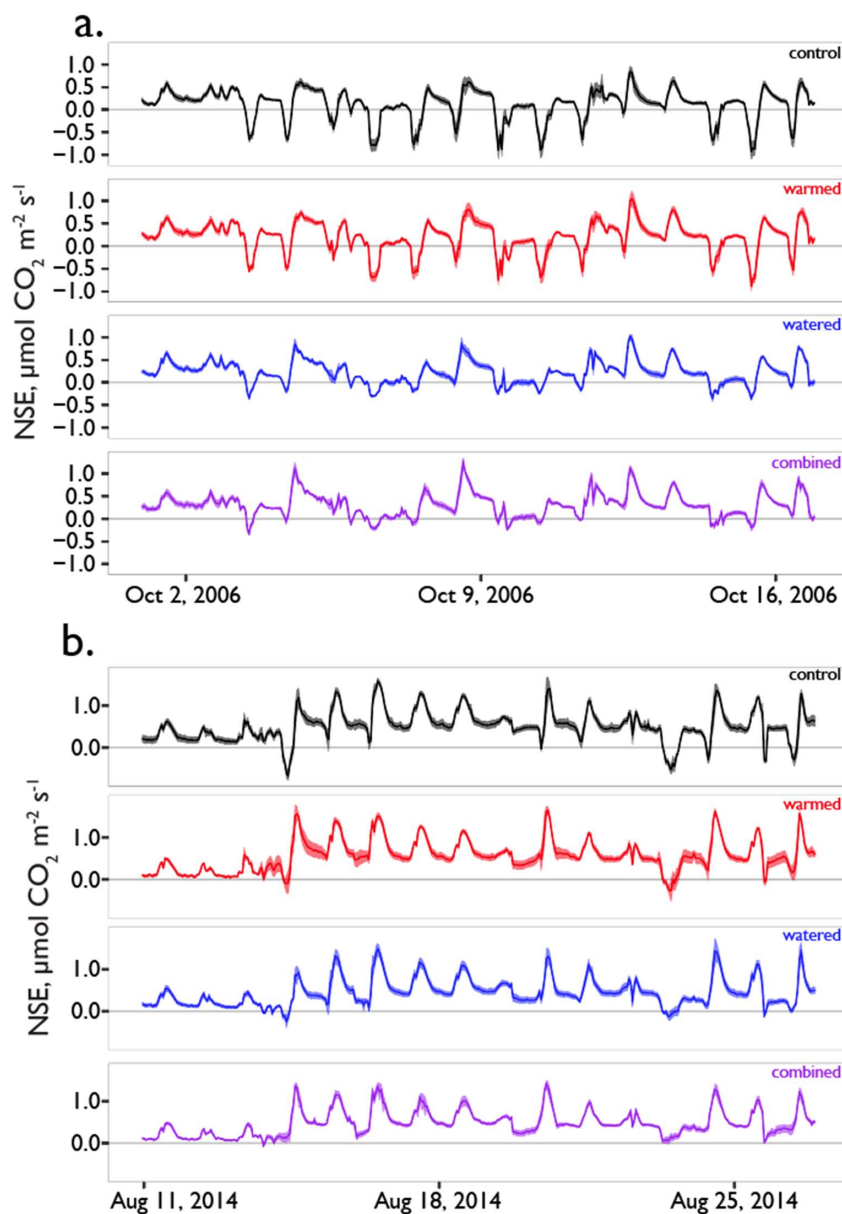


622
623 Fig. 2. Interannual comparison of “puffs” of CO₂ from a single automated flux chamber
624 (watering treatment, block 2) observed in response to mid-summer experimental watering
625 treatments. Time resolution is hourly. Plots were experimentally watered from 2005-2012, with
626 no watering in the final panel (2014). Timing of the watering treatments are shown by the
627 vertical dotted lines. The puffs shown here are CO₂ fluxes at or above ~1 μmol CO₂ m² s⁻¹ and
628 these occurred in response to active watering treatments.



629

630 Fig. 3. (a). Seven-month cumulative CO₂ fluxes during 4 measurement years: 2006, 2007, 2013,
631 and 2014 for the period of February 19 - September 18, a period chosen due to availability of
632 data in all measurement years. (b) Cumulative CO₂ flux during periods with active
633 photosynthesis (defined as days during which NSE was < -0.2 μmol CO₂ m⁻² s⁻¹ or lower, largely
634 corresponding with wet periods). Though selection was made on this daily minimum, numbers
635 are positive because 24 hour totals during these periods were still largely net sources of CO₂ to
636 the atmosphere despite active photosynthesis during peak hours. Dots indicate values from
637 individual automated chambers and horizontal and vertical bars indicate mean ± SE. For effect
638 sizes associated with each treatment, see Table 2.



639

640 Fig. 4. Examples of hourly CO₂ flux patterns during rain events (a) early in the experiment and
 641 (b) in the final season of measurement. Solid lines are the mean and ribbons indicate ± 1 SE. See
 642 Fig. 1a for rainfall patterns at these times.

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