

## Reviewer 1 Response

We are pleased to report that we have included our R script for the analyses in this paper as part of the supplemental information. We have also made sharing R script sharing a policy for papers produced in my lab going forward. The data in this manuscript are now available on ESS DIVE (doi:10.15485/1596312).

We edited our second paragraph slightly. We still wanted to introduce apparent after respiration quotients are defined in their “ideal” form so as not to confuse the reader.

Specific changes:

- 1: Soil respiration was redefined.
- 2: Cited Subke et al. 2006
- 3: Removed definition of OR and cleared up ARQ/RQ confusion.
- 4: Based on its elemental structure
- 5: Fixed
- 6: Added “same”
- 7: Started new paragraph.
- 8: I am not a fan of MASS: stepAIC() as I find it is too conservative in regards to the predictor variables it leaves in a model. I prefer to remove variables when their removal does not change the AIC or significantly change the results of the LRT based on Occam’s razor. Anyways, the R code is now available so it can be replicated.
- 9: Started new paragraph.
- 10: We recalculated using this command, R squared were either the same or within 0.02. Great tip, thank you!
- 11: The R code is now SI. The data have been submitted to ESS DIVE.
- 12: Changed.
- 13: Defined the circles in the caption.
- 14: Thanks
- 15: Added.
- 16: ?
- 17: Yes, SOC. Good catch.
- 18: Since those conditions were met in our soils, we do not think discussing it further is relevant to this manuscript. There is a good discussion of it in the Angert paper we cited.
19. Thanks

## Reviewer 2 Response

We added the height of ambient air sampling (0.5 to 1 m aboveground).

We added a citation for the atmospheric concentration of oxygen.

We changed enriched and depleted to higher/greater and lower when referring to delta values.

We rewrote that results paragraph with better parallel construction of the sentences. Since these were mixed model multiple regressions, we do not have traditional ANOVA tables to report.

We fixed the table number.

The suggestion that we investigate the effect of the warming on temperature sensitivity was a great one. We re-ran our linear models of ARQ and  $^{13}\text{C}$  vs climate (soil T or VWC) with a climate by warming treatment interaction, which improved the model in all cases except for one ( $^{13}\text{C}$  vs VWC). The reviewer was correct in stating that this was a missed opportunity. These new analyses make a much stronger case for the experimental warming treatment affecting the substrates being used to fuel soil respiration. We have thus expanded our discussion section to include more about how warming and soil moisture can affect root respiration and substrate utilization.

We added the sample size ( $n=4$ ) for the incubations. We did not have  $^{13}\text{C}$  values as we had issues with our Picarro at that time.

We reworded line 242.

We added your comment about advection possibly leading to erroneous diffusive fractionation corrections to the manuscript.

The data ([doi:10.15485/1596312](https://doi.org/10.15485/1596312)) are available on ESS DIVE now.

We added a range of RQ values for the molecules in table 1.

We have added sample sized to all the captions of all tables and figures.

In figure 1, we chose to keep the lines connecting the ARQ points as the point of figure 1 is to show how the ARQ and  $^{13}\text{C}$  patterns are similar. We added the fit statistics to the caption.

In figure 2, we changed the x-axis so they are the same for both panels, and, as requested, we include all the data points for the ARQ data as well.

# 1 Using Respiration Quotients to Track Changing Sources of Soil 2 Respiration Seasonally and with Experimental Warming

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11 **Abstract.** Developing a more mechanistic understanding of soil respiration is hampered by the difficulty in  
12 determining the contribution of different organic substrates to respiration and in disentangling autotrophic versus  
13 heterotrophic and aerobic versus anaerobic processes. Here, we ~~use~~ a relatively novel tool for better understanding  
14 soil respiration: the apparent respiration quotient (ARQ). ARQ is the amount of CO<sub>2</sub> produced in the soil divided by  
15 the amount of O<sub>2</sub> consumed and it changes according to which organic substrates are being consumed and whether  
16 oxygen is being used as an electron acceptor. We investigated how the ARQ of soil gas varied seasonally, by soil  
17 depth, and by *in situ* experimental warming (+4°C) in a coniferous forest whole-soil-profile warming experiment over  
18 two years. We then compared the patterns in ARQ to those of soil δ<sup>13</sup>CO<sub>2</sub>. Our measurements showed strong seasonal  
19 variations in ARQ from ≈0.9 during the late spring and summer to ≈0.7 during the winter. This pattern likely reflected  
20 a shift from respiration being fueled by oxidized substrates like sugars and organic acids derived from root and root  
21 respiration during the growing season to more reduced substrates such as lipids and proteins derived from microbial  
22 necromass during the winter. This interpretation was supported by δ<sup>13</sup>CO<sub>2</sub> values, which were ~~relatively lower~~, like  
23 lipids, in the winter and ~~relatively higher~~, like sugars, in the summer. Furthermore, ~~experimental warming significantly~~  
24 ~~changed how both ARQ and δ<sup>13</sup>CO<sub>2</sub> responded to soil temperature.~~ Wintertime ARQ and δ<sup>13</sup>CO<sub>2</sub> values were higher  
25 in ~~heated~~ than in control plots, ~~probably due to the warming-driven increase in microbial activity that may have utilized~~  
26 ~~oxidized carbon substrates, while growing season values were lower in heated plots.~~ Experimental warming and  
27 ~~phenology change the sources of soil respiration throughout the soil profile. The sensitivity of ARQ to these changes~~  
28 ~~demonstrates its potential as~~ a tool for disentangling the biological sources contributing to soil respiration.

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Deleted: . probably due to an increase in the use of more oxidized carbon substrates with warming.

Deleted: Our results demonstrate that soil ARQ shows strong seasonal patterns in line the phenology of carbon inputs and patterns in soil δ<sup>13</sup>CO<sub>2</sub>, verifying ARQ as

41 **1 Introduction**

42 Despite making extensive measurements of soil respiration (Bond-Lamberty and Thomson, 2010), scientists lack methods to  
43 disentangle the processes underlying, and substrates contributing to, soil respiration, which hampers predictions of terrestrial  
44 carbon cycle responses to global change (Phillips et al., 2017). Mechanistic uncertainty surrounding soil respiration is partly  
45 responsible for the 1000 Pg spread in model predictions of end-of-century terrestrial carbon-climate feedbacks (Friedlingstein  
46 et al., 2013). [Soil respiration is the flux of CO<sub>2</sub> from the soil surface to the atmosphere, which is dominated by autotrophic  
47 respiration from plant roots and heterotrophic respiration from soil microbes.](#) Heterotrophic respiration, which has increased  
48 globally over the past three decades (Bond-Lamberty et al., 2018), is itself the sum of various processes using different sources  
49 of energy. For example, microbes consume different organic substrates depending on what molecules are accessible and  
50 whether the microbes are living in the rhizosphere or bulk soil, and microbes utilize different terminal electron acceptors  
51 depending on O<sub>2</sub> availability in the microsites in which they reside (Keiluweit et al., 2016; Liptzin et al., 2011). The electron  
52 donors (the organic substrates) and the electron acceptors used by soil microbes during respiration cannot be resolved by  
53 measuring the CO<sub>2</sub> flux alone. Previous studies have used measurements of δ<sup>13</sup>C to partition respiration into autotrophic and  
54 heterotrophic components (e.g., Dorrepaal et al., 2009), radiocarbon to partition respiration sources by age (e.g., Trumbore,  
55 2000), or both isotopes in combination to more finely separate respiration among sources (e.g., Hicks Pries et al., 2013;  
56 Hopkins et al., 2012). However, isotopes are not the only way to disentangle soil respiration's various components (Subke et  
57 al., 2006).

58  
59 Our ability to understand soil respiration is limited by measuring only one half of the respiration equation, the CO<sub>2</sub> produced.  
60 Simultaneously measuring the O<sub>2</sub> consumed can provide a more mechanistic understanding of the processes and substrates  
61 contributing to soil respiration (Phillips et al., 2017). The paired measurements of CO<sub>2</sub> and O<sub>2</sub> can be used to calculate a  
62 respiration quotient (RQ; Angert and Sherer, 2011). All organic matter has an oxidative ratio (I/RQ), which can be calculated  
63 based on an elemental analysis of its C, H, O, and N (Masiello et al., 2008). The oxidation state of carbon in carbohydrates is  
64 0 with a corresponding RQ of 1 [based on its elemental structure](#). More reduced energy sources such as lipids have lower RQ  
65 values (≈0.73) and the RQ of proteins range from 0.67 to 1; more oxidized sources such as organic acids have RQ ranges from  
66 1 to 4 (Masiello et al., 2008; Table 1). The RQ of aerobic respiration therefore changes based on what substrates are being  
67 consumed (Dilly, 2001; Theenhaus et al., 1997). Anaerobic respiration increases RQ to values greater than one, as electron  
68 acceptors like Fe(III) and NO<sub>3</sub><sup>-</sup> replace O<sub>2</sub>. Thus, RQ can help differentiate between the electron donors (organic substrates)  
69 and terminal electron acceptors used during soil respiration. We will refer to the 'apparent' [respiration quotient \(ARQ\)](#) because  
70 not all ecosystem CO<sub>2</sub> or O<sub>2</sub> fluxes are due to respiratory processes (Angert and Sherer, 2011). For example, fluctuating redox  
71 conditions can lead to consumption of O<sub>2</sub> during metal oxidation and drive ARQ below the value of the most reduced organic  
72 matter (Angert et al., 2015).

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79 Thus far, CO<sub>2</sub>:O<sub>2</sub> ratios have been primarily used to understand large scale earth system processes and only few studies have  
80 examined processes within ecosystems. This ratio in atmospheric samples has been used to estimate a) the magnitude of the  
81 terrestrial carbon sink, because carbon uptake by terrestrial ecosystems is balanced by O<sub>2</sub> production whereas ocean CO<sub>2</sub>  
82 uptake is decoupled from O<sub>2</sub>, (Keeling, 1988; Keeling et al., 1996; Randerson et al., 2006; Worrall et al., 2013) and b)  
83 anthropogenic impacts on the carbon cycle, based on the principle that burning of reduced fossil fuels results in a different  
84 oxidative ratio than does photosynthesis and subsequent respiration of carbohydrates (Keeling, 1988). The CO<sub>2</sub>:O<sub>2</sub> ratio of  
85 ecosystem-atmosphere exchanges is an essential quantity in these carbon cycle calculations. CO<sub>2</sub>:O<sub>2</sub> ratios have been estimated  
86 from measurements of net ecosystem exchange of CO<sub>2</sub> and O<sub>2</sub> (e.g., Seibt et al., 2004) and from elemental analysis of biomass  
87 (Hockaday William C. et al., 2015; e.g., Masiello et al., 2008), both of which are assumed to be similar over multiyear  
88 timescales. In early carbon sink calculations, the oxidative ratio of ecosystem fluxes was assumed to be 1.1 (ARQ=0.9) based  
89 on a single study of temperate soils (Severinghaus, 1995). However, the few subsequent studies examining the CO<sub>2</sub>:O<sub>2</sub> ratio  
90 of soil respiration fluxes have shown soil fluxes can deviate widely from that value.

91

92 Soil ARQ from incubations shift as a result of temperature changes, substrate additions, and soil management. For example,  
93 the ARQ of peat soils decreased from about 1.1 to about 0.6 when temperatures increased from 0 to 20°C, attributed to changing  
94 substrate use (Chapman and Thurlow, 1998). Glucose additions to German forest soils increased soil ARQ to 0.95-1.0 from a  
95 basal value around 0.7 (Dilly, 2001; Theenhaus et al., 1997). Soils under organic agriculture were found to have a greater ARQ  
96 (1.19) than the same soils under conventional agriculture (0.72; Theenhaus et al., 1997). Soil ARQ in mesocosms containing  
97 pine seedlings changed seasonally and when the pine seedlings were cut, indicating the ratio is responsive to changes in  
98 vegetation (Andersen and Scagel, 1997; Scagel and Andersen, 1997).

99

100 Lastly, in one of the only studies using *in situ* measurements, soil ARQ taken from gas wells across multiple forested  
101 ecosystems ranged widely from 0.14 to 1.23 indicating the influence of abiotic processes that consume O<sub>2</sub> (Angert et al. 2015).  
102 The wide range in soil ARQ values associated with different biochemical conditions indicates the ratio has the potential to  
103 provide insight into the substrates contributing to respiration as well as into abiotic O<sub>2</sub> consumption. Finer scale research is  
104 needed, however, to explore ARQ values in the same soils under different conditions to learn what these values indicate about  
105 the processes and substrates contributing to soil respired CO<sub>2</sub>.

106

107 Here we investigated how the ARQ of soil gas *in situ* varied seasonally, by soil depth, and by experimental warming in a  
108 whole-soil-profile warming experiment in a well-drained, oxygenated coniferous forest soil (Hicks Pries et al., 2017). We  
109 characterized soil ARQ at 30 and 90 cm depths in the winter and growing season over two years and compared the patterns in  
110 ARQ to monthly patterns in soil profile δ<sup>13</sup>C. We hypothesized that ARQ values would change seasonally and with warming  
111 reflecting the values of the organic carbon substrates being consumed by microbes. Like ARQ, the δ<sup>13</sup>C of soil CO<sub>2</sub> is

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112 influenced by the use of different organic substrates since more reduced substrates tend to [have lower  \$\delta^{13}\text{C}\$  values](#) (Bowling et  
113 al., 2008). By comparing ARQ values to other indicators of respiration sources, such as  $\delta^{13}\text{C}$ , augmented by what we  
114 understand about plant allocation of carbon substrates belowground, we aim to advance the utility of ARQ as a tracer of  
115 respiration processes.

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## 116 2 Methods

### 117 2.1 Warming Experiment

118 The whole soil profile warming experiment is located at the University of California Blodgett Forest Research Station, in the  
119 Sierra Nevada foothills near Georgetown, CA at 1370 m above sea level. Mean annual precipitation is 1774 mm with most of  
120 it occurring from November through April and mean annual temperature is about 12.5°C (Bird and Torn, 2006). The  
121 experiment is in a thinned 80-year-old stand of mixed conifers including ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus*  
122 *lambertiana*), incense cedar (*Calocedrus decurrens*), white fir (*Abies concolor*), and douglas fir (*Pseudotsuga menziesii*). The  
123 soils are Holland series: fine-loamy, mixed, superactive, mesic Ultic Haploxeralfs of granitic origin with thick, >5 cm O  
124 horizons, minimal carbonates (Rasmussen et al., 2005), and a pH that ranges from 5.6 to 6.5 (Hicks Pries et al., 2018). The  
125 warming treatment warmed the soil +4°C to 1 m depth while maintaining the natural temperature gradient with depth and  
126 temporal variations in soil temperature as described in Hicks Pries et al. (2017). Briefly, there were three pairs of control and  
127 heated 3 m diameter circular plots heated by 22 vertical resistance heater cables in metal conduit (BriskHeat, Ohio, USA) that  
128 surrounded them. To compensate for surface heat loss, two concentric rings of heater cable at 1 and 2 m in diameter were  
129 installed 5 cm below the soil surface in heated plots. Unheated cables were installed similarly in control plots. Heating  
130 throughout the plot volume was generally even, ranging from 3.5 to 4.5°C except at 5 cm depth where the heated plots were  
131 on average only  $2.4 \pm 1.2^\circ\text{C}$  warmer than the control due to a lack of aboveground heating. Soil moisture was slightly decreased  
132 in the warmed plots by an average of 1.5-3.5% volumetric water content (Hicks Pries et al., 2017).

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### 133 2.2 Sample Collection and Analysis

134 Dataloggers (CR1000, Campbell Scientific, Utah, USA) continuously recorded soil temperature and moisture at 30 min  
135 intervals. Temperature was monitored at 5, 15, 30, 50, 75, and 100 cm depths at a radial distance of 0.75 m from the center of  
136 each plot. Temperature probes consisted of thermistors (Omega 44005) epoxied to PVC rods, placed inside thin-walled steel  
137 conduit. To monitor soil moisture, we used an enviroSCAN (Sentek, Australia) probe fitted with capacitance sensors at 10, 30,  
138 50, and 90 cm at a radial distance of 0.75 m from the center of each plot. We calibrated the soil moisture measurements by  
139 comparing the sensor values at each depth to the volumetric water content measured in nearby (within 0.5 m) soil cores that  
140 were sampled five times over two years.

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145 Each of the six plots has a set of gas wells at 15, 30, 50, 75, and 90 cm. The gas wells were 6.35 mm diameter stainless steel  
146 tubes inserted into the soil at a 45° angle to the desired depth and topped with straight swage pipefittings (Swagelok Ohio,  
147 USA) with septa. For CO<sub>2</sub> and δ<sup>13</sup>C measurements, samples were collected from the wells with a syringe on a nearly monthly  
148 basis from March 2014 through June 2017 (32 months total) and always during morning hours. After clearing the headspace  
149 in each well, a 25 ml gas sample was transferred to an evacuated 20 ml septum-topped glass vial. For analysis, 5 ml samples  
150 were injected into the small sample isotope module of a cavity ring down spectrometer (CRDS, Picarro, Santa Clara,  
151 California) where they were diluted with ultra zero air (without CO<sub>2</sub>). A four-point calibration curve ranging from 2,000 to  
152 20,000 ppm (δ<sup>13</sup>C=-26.7‰) was used to calculate the CO<sub>2</sub> concentration from the CRDS data and to correct for mass  
153 dependency of the δ<sup>13</sup>C measurement.

154

155 In July 2015, February 2016, April 2016, August 2016, March 2017, and June 2017, we collected additional samples from the  
156 30 (except July 2015) and 90 cm gas wells into 13 ml flasks equipped with O-ring valves (LouwersHanique, Hapert,  
157 Netherlands) to simultaneously measure CO<sub>2</sub> and O<sub>2</sub> concentrations in order to calculate ARQ. The flasks were analyzed in  
158 the laboratory at the Hebrew University by a closed system (The Hampadah; Hilman and Angert, 2016). This fully automated  
159 system uses an infra-red gas analyzer (IRGA) for CO<sub>2</sub> measurement (LI 840A LI-COR; Lincoln, NE, USA) and a fuel-cell  
160 based analyzer (FC-10; Sable Systems International, Las Vegas, NV, USA) for measuring O<sub>2</sub>. The flasks were analyzed within  
161 2-3 weeks of collection.

162

163 In June 2017, we also ran a set of short (3 hour) incubations of root-free soil and of excised roots collected adjacent to the  
164 experimental plots. We collected four mineral soil cores with a 5 cm diameter hammer corer, separated the cores into 0-20 and  
165 20-40 cm depths, and removed roots >1 mm diameter. Roots were collected from four 25 cm x 25 cm x 25 cm soil pits. We  
166 rinsed roots with water to remove soil and blotted them dry before placing them into mason jars. The root-free soil was also  
167 placed into mason jars, and both sets of mason jars were flushed with ambient, outside air. After a three-hour incubation of the  
168 root samples and a 21-hour incubation of the soil samples, the headspace was sampled for CO<sub>2</sub> and O<sub>2</sub> and analyzed as  
169 described above. Incubations were run at room temperature, which was similar to the field temperature at the time of collection.

### 170 2.3 Sample Calculations and Statistics

171 To calculate ARQ, we used the following equation from Angert et al. (2015):

$$172 \quad ARQ = -0.76 \frac{\Delta CO_2}{\Delta O_2}$$

173 Where ARQ is the apparent respiratory quotient, ΔCO<sub>2</sub> (ppmv) is the difference between CO<sub>2</sub> concentrations in the soil pore  
174 space gas and ambient (i.e., ~~0.5 to 1m~~ aboveground) samples, ΔO<sub>2</sub> (ppmv) is the difference of the soil pore space O<sub>2</sub>  
175 concentration and ambient O<sub>2</sub> concentration, and 0.76 is the ratio of CO<sub>2</sub> to O<sub>2</sub> diffusivity in air (Massman, 1998). The negative  
176 sign is for convenience so the ARQ value will typically be positive, because the difference in O<sub>2</sub> concentration is always

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178 negative. For the jar incubations we used the same equation without the 0.76 factor. Ambient CO<sub>2</sub> concentrations were  
179 measured in the field at the time of sampling with the CRDS, while the ambient O<sub>2</sub> concentration was assumed to be 20.95%  
180 (Rumble, 2019). To relate the δ<sup>13</sup>C value of soil pore space CO<sub>2</sub> to the δ<sup>13</sup>C of CO<sub>2</sub> production, we corrected the pore-space  
181 δ<sup>13</sup>C value for diffusion since <sup>13</sup>C diffuses slower in air than <sup>12</sup>C and thus the measured value does not accurately represent the  
182 value of production. For the correction, we used the following equation from Bowling et al. (2015):

$$183 \quad \delta_{production} = \frac{C_s(\delta_s - 4.4) - C_a(\delta_a - 4.4)}{1.0044(C_s - C_a)}$$

184 Where C<sub>s</sub> is the soil pore space CO<sub>2</sub> concentration (ppmv), δ<sub>s</sub> (‰) is the isotopic composition of soil pore space CO<sub>2</sub> and C<sub>a</sub>  
185 and δ<sub>a</sub> are the CO<sub>2</sub> concentration and isotopic composition of ambient air, respectively. The ambient CO<sub>2</sub> concentrations and  
186 δ<sup>13</sup>C values needed for these corrections were measured in the field at the time of sampling with the CRDS.

187  
188 To investigate the effects of season, warming treatment, and soil depth on ARQ and δ<sup>13</sup>C, we ran multiple regressions in R (R  
189 Development Core Team, 2017). Because ARQ was not sampled from both depths on all dates, we ran separate regressions  
190 for each depth (30 and 90 cm) and then ran a regression that included a depth effect while dropping the first sampling date. In  
191 all regressions, treatment and sampling date (as a factor) were fixed effects. Following Zuur et al. (2009), we used a full model  
192 with all fixed effects and their interactions to optimize the random effects and autocorrelation structure based on AIC. For both  
193 versions, we used the individual gas well as a random effect and a temporal autocorrelation did not improve the model, nor  
194 did an autocorrelation function graph indicate one was needed. We chose the significant fixed effects by performing a series  
195 of pairwise model comparisons using AIC and the *F* test, dropping the least significant variables each time until only variables  
196 that improved the model fit remained. The p-values reported are those from the t-tests of the summary.lme function of best fit  
197 model. [We report conditional R<sup>2</sup> values calculated using the rsquared command in the piecewiseSEM package.](#)

198  
199 To investigate seasonal patterns in δ<sup>13</sup>CO<sub>2</sub>, we had more data in terms of both length of time and temporal density of sampling  
200 and were thus able to treat month as a continuous variable. We fit a sine function and tested models including the first and  
201 second harmonics of the month effect as well as linear fixed effects of depth, treatment, and a depth by treatment interaction.  
202 Graphical exploration indicated the sinusoidal pattern differed slightly by year, so we also added a year effect to the second  
203 harmonic of the month effect. As above, we used the full fixed effect model to test the best random and autocorrelation  
204 structure. Individual gas well depth was used as a random effect and a correlation structure did not improve the model.

205  
206 To test relationships between ARQ and δ<sup>13</sup>CO<sub>2</sub>, and both ARQ and δ<sup>13</sup>CO<sub>2</sub> individually versus soil temperature and volumetric  
207 water content, we ran mixed-model regressions with individual gas well as a random effect. [For the soil climate relationships,](#)  
208 [we used AIC and the \*F\* test to investigate whether the warming treatment and its interaction with soil temperature or VWC](#)  
209 [were significant fixed effects.](#) We tested the need for autocorrelation structures based off of AIC and none improved the  
210 models. For all models, we graphically checked the residuals for violations of normality and heterogeneity of variance. For

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Deleted: For these regressions, we report pseudo R<sup>2</sup> values calculated from a linear regression of the actual data versus the model predicted data.



218  $\delta^{13}\text{CO}_2$  analyses, we dropped the 15 cm depths due to their unusually low  $\delta^{13}\text{C}$  value ( $<-32\%$ ) after correction (Eq. 1), which  
219 indicated potential intrusion of atmospheric air during sampling that led to an overcorrection. We used one-way ANOVA's to  
220 compare the ARQ of soil and root incubations and the ARQ of two soil depths we incubated. All statistics were performed in  
221 R v 3.4.1 and regressions were done using the lme function (R Development Core Team, 2017).

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### 222 3 Results

223 Both ARQ and  $\delta^{13}\text{CO}_2$  had similar, strong seasonal patterns (Fig. 1a and 1b). ARQ values were higher during the growing  
224 season ( $0.89 \pm 0.01$ ,  $n=42$ ) and lower during the winter ( $0.70 \pm 0.02$ ,  $n=23$ ). In ARQ regression analyses for both depths, there  
225 was a significant effect of date ( $p<0.0001$ ,  $n=59$ ) with February 2016 and March 2017 differing significantly from July 2015  
226 (90 cm only), April 2016, August 2016, and June 2017. Similarly,  $\delta^{13}\text{C}$  was higher during the summer (June through October,  
227  $-27.97 \pm 0.06$ ,  $n=311$ ) and lower during the winter and spring (November through May,  $-29.01 \pm 0.04$ ,  $n=447$ ). While individual  
228 dates were not compared statistically for  $\delta^{13}\text{CO}_2$ , the vast improvement in model fit using month as a sine function instead of  
229 a linear function or factor ( $\Delta\text{AIC}=114$ ) is strong statistical evidence for a seasonal effect (Fig. 2b). ARQ and  $\delta^{13}\text{CO}_2$  were  
230 significantly related according to the mixed effect regression model (Fig. 1c,  $p<0.0001$ ,  $n=64$ ,  $R^2=0.20$ ). However, the patterns  
231 in ARQ and  $\delta^{13}\text{CO}_2$  did not match during April.

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233 Both ARQ and  $\delta^{13}\text{CO}_2$  differed by warming treatment (Fig. 2) and by depth (Table 2). For the ARQ of 30 cm depths, there  
234 was a significant treatment-by-date interaction ( $p=0.051$ ,  $n=30$ ) whereby heated plots had greater ARQ values during the  
235 winter months (February 2016 and March 2017; Fig. 2a). For the ARQ of 90 cm depths, the best fit model did not include a  
236 significant treatment effect or treatment-by-date interaction (Fig. 2a,  $n=35$ ). For  $\delta^{13}\text{CO}_2$  across all depths, treatment was a  
237 significant effect ( $p=0.0065$ ,  $n=758$ ) with warmed soil on average having a slightly higher  $\delta^{13}\text{CO}_2$  ( $-28.33 \pm 0.05$ ) than the  
238 control soil ( $-28.83 \pm 0.06$ ; Fig 2b). The treatment-by-depth interaction was not significant for  $\delta^{13}\text{CO}_2$  and was not included in  
239 the best fit model. Looking at depth only (Table 2), ARQ at 30 cm was marginally significantly greater than ARQ at 90 cm by  
240 0.07 units ( $p=0.099$ ,  $n=59$ ), while  $\delta^{13}\text{CO}_2$  increased with depth from  $-28.98$  at 30 cm to  $-28.34$  at 90 cm ( $p=0.0089$ ,  $n=758$ ).

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242 Both ARQ and  $\delta^{13}\text{CO}_2$  showed strong relationships with soil climate that were significantly affected by the warming treatment  
243 (Fig 3). We tested relationships with soil temperature and soil moisture individually because of the strong negative correlation  
244 between temperature and moisture in this Mediterranean climate (pearson's  $r=-0.76$  to  $-0.78$ ). ARQ increased significantly  
245 with increasing soil temperatures ( $p<0.0001$ ,  $n=65$ ,  $R^2=0.52$ ; Fig 3a) with values increasing faster in control plots than in  
246 warmed plots ( $p=0.0051$ ). ARQ decreased with increased soil moisture ( $p<0.0001$ ,  $n=60$  due to missing VWC values,  $R^2=0.24$ ;  
247 Fig. 3b), and the decrease was faster in the control than in the warmed plots.  $\delta^{13}\text{CO}_2$  became higher with increasing soil  
248 temperatures ( $p<0.0001$ ,  $n=375$ ,  $R^2=0.33$ ; Fig. 3c) with values again increasing faster in the control than in the warmed plots

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269 ( $p=0.02$ ).  $\delta^{13}\text{CO}_2$  decreased with increased soil moisture ( $p<0.0001$ ,  $n=345$  due to missing VWC values,  $R^2=0.30$ ; Fig. 3d),  
270 and treatment did not have a significant effect.

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272 Our incubations of roots ( $n=4$ ) and of root-free soil ( $n=4$  per depth increment) indicated that heterotrophic and autotrophic  
273 respiration had significantly different ARQ values, at least during the summer when we performed the incubations. Roots had  
274 a greater ARQ ( $0.87 \pm 0.03$ ) than did root-free soil ( $0.78 \pm 0.02$ ; one-way ANOVA,  $p=0.029$ ). Furthermore, ARQ of the soil  
275 incubations significantly declined with depth from  $0.82 \pm 0.01$  at 0-20 cm to  $0.74 \pm 0.02$  at 20-40 cm (one-way ANOVA,  
276  $p=0.0053$ ).

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#### 277 4 Discussion

278 There are many factors that can affect ARQ; however, our evidence indicates the strong seasonal patterns in ARQ and  $\delta^{13}\text{CO}_2$   
279 were likely driven by changes in the amount of root-derived organic substrates providing energy for heterotrophic microbial  
280 respiration and changes in the contributions of autotrophic root respiration. This interpretation is supported by previous soil  
281 ARQ studies, our incubations, and the scientific understanding of how plant carbon inputs change seasonally. The seasonal  
282 range in ARQ from  $\approx 0.9$  during the growing season to  $\approx 0.7$  during the winter may reflect a shift in the molecules fueling  
283 respiration from more oxidized substrates like sugars and organic acids derived from roots in the summer to more reduced  
284 substrates in the winter such as lipids and proteins derived from microbial necromass. Previous incubations found that glucose  
285 additions increased ARQ (Dilly, 2001; Theenhaus et al., 1997). Other studies attributed a decline in ARQ during the time  
286 course of incubation to the depletion of labile carbon sources (Angert et al., 2015; Severinghaus, 1995). Our short-term  
287 incubations demonstrated that root respiration has a greater ARQ than microbial respiration from root-free soils. During the  
288 growing season, root respiration and exudation increase, which should increase ARQ, as seen in our data. In Eastern U.S.  
289 deciduous forests, root exudation rates tend to be lower in the winter and spring than in the summer and fall (Abramoff and  
290 Finzi, 2016; Phillips et al., 2008). Mass-specific fine root respiration rates were greater during the growing season (up to 8  
291  $\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$ ) than in the winter ( $<1 \text{ nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$ ) and total belowground carbon flux was greatest from May through  
292 October (Abramoff and Finzi, 2016). Though these root studies were not from the western United States, eddy covariance data  
293 from a coniferous forest near our study site found that primary production was greatest during the summer months from June  
294 through mid-September (Goldstein et al., 2000).

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296 Beyond the results of our root and root-free soil incubations, there is additional evidence that root and rhizosphere respiration  
297 should have a greater ARQ than microbial-derived respiration. For example, respiration of root tips is driven by sugar content  
298 and has an RQ of 1.0 (Saglio and Pradet, 1980). Furthermore, recent metabolomic analysis of root exudates identified sugars,  
299 carboxylic acids, amino acids, and phenolics as the main metabolites (Zhalnina et al., 2018), most of which are relatively  
300 oxidized energy sources with relatively high respiratory quotients. Thus, we would expect greater ARQ values during the

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306 summer due to higher root activity. When trees are dormant, the lack of fresh inputs from roots may lead to more recycling of  
307 organic carbon within microbial biomass, wherein proteins and lipids are the first and third largest constituents by weight,  
308 making up to 55% and from 10-35% of a typical bacterial cell's dry mass, respectively (Kleber and Reardon, 2017; Neidhardt,  
309 1987). Lipids and proteins tend to be reduced and have the lowest RQ values of common organic substrates, likely explaining  
310 the lower wintertime ARQ values in our soils.

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312 The seasonal pattern in  $\delta^{13}\text{CO}_2$  reinforces our interpretation that changes in respiration carbon sources were driving changes  
313 in ARQ. Soil  $\delta^{13}\text{CO}_2$  was more enriched in the summer and became more depleted in the winter by up to 2‰. In a  
314 comprehensive review of carbon isotopes in terrestrial ecosystems, Bowling et al. (2008) showed that plant lipids tend to be  
315 more depleted in  $^{13}\text{C}$  while sugars and organic acids tend to be more enriched in  $^{13}\text{C}$  relative to bulk leaf  $\delta^{13}\text{C}$ . While these  
316 numbers are based on plant lipids, if we assume microbial lipids are similarly depleted relative to other organic compounds,  
317 an increase in microbial necromass as an organic matter source relative to root-derived sources during the winter would cause  
318 the observed fluctuation in  $\delta^{13}\text{CO}_2$ . Furthermore, a chemical fractionation of soil organic matter found that the water-soluble  
319 fraction, which includes sugars, was 3-4‰ more enriched than the acid-insoluble pool (Biasi et al., 2005). While the  
320 interpretation of respiration  $\delta^{13}\text{C}$  by itself in  $\text{C}_3$  ecosystems can be difficult due to the small ‰ differences among carbon  
321 sources (e.g., Bowling et al., 2015), the simultaneous use of ARQ and  $^{13}\text{CO}_2$  helps strengthen interpretations.

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323 Seasonality encompasses changes to phenology and soil climate, among other factors. Both ARQ and  $\delta^{13}\text{C}$  had significant  
324 positive relationships with soil temperature. In addition to the importance of plant phenology described above, temperature  
325 could have direct effects on respiration sources. Specifically, warmer temperatures can increase root exudation rates (Yin et  
326 al., 2013) and the relative contribution of autotrophic-derived, if not directly autotrophic, respiration to total soil respiration.  
327 In two subarctic ecosystems, warming increased the proportion of ecosystem respiration derived from autotrophs (which, using  
328 natural abundance radiocarbon as a tracer, included heterotrophic respiration of root exudates) relative to heterotrophs (Hicks  
329 Pries et al., 2015). However, temperatures can affect ARQ through more than just changing the contributions of autotrophic  
330 sources. Lower temperatures increase the thermodynamic favorability of the oxidation of reduced carbon in compounds like  
331 lipids (LaRowe and Van Cappellen, 2011), which could also explain the decrease in ARQ values at lower temperatures. For  
332  $\delta^{13}\text{C}$ , it is likely that phenological changes to organic carbon sources were more important than temperature per se. Several  
333 soil incubation studies show that increases in temperature cause respired  $\delta^{13}\text{CO}_2$  to decrease by about 0.12–0.35‰ for each  
334 1°C rise in temperature—the opposite of the relationship we found (Andrews et al., 2000; Biasi et al., 2005; Hicks Pries et al.,  
335 2013). In these incubations, which were devoid of new organic carbon inputs, unlike in situ conditions, the shift was attributed  
336 to changes to the microbial community that affected carbon source preferences (Andrews et al., 2000; Biasi et al., 2005).  
337 Furthermore, in a Mediterranean climate, phloem sap from trees has been shown to become more enriched in  $^{13}\text{C}$  during the  
338 summer (Merchant et al., 2010), matching our pattern in soil  $\delta^{13}\text{CO}_2$ .

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342 [While ARQ and  \$\delta^{13}\text{CO}\_2\$  increased with soil temperature, experimental warming slowed that rate of increase so that both ARQ](#)  
343 [and  \$\delta^{13}\text{CO}\_2\$  values were generally greater in the control than in the heated treatment at the warmest soil temperature.](#)  
344 [Concurrently, during the colder months, experimental warming caused greater ARQ values \(as at 30 cm depths in February](#)  
345 [2016 and March 2017\) and slightly higher  \$\delta^{13}\text{CO}\_2\$  relative to the controls. The increase in ARQ and  \$\delta^{13}\text{CO}\_2\$  with experimental](#)  
346 [warming during the colder soil temperatures of winter indicates proportionately more respiration of relatively oxidized, labile](#)  
347 [organic substrates in the heated treatment. Perhaps enhanced root growth and exudation in the heated treatment \(Yin et al.,](#)  
348 [2013\) could result in the increased availability of labile organic substrates, but this increase occurred in winter when trees were](#)  
349 [less active and was not seen during the growing season. The increase in ARQ and  \$\delta^{13}\text{CO}\_2\$  could also be the result of preferential](#)  
350 [decomposition of more highly oxidized, labile substrates by a more active microbial population during the winter.](#)  
351 [Experimental warming increased microbial activity at all soil depths; warming increased  \$\text{CO}\_2\$  production by 34 to 37% overall](#)  
352 [with about 40% of the warming response occurring below 15 cm in the soil profile \(Hicks Pries et al., 2017\). A warming-](#)  
353 [induced increase in the consumption of labile substrates could lead to exhaustion of the labile pool and eventually smaller](#)  
354 [warming-induced SOC losses as seen at Harvard Forest \(Melillo et al., 2002, 2017\). In fact, the trend towards decreased ARQ](#)  
355 [and  \$\delta^{13}\text{CO}\_2\$  values during the warmer soil temperatures of the growing season could be due to a depletion of the labile SOC](#)  
356 [pool during the winter. Another potential explanation for lower values during the growing season could be a reduction in the](#)  
357 [proportion of soil respiration derived from roots. In one warming study, root respiration was less sensitivity to warming relative](#)  
358 [to heterotrophic respiration \(Hartley et al., 2007\). The warming treatment dried the soil slightly at Blodgett \(Hicks Pries et al.,](#)  
359 [2017\), which could stress roots during California's essentially rainless growing season. Future measurements of  \$\text{CO}\_2\$](#)   
360 [production, ARQ, and  \$\delta^{13}\text{CO}\_2\$  in trenched and untilled plots could help distinguish these possibilities.](#)

361  
362 Soil temperature and soil moisture were so strongly negatively correlated due to our study site's Mediterranean climate that it  
363 is difficult to separate their effects. ARQ and  $\delta^{13}\text{CO}_2$  were negatively correlated with volumetric water content, which was  
364 greatest when soil temperatures were coldest. Volumetric water content has the potential to control ARQ in several ways. First,  
365 increased soil moisture reduces  $\text{O}_2$  availability, which could increase ARQ values  $>1$  as  $\text{CO}_2$  is produced without  $\text{O}_2$   
366 consumption. However, during our study the soil remained oxic (soil  $\text{O}_2$  averaged 20% and the minimum was 17.38%). The  
367 negative relationship between ARQ and soil moisture indicates that anaerobic respiration was not a driver, and we only  
368 measured one ARQ value greater than one (1.03) during our study. However, diffusion rates are lower with higher soil  
369 moisture, which could make detection of high ARQ values difficult if anoxic conditions occur within microaggregates. In  
370 anoxic microaggregates, iron (II) is produced anaerobically, which is subsequently oxidized to iron (III) as the aggregate dries  
371 and becomes aerobic, a process that consumes  $\text{O}_2$  without producing  $\text{CO}_2$ , resulting in low ARQ values that can be detected  
372 as drying soils increase diffusion (Angert et al., 2015). In our soils, which tend to contain relatively high amounts of iron  
373 oxides (Rasmussen et al., 2005), iron oxidation could explain the 15% of ARQ values that were less than the reduced organic  
374 matter value of 0.7. Lastly, since  $\text{CO}_2$  is more soluble in water than is  $\text{O}_2$ , more  $\text{CO}_2$  relative to  $\text{O}_2$  is expected to dissolve in  
375 soil water, which would reduce ARQ values at higher moisture contents. However, different dissolution rates and iron

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377 oxidation do not fully explain our data as the wide variability in ARQ values (0.44 to 0.94) at high volumetric water contents  
378 (0.27 to 0.31) can be best explained by time of year (Fig. A1), which again points to phenology as the main driver; the greater  
379 ARQ values are from April and June while the lower values are from February and March. Furthermore, there was a stronger  
380 relationship between observed and predicted ARQ in the temperature model than in the soil moisture model.

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382 Experimental warming affected the relationship between ARQ and soil moisture. ARQ was greater in the heated treatment  
383 when soil moisture was high (winter) and lower in the heated treatment when soil moisture was low (growing season). Soil  
384 water sampled from lysimeters had a greater concentration of dissolved organic carbon in the warming treatment than in the  
385 control (unpublished data), which could deliver oxidized substrates to microbes during the winter rainy season.

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387 The reasons for  $\delta^{13}\text{CO}_2$  decreasing with increasing volumetric water content are not clear. Based on kinetics, we would expect  
388 that as more  $\text{CO}_2$  dissolves in water, the soil air should become enriched in  $^{13}\text{CO}_2$  because dissolution discriminates against  
389 the heavy isotope and increasingly so at lower temperatures (Zhang et al., 1995), but our data were not consistent with this  
390 explanation. Another possibility is that advective transport of atmospheric  $\text{CO}_2$  through the soil is more likely at lower soil  
391 moisture content. While intrusion of atmospheric  $\text{CO}_2$  would increase the  $\delta^{13}\text{C}$  of soil air, it reduces the effective diffusion  
392 fractionation to <4.4 %, leading to overcorrected, and thus unrealistically low  $\delta^{13}\text{C}$  values, of which we did have several.

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**Deleted:** The warming treatment caused slightly greater ARQ values (only in the winter) and slightly more enriched  $\delta^{13}\text{CO}_2$  relative to the controls; trends that are similar to those followed by ARQ and  $\delta^{13}\text{CO}_2$  with soil temperature. The warming treatment effect in terms of ARQ and  $\delta^{13}\text{CO}_2$  was relatively small (0.07 units and 0.48‰), but its effect on soil carbon flux was large. Warming increased  $\text{CO}_2$  production by 34 to 37% with about 50% of the respiration and 40% of the warming response occurring below 15 cm in the soil profile (Hicks Pries et al., 2017). ¶

393  
394 Depth was the only parameter by which ARQ and  $\delta^{13}\text{CO}_2$  did not change in concert with one another. ARQ decreased with  
395 depth while  $\delta^{13}\text{CO}_2$  increased. The decrease in ARQ with depth, which was more dramatic in the root-free soil incubations  
396 than in soil air (difference of 0.08 versus 0.03), is likely due to decreased plant inputs with fewer fine roots and less root  
397 exudation at depth (Hicks Pries et al., 2018; Tüchtmantel et al., 2017). The enrichment of soil  $\delta^{13}\text{CO}_2$  likely reflects the near-  
398 universal enrichment of soil organic carbon with depth due to catabolic carboxylation reactions (as microbial byproducts and  
399 necromass become a larger proportion of soil organic matter; Ehleringer et al., 2000; Torn et al., 2002) or the Suess effect (the  
400 continuing depletion of atmospheric  $\text{CO}_2$  over time due to the burning of fossil fuels). In our soils, there was about a 2‰  
401 enrichment in bulk soil organic  $\delta^{13}\text{C}$  with depth (Hicks Pries et al., 2018).

**Deleted:** The direction of the shift in ARQ and  $\delta^{13}\text{CO}_2$  with warming to slightly higher ARQ and more enriched  $\delta^{13}\text{CO}_2$  values indicates proportionately more respiration of relatively oxidized, labile organic substrates. In principle, the shifts in ARQ and  $\delta^{13}\text{CO}_2$  could also result from a relative increase in availability of labile organic substrates, perhaps as a result of enhanced root growth and exudation (Yin et al., 2013). Given that ARQ only differed by treatment in the winter when trees were less active, however, the former situation of preferential decomposition seems more likely. If so, this could lead to exhaustion of that pool and eventually lower warming-induced  $\text{CO}_2$  losses as seen at Harvard Forest (Melillo et al., 2002, 2017). Further measurements of  $\text{CO}_2$  production, ARQ, and  $\delta^{13}\text{CO}_2$  as warming progresses will help distinguish these cases. ¶

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## 402 5 Conclusion

403 Here we have shown, for the first time, both annual patterns in soil ARQ and how ARQ is affected by experimental warming.  
404 We inferred that seasonal patterns in ARQ were likely due to changes in the dominant substrates providing the energy for soil  
405 respiration with root-derived sugars and organic acids being the dominant substrates during the growing season and microbial  
406 necromass being the dominant substrate during the winter. These inferences of organic substrates were supported by soil  
407  $\delta^{13}\text{CO}_2$  measurements, which showed clear patterns despite our study system containing only  $\text{C}_3$  plants. We caution that direct  
408 experimental evidence of how ARQ changes with sources is needed before our inferences of substrate use can be proven.

442 [However, our data indicate](#) ARQ measurements can help to disentangle the biological sources contributing to soil respiration  
443 and to understand how sources are shifting due to global change. This application of ARQ worked well in our soils, which  
444 were well-drained, oxygenated, and lacked carbonates. The interpretation of soil ARQ values becomes more complex if those  
445 conditions are not met ([Angert et al., 2015](#)). The autotrophic and heterotrophic source separation in our incubations indicates  
446 ARQ has the potential to be used to partition soil respiration in a similar manner to natural abundance  $\delta^{13}\text{C}$  (e.g., [Dorrepaal et](#)  
447 [al., 2009](#); [Hicks Pries et al., 2013](#)). To enable further applications of ARQ, more characterization is needed of the controls of  
448 the ratio, including incubation studies of sterile and 'live' soils under aerobic and anaerobic conditions and co-located  
449 measurements of ARQ fluxes and the oxidative ratio of organic matter sources as in [Masiello et al. \(2008\)](#). Such future  
450 investigations will help determine whether ARQ deserves a prominent place alongside natural abundance isotopes in the  
451 ecosystem ecology and biogeochemistry toolkit.

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#### 452 Data Availability

453 Data ([doi:10.15485/1596312](https://doi.org/10.15485/1596312)) are publicly available on ESS-DIVE (<http://ess-dive.lbl.gov/>).

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#### 454 Author Contribution

455 CHP, AA, and MST conceived of the study. Field measurements were conducted by CHP and CC. Lab analyses were  
456 conducted by CHP and BH. Statistical analyses were conducted by CHP. CHP wrote the manuscript with feedback from all  
457 authors.

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462 their contributions to setting up the warming experiment.

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Molecule	RQ <sup>a</sup>	$\delta^{13}\text{C}$ (relative to bulk leaf) <sup>b</sup>
Organic acids	1.4 (0.97-4.2)	+0.75
Sugars	1.0	+1.5-2
Phenolics	0.95 (0.92-1.3)	NA
Proteins	0.77 (0.67-1.01)	+1
Lignin	0.88 (0.88-0.94)	-3
Lipids	0.73 (0.68-0.80)	-4

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733 <sup>a</sup>Data from Masiello et al. 2008  
734 <sup>b</sup>Data from Bowling et al. 2008

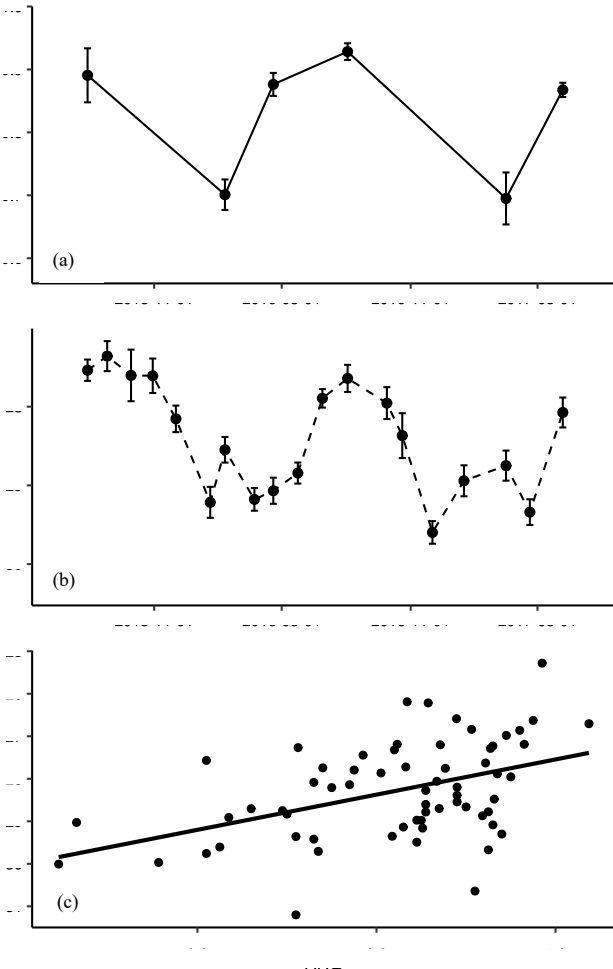
735 **Table 1. Respiration quotients (RQ; the inverse of reported oxidative ratios, which are based on elemental analyses) and relative**  
736 **isotopic enrichment of common molecules/substrates for respiration found in soils. The most common RQ value is listed followed by**  
737 **the range of potential RQ values in parentheses. The apparent respiration quotient is based on the simultaneous measurement of**  
738 **soil CO<sub>2</sub> and O<sub>2</sub>.**

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Depth (cm)	$\delta^{13}\text{CO}_2$ (‰)	ARQ
30	-29.0 ± 0.09 (191)	0.84 ± 0.02 (30)
50	-28.6 ± 0.08 (190)	
70	-28.4 ± 0.07 (191)	
90	-28.3 ± 0.08 (186)	0.81 ± 0.02 (35)

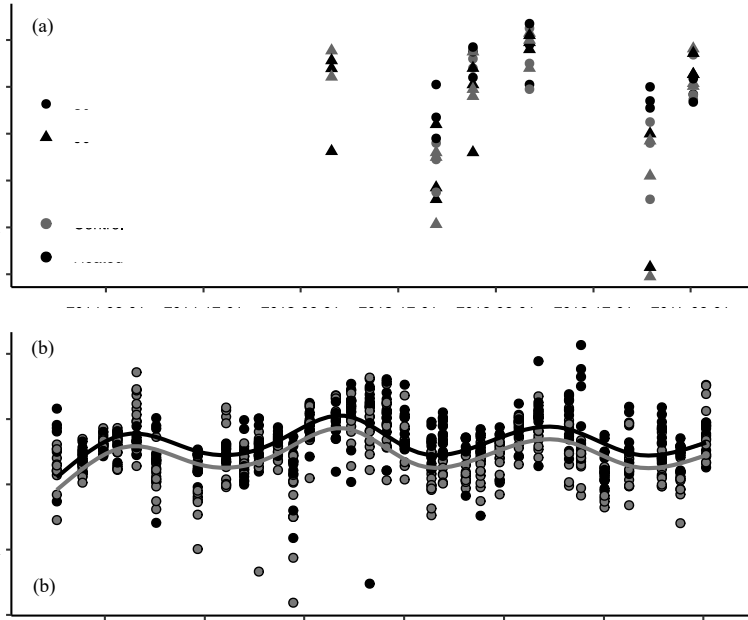
744 **Table 2. The mean ± SE (number of samples) of corrected  $\delta^{13}\text{CO}_2$  and ARQ of soil pore space by depth averaged over all timepoints.**  
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751 Figure 1. Mean ( $\pm$  SE) apparent respiration quotient (ARQ,  $n=12$  except  $n=6$  for 07/2015; a) and corrected  $\delta^{13}\text{CO}_2$  ( $n=24$  per date;  
752 b) in soil pore space air averaged across all depths and treatments by sampling month. The relationship between ARQ and  $\delta^{13}\text{CO}_2$   
753 values over the months when they were sampled simultaneously (c). The line shows the fit of a linear regression ( $p<0.0001$ ,  $n=64$ ,  
754  $R^2=0.20$ ).

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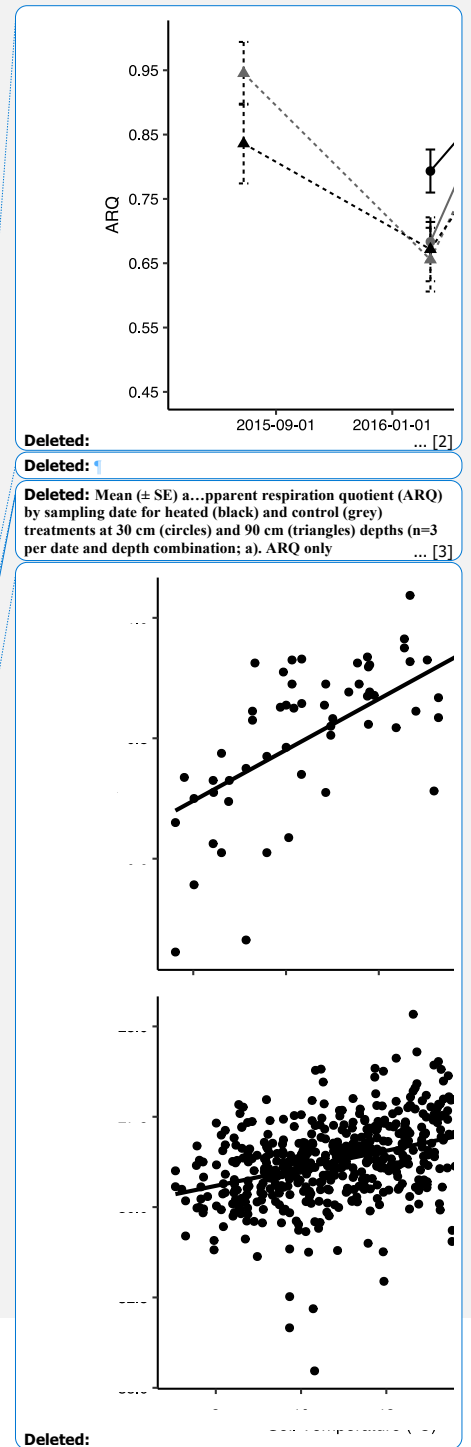
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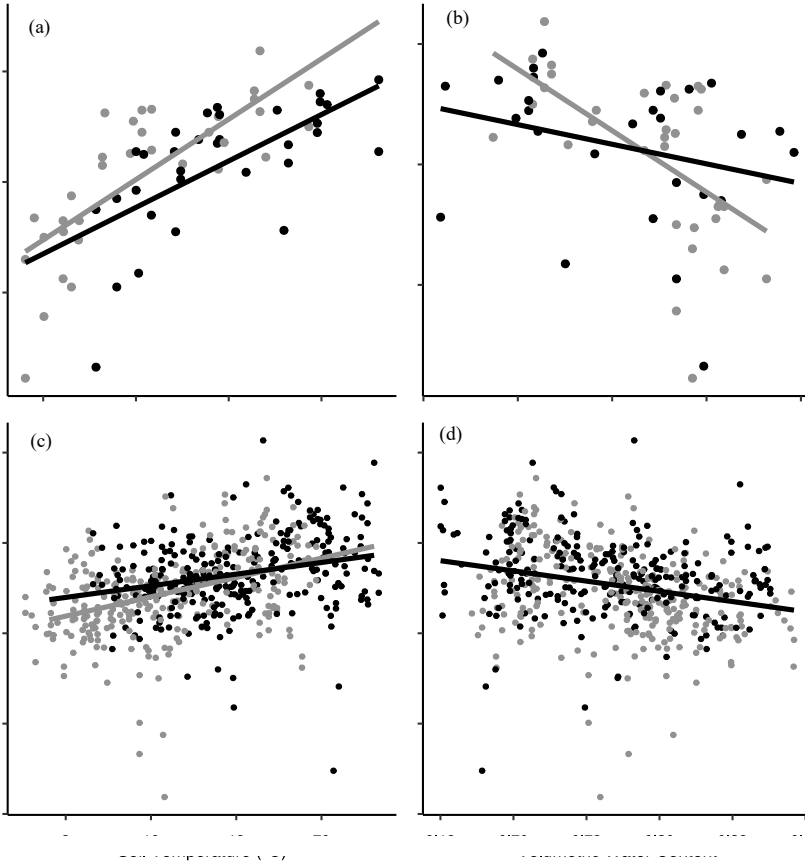


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 759 Figure 2. Apparent respiration quotient (ARQ) by sampling date for heated (black) and control (grey) treatments at 30 cm (circles)  
 760 and 90 cm (triangles) depths (n=3 per date and depth combination; a). ARQ differed significantly among treatments during the  
 761 winter at 30 cm. Corrected  $\delta^{13}\text{CO}_2$  for all depths (30, 50, 70, and 90 cm) and months sampled (b). The lines represent the predicted  
 762 fit of a sinusoidal regression (see text) for an average soil depth in control (grey) and heated (black) treatments (n=758).

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(c)





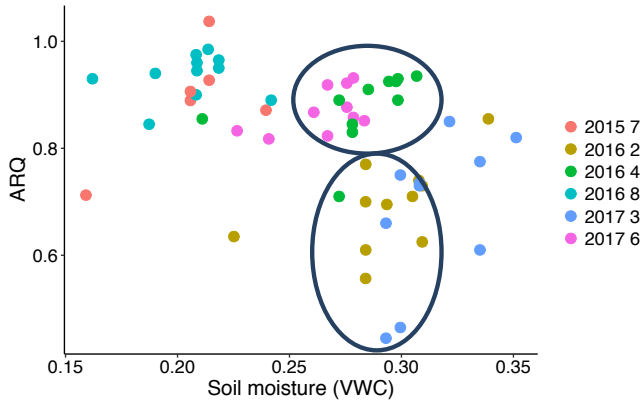
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781 Figure 3. The relationships of apparent respiration quotient (ARQ) by soil temperature (a, n=65) and soil moisture (b, n=60) and  
 782  $\delta^{13}\text{CO}_2$  by soil temperature (n=565, c) and soil moisture (n=535, d). Gray and black points represent data from control and heated  
 783 gas wells, respectively. The lines show the fit of a mixed model regression between each variable where individual gas well was  
 784 treated as a random effect. Separate grey (control) and black (heated) lines indicate there was a significant effect of warming  
 785 treatment on the relationship between the response variable and soil temperature.

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Figure A1. The variability in the apparent respiration quotient's (ARQ) relationship with soil moisture at 0.25 to 0.30 VWC can be explained by time of year. The greater ARQ values (in the top circle) are from April and June while the lower values (in the bottom circle) are from February and March. Colors are by sampling date shown as year and month.

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