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Can current moisture responses predict soil CO₂ efflux under altered precipitation regimes? A synthesis of manipulation experiments

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Abstract. As a key component of the carbon cycle, soil CO₂ efflux (SCE) is being increasingly studied to improve our mechanistic understanding of this important carbon flux. Predicting ecosystem responses to climate change often depends on extrapolation of current relationships between ecosystem processes and their climatic drivers to conditions not yet experienced by the ecosystem. This raises the question of to what extent these relationships remain unaltered beyond the current climatic window for which observations are available to constrain the relationships. Here, we evaluate whether current responses of SCE to fluctuations in soil temperature and soil water content can be used to predict SCE under altered rainfall patterns. Of the 58 experiments for which we gathered SCE data, 20 were discarded because either too few data were available or inconsistencies precluded their incorporation in the analyses. The 38 remaining experiments were used to test the hypothesis that a model parameterized with data from the control plots (using soil temperature and water content as predictor variables) could adequately predict SCE measured in the manipulated treatment. Only for 7 of these 38 experiments was this hypothesis rejected. Importantly, these were the experiments with the most reliable data sets, i.e., those providing high-frequency measurements of SCE. Regression tree analysis demonstrated that our hypothesis could be rejected only for experiments with measurement intervals of less than 11 days, and was not rejected for any of the 24 experiments with larger measurement intervals. This highlights the importance of high-frequency measurements when studying effects of altered precipitation on SCE,

probably because infrequent measurement schemes have insufficient capacity to detect shifts in the climate dependencies of SCE. Hence, the most justified answer to the question of whether current moisture responses of SCE can be extrapolated to predict SCE under altered precipitation regimes is “no” – as based on the most reliable data sets available. We strongly recommend that future experiments focus more strongly on establishing response functions across a broader range of precipitation regimes and soil moisture conditions. Such experiments should make accurate measurements of water availability, should conduct high-frequency SCE measurements, and should consider both instantaneous responses and the potential legacy effects of climate extremes. This is important, because with the novel approach presented here, we demonstrated that, at least for some ecosystems, current moisture responses could not be extrapolated to predict SCE under altered rainfall conditions.

1 Introduction

Soil respiration (SCE) is a crucial component of the terrestrial carbon cycle. Comprising about 100 Pg C yr⁻¹ (Bond-Lamberty and Thomson, 2010b), SCE represents the largest terrestrial carbon flux to the atmosphere. Furthermore, because SCE includes both autotrophic and heterotrophic components, it reflects the performance of both plants and microbes. Soil respiration depends on available substrates and, accordingly, differences in SCE across different

ecosystems have been related to photosynthetic productivity (e.g., Janssens et al., 2001; Vargas et al., 2010; Högberg et al., 2001; Bahn et al., 2008), thereby emphasizing the interdependence of microbes and plants. The two key abiotic climate-related factors that influence SCE dynamics in terrestrial ecosystems are temperature and soil moisture (Raich and Schlesinger, 1992).

Raising temperature increases metabolic reaction rates, and hence microbial and plant respiration (Larcher, 2003). The temperature response of SCE can usually be expressed as an exponential curve, such as the frequently used Arrhenius function or Q_{10} function (Davidson and Janssens, 2006). The relationship of SCE with moisture is less straightforward than that with temperature. Briefly, at suboptimal soil moisture, osmotic stress and substrate diffusion limit microbial activity (Moyano et al., 2013; Schimel et al., 2007). In addition, root respiration typically declines when soil moisture decreases below optimal levels (Heinemeyer et al., 2012; Bryla et al., 2001; Burton et al., 1998; Thorne and Frank, 2009) due to reduced root growth and ion uptake, as well as reduced maintenance costs following protein degradation, lower membrane potentials and increased root death (Huang et al., 2005; Eissenstat et al., 1999). At supra-optimum soil moisture levels, SCE decreases with increasing soil moisture, primarily because of reduced oxygen levels available to microbes (Moyano et al., 2013; Jungkunst et al., 2008; Vicca et al., 2009) and plant roots (Mäkiranta et al., 2008). In summary, the short-term response of SCE to changes in soil moisture is not monotonic; SCE increases from low to intermediate soil moisture, reaches a plateau at optimum moisture, and decreases again at high soil moisture.

1.1 Responses of soil CO₂ efflux to precipitation manipulations

Given the strong non-monotonic response of SCE to soil moisture, changes in the hydrological cycle with climate change may have a large and nonlinear impact on this carbon flux. Impacts of altered precipitation on ecosystem processes have been studied less extensively than those of warming and elevated atmospheric CO₂ concentrations (Jentsch et al., 2007), but multiple precipitation manipulation experiments have been conducted in several biomes in recent years (Beier et al., 2012). Wu et al. (2011) conducted a first meta-analysis of these experiments, reporting overall effects of altered rainfall on plant productivity and SCE. Because most of these experiments are conducted in ecosystems where water availability is at or below optimum levels, drought is generally reported to reduce SCE, whereas SCE usually increases in response to water addition (Wu et al., 2011). The non-monotonic relationship between SCE and soil moisture, however, suggests that the influence of altered rainfall patterns depends not only on the direction and magnitude of change in precipitation but also on ecosystem characteristics such as climate (wet or dry region), soil type (defining water

holding capacity), and timing of the rain or drought events (e.g., spring versus summer) (Knapp et al., 2008). Soil type strongly affects responses to drought events (Kljun et al., 2006) by determining water holding capacity and thus water availability. However, the manipulation experiments conducted to date have rarely provided the necessary data (e.g., soil water potential) for estimation of available soil water to plants and microbes (Vicca et al., 2012a), which considerably hampers our ability to characterize global patterns of ecosystem responses to altered precipitation regimes.

1.2 Extrapolation to different climate scenarios

Because model projections of future climate are highly sensitive to the assumed response of SCE to changes in its abiotic drivers (Friedlingstein et al., 2006; Wieder et al., 2013), a current challenge for ecologists is to test whether existing relationships between SCE and soil water content (SWC) can be extrapolated to predict future ecosystem–atmosphere feedbacks. Soil respiration has been measured in many observational studies, and data were recently collated into a global database (Bond-Lamberty and Thomson, 2010a). Such large data sets have great potential for improving our understanding of terrestrial carbon cycling and for improving Earth system models. Nonetheless, it remains unclear to what extent current-climate observations are actually suitable for predicting future patterns of SCE, given that rainfall patterns are expected to change in the future. Extreme events such as severe heat waves and droughts are expected to increase in intensity and periodicity. Although current model projections of climate extremes remain uncertain (with contradicting results from different models), consensus is growing that, for example, the number of consecutive dry days will increase in the drier temperate regions (Orlowsky and Seneviratne, 2012; Seneviratne et al., 2012). In the Mediterranean region, longer dry spells and more intense precipitation events are very likely (Seneviratne et al., 2012).

Altered precipitation patterns, and extreme drought and rainfall events in particular, may cause structural changes in the ecosystem (for a detailed overview, see van der Molen et al., 2011). For example, changes in precipitation patterns can decrease microbial biomass and alter microbial community composition (Curiel Yuste et al., 2012; Jentsch et al., 2011; Sanaullah et al., 2011; Tian et al., 2012) as well as soil structure (Sowerby et al., 2008) and vegetation structure (e.g., root-to-shoot ratio) and composition (De Dato et al., 2008; Morecroft et al., 2004). Extreme drought events can also affect soil water availability and nutrient retention via increases in soil hydrophobicity (Bloor and Bardgett, 2012; Goebel et al., 2011; Muhr et al., 2010). Such structural changes can alter SCE in a way that may not be predictable from current-climate observations. Moreover, the relationships between SCE and soil moisture could change, or show large time lags in response to rewetting (Joos et al., 2010), rendering

relationships based on current-climate observations invalid for predictions of SCE under altered precipitation regimes.

We use the most comprehensive data set of ecosystem precipitation manipulation experiments currently available to explore whether response functions for SCE established under ambient conditions are useful for explaining variation in SCE under altered precipitation regimes. Specifically, for each experiment, we tested the hypothesis (H1) that the soil moisture response of SCE as observed from fluctuations over time in the control plots can be extrapolated to predict SCE in plots exposed to a different precipitation regime. Testing this hypothesis is important because ecosystem models usually use functions dependent on soil moisture to predict SCE under current and future climate scenarios. Rejection of H1 would suggest that the manipulation of precipitation altered the relationship of SCE with soil moisture. We further examined the vegetation types, climate zones, soil types and manipulation regimes for which H1 was and was not rejected. Finally, for the experiments where H1 was rejected, we tested whether rejection of our hypothesis was caused by SWC in manipulated treatments exceeding the range of SWC encountered in the control plots, or whether this rejection more likely resulted from structural changes within the ecosystem. Based on the above-mentioned mechanisms, we expect H1 to be rejected, not only when SWC in the treatment exceeds SWC in the control but also after SWC recovered but other ecosystem properties did not.

2 Methods

2.1 Data collection and analysis

We gathered information from single-factor field experiments in which precipitation was altered, and where SCE, ST and SWC were measured in both control and treatment plots (further referred to as SCE_{control} and SCE_{treatment}, SWC_{control} and SWC_{treatment}). Whenever available, we collected high-frequency data (i.e., daily values; if hourly measurements were available, these were averaged to obtain daily values) of SCE, soil temperature (ST) and SWC. In the majority of the experiments, however, the measurement interval for SCE was larger than a day. Detailed information for all manipulation experiments and the SCE data used in this study is given in Appendix Tables A1, B1 and C1; species composition for each site is provided in Supplement Table S1. The timing of measurements and manipulation for all experiments is shown in Figs. S1 and S2. The individual responsible for data availability in each experiment, along with contact details, is provided in Supplement Table S2. An overview of the average change in annual precipitation and the direction of the manipulation effect on SCE is presented in Fig. 1, for which differences in SCE between control and treatment were analyzed using repeated measures ANOVA, with measurement day as the within-subject factor.

In order to test whether the moisture response of SCE as observed in the control plots can be used to predict SCE under altered rainfall patterns, we followed the protocol presented in Fig. 2. We first tested which of four models best fitted SCE_{control}. These models take into account SWC as well as ST, because the latter is an important driver of fluctuation in SCE over time. Soil temperatures hardly differed between control and treatment plots (data not shown). For this and further analyses, experiments with no more than 10 data points were discarded. The four models (which have been used previously, see, for example, Curiel Yuste et al., 2003; Kopittke et al., 2013) were

$$\log(\text{SR}) = a + b\text{ST} + c\text{SWC}, \quad (1)$$

$$\log(\text{SR}) = a + b\text{ST} + \log(c + d\text{SWC}), \quad (2)$$

$$\log(\text{SR}) = a + b\text{ST} + \log(c + d\text{SWC} + e\text{SWC}^2), \quad (3)$$

$$\log(\text{SR}) = a + b\text{ST} + c\text{SWC} + d\text{SWC}^2. \quad (4)$$

These four models all reflect an exponential relationship between SCE and ST; the relationship between log(SCE) and SWC is linear, quadratic, exponential linear and exponential quadratic for models 1, 2, 3 and 4, respectively. The first two models characterize soil moisture response as a monotonic function (increasing when d is positive), whereas models 3 and 4 allow non-monotonic responses. Model coefficients and goodness-of-fit parameters for all sites and models are presented in Supplement Tables S3 and S4.

Model selection was based on the second-order Akaike information criterion (AICc). Across all sites, model 4 showed a significantly lower AICc than all other models (Wilcoxon sign rank test, $p < 0.05$). Therefore, we opted to use model 4 for all subsequent analyses. However, residuals were not normally distributed for seven experiments, which were therefore discarded from the subsequent analyses (note that for these experiments the normal distribution criterion was usually not met for any of the other three models either). Arguably, we could have opted for the best of the four models for a given experiment instead of the best model across experiments. We opted for the latter to avoid possible artifacts related to using different models for different sites. Moreover, results were similar when using models 1–3 (but fewer sites were eligible for the tests, data not shown).

We parameterized model 4 for each of the 45 remaining experiments using the control data, and used the resulting model coefficients specific to each site to test whether SCE_{treatment} could be predicted. Subsequently, these results were used to test our hypothesis that the moisture response of SCE as observed in the control plots can be extrapolated to predict SCE_{treatment}. We set forward two criteria indicative for goodness of extrapolation from control conditions to treatment conditions:

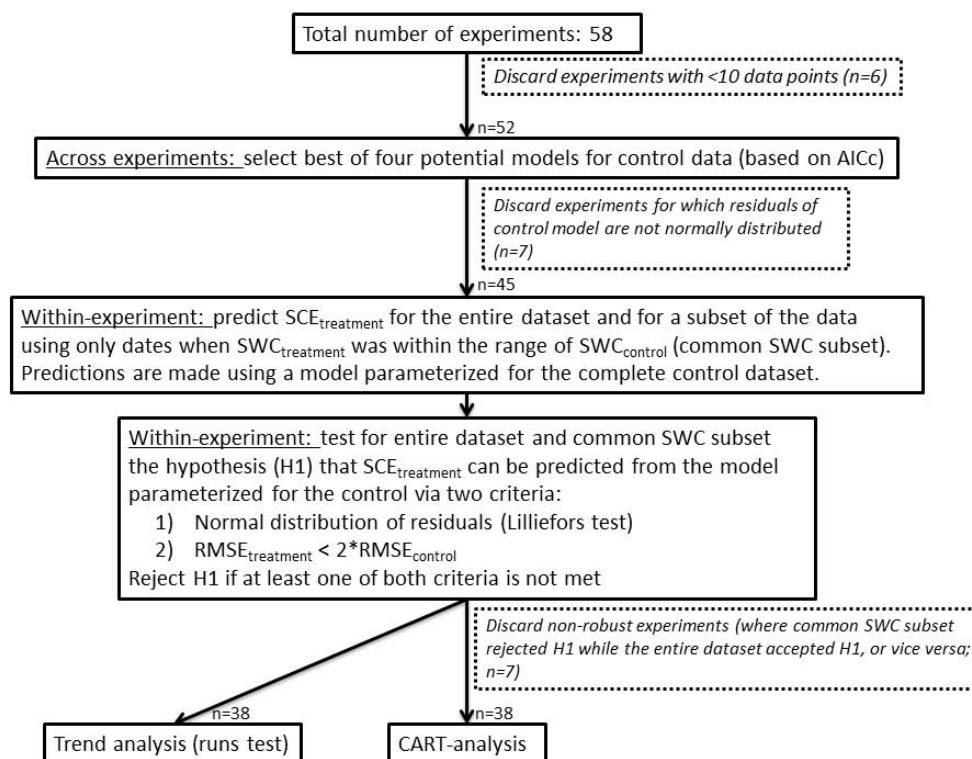


Figure 1. (a) Overview of the magnitude and direction of precipitation effect on soil CO₂ efflux (SCE) for the different experiments. Arrows point from control precipitation to treatment precipitation (averaged over different years in case of multi-year data). Crosses localize control conditions in terms of annual precipitation and mean annual temperature (MAT). Black arrows indicate a positive correlation between precipitation manipulation and SCE, i.e., an increase of SCE when precipitation increases, or a decrease of SCE when precipitation is reduced. Gray arrows indicate negative correlations (which could be considered to reflect somewhat unexpected results). Bold arrows represent significant differences between SCE treatment and SCE control ($p < 0.05$), while thin arrows reflect non-significant differences (repeated measures ANOVA). Panel (b) shows the biomes that are represented by our data set (biome figure adapted from Chapin et al., 2002).

1. The difference between SCE_{treatment} predicted by the control model (further termed “predicted SCE_{treatment}”) and observed SCE_{treatment} followed a normal distribution (Lilliefors test).
2. The root-mean-square error (RMSE) for predicted SCE_{treatment} was less than double the RMSE for predicted SCE_{control}. This second criterion is critical, because it indicates the goodness of fit to SCE_{treatment}, taking into account the performance of the control model. Because no generally accepted threshold for accurate data–model agreement exists, we opted for a stringent threshold where $RMSE_{treatment} < 2RMSE_{control}$, which in our case was exceeded in only a few sites (Appendix Table C1). Visual inspection of the figures for predicted versus measured values (Fig. S3) and the residuals (Fig. S1) indicated that this criterion was justified for rejecting H1.

When both conditions were fulfilled, the prediction of SCE_{treatment} was considered reasonable and H1 was not rejected. It was rejected when at least one of both criteria was not met.

Rejection of H1 may have resulted from structural changes in the ecosystem, or may merely reflect erroneous extrapolation beyond the range of the conditions observed in the control. To test whether such erroneous extrapolation was responsible for rejection of H1, we performed the two tests for H1 also on a subset of the data, using only dates when SWC_{treatment} was within the range of SWC_{control} (further simply referred to as “common SWC subset”). We consider the results robust when the outcomes of the analysis for the entire data set and for the common SWC subset agree and potential rejection of H1 is unlikely due to extrapolation. Only for such robust sites were subsequent analyses performed.

We used classification and regression tree (CART) analysis to investigate whether rejection of H1 was related to site or experimental characteristics. For this analysis, we included only the robust experiments ($n = 38$; see also Fig. 2). Predictor variables used in the CART analysis were vegetation type (grassland, forest, shrubland or agricultural land), hydrology (xeric, mesic or hydric – classification based on Köppen climate classification; see also Appendix A), percentage clay in the soil, mean annual precipitation

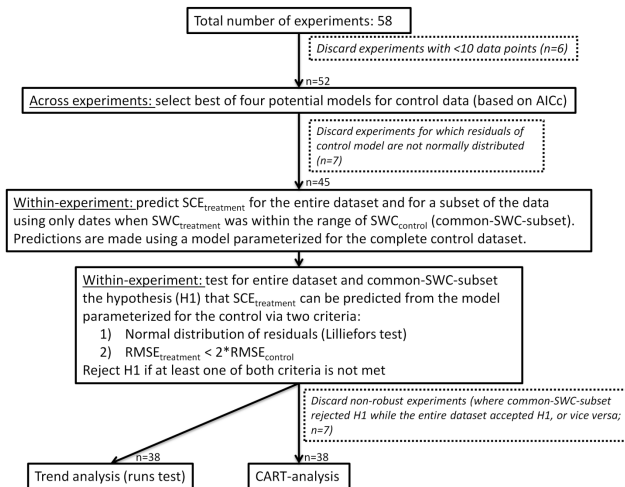


Figure 2. Protocol of the analyses performed to test the hypothesis (H1) that the moisture response of soil CO₂ efflux as observed in the control plots (SCE_{control}) can be used to predict soil CO₂ efflux in the precipitation manipulation treatment (SCE_{treatment}). The number of sites for each step and the reasons for discarding experiments from further analyses are displayed.

(MAP), mean annual temperature (MAT), an aridity index (MAP/2MAT), treatment manipulation type (drought or irrigation experiment or altered precipitation pattern without a change in total precipitation) and manipulation technique (roofs, shelters, retractable curtains, troughs or irrigation), treatment manipulation duration (continuous manipulation, episodic manipulation or altered pattern during the entire experiment), number of years of experimental manipulation, and the percentage of measurement days for which SWC_{treatment} was either above or below the natural boundaries of SWC_{control} (i.e., an indication of potentially erroneous extrapolations beyond the range for which the model was parameterized). We further included as predictor variables the total number of SCE measurements (N), the median of the measurement interval (I, number of days), and N/I (which is low for sites with few and/or infrequent measurements; highest N/I is obtained for experiments with daily SCE measurements). As several experimental sites were represented by more than one experiment, we weighted the CART analysis by the inverse of the number of experiments per site. For example, the Sevilleta experiment consisted of two different irrigation experiments, and therefore each experiment was weighted by 0.5 (Appendix Table C1).

To further analyze the possible cause for the failure of the control model to predict SCE_{treatment}, we examined the course of a predictability index over time, which was calculated for each measurement day as

$$Pi = \frac{|\text{predicted } SCE_{control} - \text{observed } SCE_{control}|}{|\text{predicted } SCE_{treatment} - \text{observed } SCE_{treatment}|} \quad (5)$$

where predicted SCE_{control} and predicted SCE_{treatment} are both calculated using model 4 (see above) and parameterized using the control data. Hence, Pi indicates the predictability of SCE_{treatment}, but taking into account the predictions of SCE_{control} at the same moment in time. Values of Pi around zero indicate that the model parameterized for the control performs similarly for control and treatment, while negative values indicate that the prediction of the treatment is worse than that of the control (and vice versa for positive values). For the current analysis, we are particularly interested in the change of Pi over time. If Pi shows a trend towards increasingly negative values over time, then the predictability of SCE_{treatment} becomes progressively worse. To test whether there was a significant trend in Pi (e.g., a decrease of Pi over time, or during part of the measurement period) we performed the runs test (non-parametric trend analysis), dichotomized around the median (Davis, 2002). This test checks the randomness of sequences. It creates “runs”, defined as uninterrupted sequences of the same state (in this case either above or below the median), and then tests whether the number of runs is significantly different from what would be expected if they were randomly drawn from the same distribution. The runs test is thus not affected by the increased serial dependence of data with increasing measurement frequency, which is important because our study includes experiments with different measurement frequencies.

2.2 Test for artifacts related to SWC measurements

Given that measurements of SWC can be incorrect when, for example, the soil dries out and the contact between sensor and soil is interrupted, or when they do not reflect available water at all depths relevant for SCE, we needed to test the robustness of the results found for Pi. To this end, we used a simple bucket model (extracted from the Rothamsted C-cycling model; Coleman and Jenkinson, 1996) to simulate water availability in the main rooting zone independently of SWC measurements. Input parameters of this model are precipitation, potential evapotranspiration, percentage of clay and main rooting zone. Potential evapotranspiration estimates were obtained via the Priestley–Taylor model, which is based on net incoming radiation (NIR), saturation vapor pressure and air temperature (Priestley and Taylor, 1972). Quantification of NIR was based on downward shortwave radiation, albedo and outgoing longwave radiation. Downward shortwave radiation was obtained via reanalysis of bias-corrected data of WATCH (ERA40; see Weedon et al., 2011) and BC_ERAinterim (ERA Interim; see Piani et al., 2010). Albedo was derived from MODIS MCD43C3.005, assuming a mean seasonal distribution. The outgoing longwave radiation was derived as a fraction of the daily temperature difference scaled by the fraction of actual vapor pressure and the ratio of downward shortwave radiation and potential shortwave radiation.

The estimate of water availability obtained from the bucket model was then used to perform analyses analogous to those described above: coefficient estimates from a control model (in model 4, SWC was replaced by the water availability estimate from the bucket model, while ST did not change) were used to predict $SCE_{\text{treatment}}$ at each measurement date. Subsequently, we tested H1 and estimated P_i , which was further analyzed for trends via the runs test. More details about this analysis based on the bucket model estimates of water availability are given in the supporting information.

All analyses were performed using Matlab (2012b, The Mathworks Inc., Natick, MA). A comprehensive list of the abbreviations used in this study is provided in Table D1.

3 Results

3.1 General response of soil CO_2 efflux to precipitation manipulation

Our data set covers different climate regions and biomes (Fig. 1 and Appendix Table A1), but the temperate zone is clearly dominant. Few experiments were conducted in the tropics ($n = 3$), and we found no precipitation manipulation experiments with SCE measurements for the boreal zone. Forests, grasslands and shrublands are all well represented, but agricultural fields are not (only one site, with three experiments – Hohenheim; Appendix Table A1), and hydric sites are also represented by only one site (Clocaenog). Overall, decreased precipitation reduced SCE, whereas enhanced precipitation increased SCE (Fig. 1), although for six experiments, we found a significant response of SCE in the opposite direction. Four of these were drought experiments (Clocaenog, Solling, Tolfa and WalkerBranch_Dry; Appendix Table B1), one was an irrigation experiment (Boston_wet) and one was an experiment where only the precipitation pattern was altered, with little effect on total precipitation (RaMPsAlt; the manipulation slightly increased total rainfall, and decreased total SCE; Appendix Table B1).

3.2 Across-experiment variation in predictability of soil CO_2 efflux

We tested the goodness of the prediction of $SCE_{\text{treatment}}$ on the entire data set for each site, as well as on the common SWC subset (i.e., excluding dates for which $SWC_{\text{treatment}}$ was outside the range of SWC_{control}). For this, we started from the 45 experiments where the control model was of sufficient quality (see protocol in Fig. 2). For 38 of these 45 experiments subjected to this analysis, both tests gave the same outcome and results are considered robust (Appendix Table C1, column “Robust?”). These sites showed both over- and underestimations of $SCE_{\text{treatment}}$ (Fig. 3a and Appendix Table B1). Across all sites, using the common SWC subset instead of the entire data set had a minor effect on the difference between predicted and observed $SCE_{\text{treatment}}$ (Fig. 3c

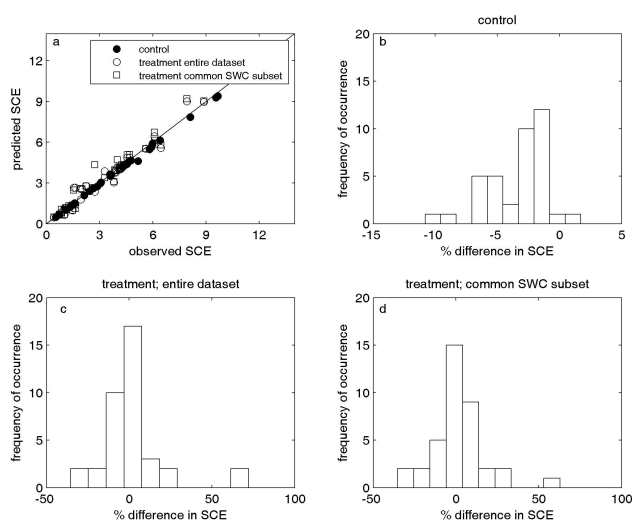


Figure 3. (a) Predicted soil CO_2 efflux (SCE , $\mu\text{mol } CO_2 \text{ m}^{-2} \text{ s}^{-1}$) versus observed SCE for control, for the treatment when using the entire data set, and for the treatment when using the common SWC subset. Predictions of treatment SCE were based on the model parameterized for the control. (b–d) Histograms showing the frequency of occurrence for the percentage difference between observed and predicted for control, for the treatment when using the entire data set and for the treatment when using the common SWC subset. The percentage difference was calculated as $100 \cdot (\text{average predicted} - \text{average observed}) / \text{average observed}$. For details, see Appendix Table C1.

and 3d), although for some sites, this reduction was substantial (see Appendix Table B1).

For the 38 experiments for which both the entire data set and the common SWC subset gave the same result (i.e., the experiments with robust results), H1 was rejected in only seven, while we could not reject the hypothesis for the remaining 31 experiments (Appendix Table C1). The seven experiments for which H1 was rejected represent six independent sites (one site was represented by two experiments, Appendix Table C1). The 31 experiments for which H1 could not be rejected represented 14 different sites (Appendix Table C1).

To test whether artifacts related to SWC measurements were responsible for rejecting H1, we replaced SWC in model 4 with the bucket model results. This exercise provided results of acceptable quality (i.e., normal distribution of the residuals and an $R^2 \geq 0.30$; see SI) for only 16 of the 45 experiments, indicating the limitations of this approach. Nonetheless, for 14 of these 16 experiments, the outcome of the bucket model approach agreed with the results of the SWC approach. Importantly, rejection of H1 was confirmed for three of the seven experiments (i.e., for Solling, Stubai and TurkeyPoint; Supplement Table S5). For the other four experiments where H1 was rejected using the SWC approach, the low quality of the fits based on the bucket model

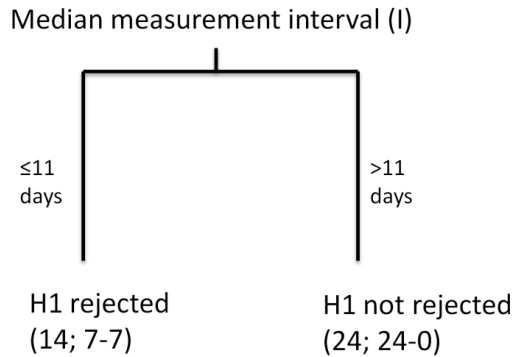


Figure 4. Classification and regression tree (CART) showing for which groups of experiments our hypothesis (H1: the moisture response of soil CO₂ efflux (SCE) as observed in the controls can be used to predict SCE in the treatment) could and could not be rejected. This CART analysis included as a weight factor the reciprocal of the number of experiments per site to take into account their interdependence. The key predictor variable (the median measurement interval) is depicted at the top, and predictor variable thresholds are at the side of each branch. Below the terminal nodes, the values between brackets display: total number of experiments; number of experiments for which H1 was not rejected - number of experiments for which H1 was rejected. A list of all predictor variables included in the CART-analysis is given in the Methods section. This analysis used the 38 experiments for which results from the entire dataset and the common SWC subset agreed (i.e., robust results).

approach did not allow for this test. In any case, the bucket model approach indicates that artifacts related to SWC measurements are unlikely responsible for rejecting H1.

The CART analysis – which accounts for the dependence of results from different experiments within a single site (Appendix Table C1) – indicated measurement frequency as the key predictor variable of whether or not H1 could be rejected. For experiments with median measurement intervals of SCE larger than 11 days, H1 was never rejected (Fig. 4), whereas H1 was rejected for 7 of the 14 experiments with intervals ≤ 11 days, which included all 5 experiments with daily measurements (Appendix Table C1). The CART analysis did not identify other predictive variables or thresholds.

3.3 Within-experiment variability in predictability of soil CO₂ efflux

A trend analysis of the predictability of SCE_{treatment} (Pi) was made for the 38 experiments for which both the entire data set and the common SWC subset gave the same result (i.e., those indicated as robust in Appendix Table C1). When Pi varies around zero, predictions of SCE_{treatment} are comparable to predictions of SCE_{control}. Negative values indicate that the prediction of SCE_{treatment} was worse than that of SCE_{control} (and vice versa for positive values – but these were less abundant and always close to zero for all sites, Supplement Fig. S2). Significant trends in Pi reveal that model per-

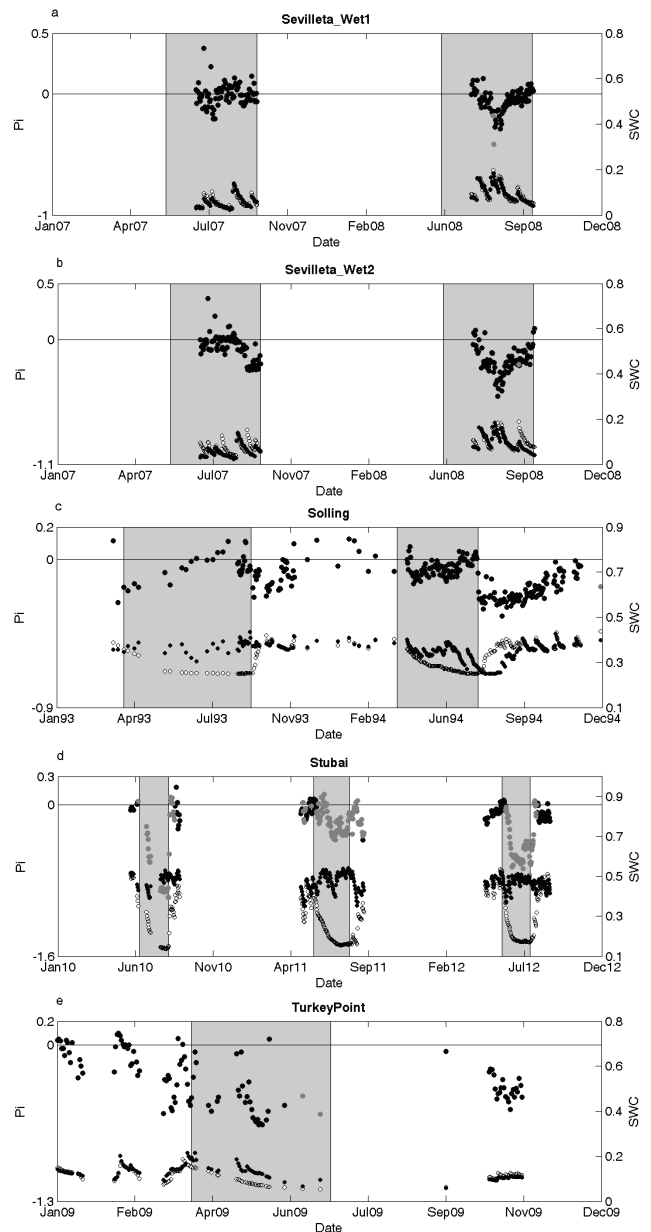


Figure 5. Time course of Pi (predictability index, large black and gray circles) for the five experiments for which our hypothesis was rejected and for which a significant trend was detected: (a) Sevilleta_Wet1, (b) Sevilleta_Wet2, (c) Solling, (d) Stubai and (e) TurkeyPoint. Pi values close to zero indicate that SCE_{treatment} was predicted similarly well compared to SCE_{control}, whereas values substantially below or above zero indicate the difference in predictability of SCE_{treatment} relative to SCE_{control}. Negative values indicate that the prediction of SCE_{treatment} was worse than that of SCE_{control}, and vice versa for positive values. Large gray circles indicate when SWC_{treatment} was outside the range of SWC_{control}. Small black and white circles represent the soil water content (SWC) for control and treatment plots, respectively. Gray areas indicate the time when water inputs were manipulated.

formance varied over time and thus suggest that the model parameterized for the control plots cannot reliably capture the variation in $SCE_{\text{treatment}}$. Whereas we detected a trend in Pi for only 1 of the 31 experiments for which H1 was not rejected (SulawesiForest; see Supplement Fig. S3 for a visual representation), we found a significant trend in the time course of Pi for five of the seven experiments for which H1 was rejected (Appendix Table C1). These five experiments were those with daily measurements of SCE. The time series of Pi for these five experiments is displayed in Fig. 5. For all other experiments, the course of Pi over time is shown in Supplement Fig. S2. Here we briefly describe the patterns observed for the five experiments for which H1 was rejected and revealed a trend in Pi (i.e., the five experiments with daily measurements of SCE). These patterns can expose the underlying reasons for rejecting H1.

The Sevilleta experiment, which consisted of two different irrigation treatments in a desert grassland, showed little effect on Pi in the first year, while a marked decrease in Pi occurred in the second year (Fig. 5a, b), particularly for the treatment plots receiving the more intense rainfall events (Sevilleta_Wet2). Here, Pi values remained below zero over two months, even though SWC was very similar in control and treatment (Fig. 5b). Such erroneous predictions of $SCE_{\text{treatment}}$ would, in the case of Sevilleta_Wet2, lead to ca. 35 % underestimation of SCE over the entire measurement period (Appendix Table B1).

Likewise for Solling, despite $SWC_{\text{treatment}}$ remaining mostly within the range of SWC_{control} (Fig. 5c), Pi remained below zero during part of the experiment. Of particular interest is the decline of Pi upon rewetting, which occurred in both treatment years and reflects an increase of $SCE_{\text{treatment}}$ (see Fig. S1). Recovery of Pi took about four months in the second treatment year, but insufficient data were available to really test for the duration of recovery. Nonetheless, estimations of $SCE_{\text{treatment}}$ based on the control model would underestimate $SCE_{\text{treatment}}$ by 33 % over the entire experimental period (Appendix Table B1).

In contrast, in Stubai, the number of measurements was substantially reduced when selecting only the dates when $SWC_{\text{treatment}}$ was within the range of SWC_{control} ($n = 103$, which is exactly one-third of the total number of data, Fig. 5d). Nonetheless, H1 was rejected also when only the common SWC subset of measurements was used (Appendix Table C1). Pi remained below zero even when $SWC_{\text{treatment}}$ had recovered after the manipulation had ended. Moreover, Pi remained negative just before the initiation of the manipulation in 2012 and across the three treatment years; this would result in an overestimation of SCE by 25 % when considering only the common SWC subset (Appendix Table B1).

At the TurkeyPoint site, Pi started declining before the onset of the manipulation (Fig. 5e). This caused difficulty in distinguishing the effects of the manipulation from pre-treatment differences. Nonetheless, analysis of the residuals revealed that the difference between SCE_{control}

and $SCE_{\text{treatment}}$ shifted after the manipulation had ended (Fig. S1); whereas residuals for $SCE_{\text{treatment}}$ were consistently lower than residuals for SCE_{control} before and during the manipulation, the opposite was true for all measurement dates after the manipulation period. This suggests that the manipulation induced substantial changes in the ecosystem. Over the entire data set, estimations of $SCE_{\text{treatment}}$ based on the control model would overestimate $SCE_{\text{treatment}}$ by 72 % (Appendix Table B1).

4 Discussion

4.1 General response of soil CO₂ efflux to precipitation manipulation

Precipitation manipulation experiments have been conducted mainly in the temperate zone, as shown in this study (with all but three experiments in temperate and subtropical regions) and in a general review by Beier et al. (2012). Particularly underrepresented in our study were the tropics and the boreal zone. Hence, it would be important to promote research in these regions for improving our global understanding of SCE responses to altered precipitation regimes. Also experiments in agricultural fields and on hydric soils are underrepresented in our data set, with only one site for each (Appendix Table A1). Forests, grasslands and shrublands in temperate and subtropical regions are all well represented in our data set.

In agreement with Wu et al. (2011), decreased precipitation typically reduced SCE, whereas enhanced precipitation increased SCE (Fig. 1). However, some responses did not fit this pattern (Fig. 1). One reason why a reduction in rainfall could stimulate SCE is related to the non-monotonic response of SCE to moisture. This is especially likely for the only hydric experiment in our data set, i.e., Clocaenog. This experiment showed a persistent increase in SCE following precipitation reduction (Sowerby et al., 2008), which is in line with the general observation of moisture responses of SCE in wetland ecosystems (Jungkunst and Fiedler, 2007). In addition, soil rewetting after a drought event can substantially increase SCE and lead to higher SCE at the annual scale in the treatment compared to the control (Borken et al., 1999). This was obviously the case in Solling (see below for more details).

4.2 Across-experiment variation in predictability of soil CO₂ efflux

The CART analysis indicated that sampling frequency was an overriding factor determining whether or not H1 was rejected. The higher the measurement frequency, the more likely H1 was rejected, and in all five experiments where SCE was measured daily, $SCE_{\text{treatment}}$ could obviously not be predicted from SCE_{control} . Indeed, even when avoiding extrapolation beyond the range for which the model was parameterized, H1 was rejected for these experiments. Measurement

frequency was thus crucial for detecting whether or not $SCE_{\text{treatment}}$ could be predicted from the ST-SWC relationship fitted to SCE_{control} . This result suggests that we may have missed important $SCE_{\text{treatment}}$ responses in experiments with larger measurement intervals. Infrequent measurement schemes have insufficient capacity to detect shifts in the climate dependencies of SCE, which implies that type 2 errors (i.e., failure to reject H1) for these experiments are probable, and this is an important call for the scientific community to revisit studies with discrete measurements. Our results emphasize the need for high-frequency SCE measurements to fully capture the fast response of SCE to changes in precipitation and other climatic variables such as temperature at multiple temporal scales (Vargas et al. 2012).

Nonetheless, of the 14 experiments with a measurement frequency < 11 days (i.e., the threshold resulting from the CART analysis), H1 could not be rejected for seven. These experiments represent in fact only four different sites (Duolun40, Duolun60, HarvardForest, Hohenheim_LA, Hohenheim_LF, RaMPs_Dry and RaMPs_DryAlt; see Appendix Table C1), and it is possible for these sites that the criteria set for rejecting H1 were too stringent. The difference in RMSE was particularly high for HarvardForest (1.72, Appendix Table C1), and it is plausible that a more complete data set (i.e., more frequent measures) would have given a different outcome (see also Supplement Fig. S2). On the other hand, experimental duration was rather short for (i) the two experiments of the Mongolian Duolun grassland site, for which SCE was measured weekly, but only for about six months (Supplement Fig. S2), and (ii) for the experiments in Hohenheim, where SCE was measured for ca. 10 months, precluding firm conclusions. Alternatively, not rejecting H1 for some experiments that provided frequent measures of SCE may reflect real variability in the potential for predicting $SCE_{\text{treatment}}$ from relations found for the control. The RaMPs experiment illustrates that in some cases, predicting $SCE_{\text{treatment}}$ from SCE_{control} could be possible. This experiment covered four manipulation years, during which SCE was measured at ca. 5-day intervals during the growing season (Appendix Table C1). The fact that H1 could not be rejected and no trend was observed for the two experiments of this site is consistent with the study by Fay et al. (2011). They reported that interannual rainfall variability was more of a determinant for most ecosystem processes studied at the RaMPs site than the manipulations applied. Hence, the experimental manipulation seems not to have pushed the system beyond a threshold that would have yielded different responses of $SCE_{\text{treatment}}$. Whether this is related to the resilience of the ecosystem, or to the manipulation applied, remains to be tested and is an important discussion pertinent for other and future experiments.

4.3 Within-experiment variability in predictability of soil CO₂ efflux

We examined in more detail the predictability index of $SCE_{\text{treatment}}$ for experiments with daily SCE measurements. This detailed analysis allows for detecting patterns and unraveling mechanisms that may remain unseen when studying only seasonal or annual totals. In our study, this analysis revealed various patterns for the five experiments providing daily SCE measurements, i.e., the experiments with the most reliable data sets. These are discussed in the following paragraphs to illustrate that various mechanisms can make the current moisture responses of SCE inappropriate for extrapolation to a future precipitation pattern, and to indicate which measurements are important to be obtained in future experiments if we are to understand the response of SCE to altered precipitation.

In the Sevilleta experiment, $SCE_{\text{treatment}}$ was equally well predicted as SCE_{control} (no marked change in Pi) in the first year. In the second year and particularly for treatment plots receiving the most intense irrigation (Sevilleta_Wet2), Pi decreased strongly. The results from this site indicate that rainfall intensity is an important factor determining variation in SCE. Vargas et al. (2012) attributed the observed increase in SCE in irrigated plots to an enhancement of the autotrophic component of SCE. This example thus illustrates that if we are to understand the mechanisms driving moisture responses of SCE, measurements of the autotrophic and heterotrophic components of SCE are required. These data are not currently available for any the experiments presented in this review.

For the Sevilleta experiment, Thomey et al. (2011) further indicated the importance of moisture in deep soil layers, which was replenished only when applying the most intense precipitation manipulation (one 20 mm rain event per month, Sevilleta_Wet2 in the current study), but not as much by more frequent but less intense rain events (four 5 mm rain events per month, Sevilleta_Wet1 in the current study). This finding emphasizes the need for precipitation experiments to measure SWC over the entire rooting zone, and not only topsoil SWC (as is typically the case; see Vicca et al., 2012a, for a discussion on this topic). Mechanistic understanding of such effects could be further improved by also measuring predawn leaf water potential, which indicates the stress level as experienced by the plants (Vicca et al., 2012a).

For the Solling experiment, Pi decreased markedly upon rewetting. The Pi decrease was due to suddenly higher observed $SCE_{\text{treatment}}$ than predicted (see residuals in Fig. S1), which reflects a pulse of SCE often observed following soil rewetting after drought events, known as the Birch effect (Birch, 1958). The Birch effect is thought to be caused by osmolyte disposal by microbes and rapid decomposition of cells that did not survive the drought or rewetting event (Birch, 1958; Jarvis et al., 2007; Schimel et al., 2007). Furthermore, when drying and wetting cycles become more pronounced, previously protected organic matter can be revealed

through reduced aggregate stability (Borken and Matzner, 2009; Deneff et al., 2001). In the case of Solling, the increase of SCE after rewetting more than compensated for reductions in SCE during the dry period (Appendix Table B1; see Borken et al., 1999, for details about SCE in the Solling experiment). Although such overcompensation for drought-related decreases of SCE after rewetting is not a universal phenomenon (Borken and Matzner, 2009), Birch effects are commonly observed in various ecosystems (Kim et al., 2012; Inglima et al., 2009; Jarvis et al., 2007), but are not usually accounted for by models. To improve our understanding of the Birch effect, and because it is supposed to be a primarily microbially mediated phenomenon, we again stress that it is necessary to separate heterotrophic from autotrophic respiration in future SCE monitoring experiments.

At the Stubai grassland site, Pi decreased sharply over the course of several drought manipulations performed in consecutive years. Pi broadly followed the course of $SWC_{\text{treatment}}$, but was mostly outside the range of SWC_{control} . In contrast to Solling, Pi returned rapidly to high values after rewetting, despite a noticeable Birch effect (Fig. S1), and appeared to be mostly determined by SWC. Nonetheless, when excluding the dates when SWC_{control} was outside the range of $SWC_{\text{treatment}}$, H1 was still rejected (Appendix Table C1) and Pi remained below zero after the precipitation manipulation, (especially after the 2012 manipulation, Fig. 5), resulting in a substantial overestimation (25 %) of $SCE_{\text{treatment}}$ when using the common SWC subset (Appendix Table B1). This indicates that SCE did not fully recover after the drought, which could be related to structural changes in soil chemical properties, soil physical properties, microbial communities and/or vegetation. This list of potential underlying reasons for the observed patterns makes clear that a holistic approach – considering also various other ecosystem properties and processes – is required if we are to mechanistically understand how SCE responds to altered precipitation.

For the TurkeyPoint experiment, Pi was low during and after the manipulation period. This pattern corresponds to aboveground observations made at the site where the rainfall exclusion was conducted during spring, when tree growth is greatest in this region (Hanson and Weltzin, 2000). Tree growth was strongly influenced by the precipitation exclusion and did not fully recover after the drought period. Moreover, tree growth terminated earlier in the drought plots as compared to the control plots (MacKay et al., 2012). Strikingly, treatment-induced changes to tree growth dynamics positively influenced SCE, as residuals in autumn were higher for the treatment than for the control (Fig. S1). Possible mechanisms to explain this lag effect could be the Birch effect as described above, or the decomposition of roots that died during drought-induced senescence. Moreover, plants can allocate large but variable fractions of their photosynthates belowground (Vicca et al., 2012b), with potentially rapid and strong effects on the autotrophic component of SCE (Bahn et al., 2008; Höglberg et al., 2001; Kuzyakov and

Gavrichkova, 2010). Hence, the results from this experiment also emphasize the need to separate autotrophic from heterotrophic respiration to fully explore the exact mechanisms underlying SCE responses.

The above list of potential mechanisms that can alter the moisture response of SCE when the precipitation regime changes is of course incomplete. Several other mechanisms can play at different levels (from community level to soil and microbial level). It is beyond the scope of this study to go into detail about all potential mechanisms. For reviews about various changes in the ecosystem under altered precipitation regimes, we refer the reader to Borken and Matzner (2009), Schimel et al., (2007) and van der Molen et al. (2011). Here, we want to emphasize the need for a holistic approach in experiments that aim to elucidate how SCE is affected by changes in precipitation regime.

4.4 A novel approach revealing limitations of current experiments and recommendations for future experiments

At present, inter-site comparison of effects of altered precipitation is seriously hampered by the lack of data necessary to quantify the treatment as experienced by the biota (i.e., the actual treatment; Vicca et al., 2012a). Without such data, conventional meta-analysis of cross-experiment variation in ecosystem responses to precipitation manipulation is prone to artifacts related to the enormous variation in the actual treatment; the magnitude, timing and duration of drought and rain events vary substantially among experiments, and soil type and rooting depth considerably influence the way plants and microbes experience a treatment (Vicca et al., 2012a). The novel approach presented here was developed specifically to avoid these problems. This is accomplished by analyzing within-experiment responses (through calculation of a predictability index) prior to across-experiment comparison (via CART analysis). Although treatments also remain largely incomparable with this method (hence, if cross-experiment differences were to occur, these could be due either to variation in the actual treatment or to differences in ecosystem response, or a combination), our method does provide mechanistic insight into the responses to altered precipitation. Importantly, the results are less prone to the large variation in the actual treatment. It would be particularly interesting to combine this approach with a quantification of the actual treatment such that moisture responses of SCE in various ecosystems can be elucidated.

The approach used in this study fully exploits the potential of the available data sets by taking advantage of the multiple measurements of SCE made in each experiment. However, this method is applicable only when sufficient data are available (we discarded six experiments with ≤ 10 data points), and when a reliable model can be fitted to the control data (in our study, seven experiments were discarded because of the poor quality of the model fit through the control data;

Fig. 2). For this reason, and because the CART analysis suggests that frequent SCE measurements are essential to detect deviations of the moisture response of SCE in the treatment as compared to the control, we recommend that future experiments that aim to test the response of SCE to altered precipitation seek to obtain high-frequency SCE measurements. This recommendation also applies to variables such as photosynthesis and ecosystem respiration that can be measured at high frequency with automated cuvettes and are therefore suitable for testing as in this study.

5 Concluding remarks

Is it possible to extrapolate the relationships between SCE and its abiotic drivers – soil temperature and soil moisture – to predict SCE responses to changes in precipitation patterns? According to our results, the most justified answer to this question is “no”; although for the majority of the experiments we could not falsify the hypothesis that we can predict SCE under altered precipitation regimes from current-climate observations. As discussed, all experiments with daily SCE measurements (i.e., the experiments with the data sets most reliable for this exercise) revealed that SCE in the altered precipitation treatment could not be predicted from the control observations. We postulate that at least some of the experiments with infrequent measurement schemes provided insufficient capacity to detect shifts in the climate dependencies of SCE. In other words, crucial patterns in SCE likely went undetected for these experiments. Importantly, the erroneous predictions in the experiments with daily SCE measurements were not related to extrapolation beyond the range for which the model was parameterized. Instead, these experiments provide insights of likely mechanisms (e.g., the Birch effect) that cause SCE in the treatment to deviate from what would be expected from the control observations.

Using single-factor experiments, our study demonstrated that current relationships between SCE and soil moisture should not be extrapolated to predict SCE when precipitation patterns change. However, climate change involves not only changes in precipitation regimes but also other environmental forcing factors. Droughts are often associated with warm periods or heat waves, and in combination with a heat wave, drought effects are typically exacerbated (Reichstein et al., 2013). This implies that thresholds for structural changes in the ecosystem may be passed earlier, which most likely makes predictions based on current-climate observations even less reliable than our analysis may suggest.

At present, the available data do not enable full elucidation of the mechanisms that complicate extrapolation of current-climate observations of the moisture response of SCE to predict SCE when rainfall patterns alter, and this likely applies also to other ecosystem and carbon cycle processes. If we are to fully understand ecosystem responses to altered precipitation, we need more experiments establishing response func-

tions across a broader range of precipitation regimes, annual temperatures, soil moisture conditions and vegetation types (especially in boreal and tropical regions). Such experiments should make accurate measurements of water availability, they should consider both instantaneous responses and the potential legacy effects of climate extremes, and would benefit from a holistic approach that allows for elucidation of underlying mechanisms. Future studies should make particular effort to obtain high-frequency measurements, which – as we demonstrated – are essential for capturing dynamic responses during drying and after rewetting, and for quantifying their implications for the carbon cycle in a more extreme climate.

Author contributions

S. Vicca conceived the manuscript, and performed the analyses and writing. M. Bahn, M. Estiarte and I. A. Janssens substantially contributed to the discussions prior to the writing. E. E. van Loon focussed specifically on the statistical analyses. All co-authors contributed with data and/or intellectual input during the writing process.

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Appendix A

General information for the experimental sites was generally obtained from the site investigators, except for the climate classification and the hydrology. For each site, we extracted the climate class from the Köppen classification (Hijmans et al. 2005) using latitude and longitude. This classification was further used to determine the hydrology. Sites classified as arid or semi-arid according to Köppen classification, i.e., those with a first letter “B”, as well as those classified as “dry-summer subtropical or Mediterranean climates” (i.e., Csa and Csb) were assigned to the xeric group. Sites classified as tropical rainforest (Af), as humid subtropical (Cfa), as maritime temperate (Cfb), or as continental with wet summer (Dfa, Dfb, Dwb, Dfc) were considered mesic. For all but two sites – Kiskunsag and Clocaenog – the resulting climate corresponded to the experience of the investigators. Kiskunsag is a shrubland on sandy soil, at the transition between deciduous forest and steppe and previously classified as xeric (Lellei-Kovacs et al., 2011); Clocaenog is a wetland with peaty soil in Wales, UK. Because the Köppen classification was clearly not indicative of the hydrology in these sites, we adjusted the hydrology to xeric and hydric for Kiskunsag and Clocaenog, respectively.

Table A1. Information about the precipitation manipulation experiments: latitude (Lat), longitude (Long), mean annual precipitation (MAP, mm), mean annual temperature (MAT, °C), Köppen classification (Köppen class.), vegetation type hydrology (Hydr.), manipulation type (Manip. type: drying experiment (–), irrigation experiment (+) or experiment in which the pattern of precipitation was altered, but not the total amount of precipitation (0)), duration of the manipulation (episodic manipulation over a few weeks while the rest of the year is unaltered (Epis) versus continuous drying/irrigation during entire growing season or year (Cont) versus altered rainfall pattern during entire year (ContAlt)), the percentage of clay in the soil, the depth of SWC measurements (cm), and a key reference for each experiment (if available). Species composition for all sites is given in Supplement Table S1. We distinguish between sites used only for Fig. 1 (not used for further analysis because there were not enough data points to generate reliable model fits ($n \leq 10$)), sites discarded from further analyses because of non-robust results (see Appendix Table C1), and sites used for all analyses.

Experiment	Lat	Long	MAP	MAT	Köppen class.	Vegetation	Hydr.	Manip. type	Duration manip.	% clay	SWC depth	Key reference
Sites included in Fig. 1, but excluded from other analyses because of too few data or non-normal distribution of model residuals for $SCE_{control}$												
Almería	37.09	–2.08	274	17	BSk	shrubland	xeric	–	Cont	7	0–5	Maestre et al. (2013)
Achenkirch	47.58	11.64	1480	5.7	Cfb	forest	mesic	–	Epis	28	5	Schindlbacher et al. (2012)
BigBend_S	29.30	–103.17	370	24.2	BWh	shrubland	xeric	+	Epis	8	15	Patrick et al. (2007)
BigBend_W	29.30	–103.17	370	24.2	BWh	shrubland	xeric	+	Epis	8	15	
BigBend_SW	29.30	–103.17	370	24.2	BWh	shrubland	xeric	+	Epis	8	15	
Garraf	41.30	1.82	552	15.6	Csa	shrubland	xeric	+	Epis	18	0–15	Beier et al. (2004)
Prades	41.35	1.03	663	11.7	Csa	forest	xeric	–	Epis	21	0–25	Ogaya et al. (2011)
RaMPs_Alt	39.10	–96.60	835	13	Cfa	grassland	mesic	0	ContAlt	32	0–15	Fay et al. (2011)
ThüringerSchiefer5	50.48	11.60	1000	6.5	Cfb	grassland	mesic	–	Epis	25	0–10	Kahmen et al. (2005)
ThüringerSchiefer6	50.48	11.58	1000	6.5	Cfb	grassland	mesic	–	Epis	25	0–10	
ThüringerSchiefer19	50.48	11.26	1000	6.5	Cfb	grassland	mesic	–	Epis	22	0–10	
Tolfa_Dry	42.15	11.93	729	13	Csa	forest	xeric	–	Cont	6	0–10	Cotrufo et al. (2011)
Tolfa_Wet	42.15	11.93	729	13	Csa	forest	xeric	+	Epis	6	0–10	
Sites included in Fig. 1 and hypothesis tests, but excluded from CART analysis because of non-robust results (see Appendix Table C1)												
Boston_dry	42.39	–71.22	1063	10.3	Dfa	grassland	mesic	–	Cont	9	0–30	Suseela et al. (2012)
Caxiúana	–1.73	–51.46	2314	26.9	Af	forest	mesic	–	Cont	10	0–30	Sotta et al. (2007)
Hohenheim_LALF	48.70	9.18	679	8.7	Cfb	agriculture	mesic	–	Epis	22	0–15	
Oldebroek	52.40	5.90	1042	10.1	Cfb	shrubland	mesic	–	Epis	8	0–50	Kopittke et al. (2013)
SulawesiCacao	–1.55	120.02	2092	25.5	Af	forest	mesic	–	Cont	14	5	van Straaten et al. (2010)
ThüringerSchiefer2	50.41	11.63	1000	6.5	Cfb	grassland	mesic	–	Epis	24	0–10	Kahmen et al. (2005)
ThüringerSchiefer3	50.41	11.63	1000	6.5	Cfb	grassland	mesic	–	Epis	23	0–10	
Sites included in all analyses												
Aranjuez	40.03	–3.54	349	15	Csa	grassland	xeric	–	Cont	6	0–5	Escolar et al. (2012)
Boston_wet	42.39	–71.22	1063	10.3	Dfa	grassland	mesic	+	Cont	9	0–30	Suseela et al. (2012)
Brandbjerg	55.88	11.97	613	8	Cfb	shrubland	mesic	–	Epis	2	20	Selsted et al. (2012)
Cloacaenog	53.05	–3.47	1550	8.2	Cfb	shrubland	hydric	–	Epis	50	7	Sowerby et al. (2008)
Coulissenhieb	50.14	11.87	1160	5.3	Cfb	forest	mesic	–	Epis	19	10	Muhr and Borken (2009)
Duolun_20	42.02	116.17	385	2.1	Dwb	grassland	mesic	–	Cont	17	0–10	
Duolun_40	42.02	116.17	385	2.1	Dwb	grassland	mesic	–	Cont	17	0–10	
Duolun_60	42.02	116.17	385	2.1	Dwb	grassland	mesic	–	Cont	17	0–10	
HarvardForest	42.54	–72.17	1100	6	Dfb	forest	mesic	+	Epis	18	5	Borken et al. (2006)
Hohenheim_LA	48.70	9.18	679	8.7	Cfb	agriculture	mesic	–	Epis	22	0–15	Poll et al. (2013)
Hohenheim_LF	48.70	9.18	679	8.7	Cfb	agriculture	mesic	0	ContAlt	22	0–15	
Kiskunsag	46.88	19.38	505	10.4	Cfb	shrubland	xeric	–	Epis	2	0–20	Lellei-Kovacs et al. (2011)
Mols	56.38	10.95	550	7.7	Cfb	shrubland	mesic	–	Epis	6	0–40	Beier et al. (2004)
PortoConte	40.62	8.17	640	16.8	Csa	shrubland	xeric	–	Epis	13	0–10	de Dato et al. (2010)
RaMPs_Dry	39.10	–96.60	835	13	Cfa	grassland	mesic	–	Cont	32	0–15	
RaMPs_DryAlt	39.10	–96.60	835	13	Cfa	grassland	mesic	–	ContAlt	32	0–15	
Sevilleta_Wet1	34.34	–106.73	250	13.2	BSk	grassland	xeric	+	ContAlt	10	0–15	Thomey et al. (2011)
Sevilleta_Wet2	34.34	–106.73	250	13.2	BSk	grassland	xeric	+	ContAlt	10	0–15	
Solling	51.52	9.56	1090	6.4	Cfb	forest	mesic	–	Epis	32	10	Borken et al. (1999)
Stubai	47.13	11.31	915	6.3	Dfc	grassland	mesic	–	Epis	16	5	
SulawesiForest	–1.49	120.05	2901	20.6	Af	forest	mesic	–	Cont	39	5	van Straaten et al. (2011)
ThüringerSchiefer1	50.41	11.63	1000	6.5	Cfb	grassland	mesic	–	Epis	24	0–10	Kahmen et al. (2005)
ThüringerSchiefer4	50.46	11.59	1000	6.5	Cfb	grassland	mesic	–	Epis	25	0–10	
ThüringerSchiefer7	50.48	11.56	1000	6.5	Cfb	grassland	mesic	–	Epis	25	0–10	
ThüringerSchiefer8	50.47	11.50	1000	6.5	Cfb	grassland	mesic	–	Epis	22	0–10	
ThüringerSchiefer9	50.43	11.51	1000	6.5	Cfb	grassland	mesic	–	Epis	23	0–10	
ThüringerSchiefer10	50.40	11.45	1000	6.5	Cfb	grassland	mesic	–	Epis	27	0–10	
ThüringerSchiefer11	50.38	11.45	1000	6.5	Cfb	grassland	mesic	–	Epis	23	0–10	
ThüringerSchiefer12	50.41	11.38	1000	6.5	Cfb	grassland	mesic	–	Epis	32	0–10	
ThüringerSchiefer13	50.42	11.39	1000	6.5	Cfb	grassland	mesic	–	Epis	31	0–10	
ThüringerSchiefer14	50.45	11.41	1000	6.5	Cfb	grassland	mesic	–	Epis	27	0–10	
ThüringerSchiefer15	50.45	11.41	1000	6.5	Cfb	grassland	mesic	–	Epis	25	0–10	
ThüringerSchiefer16	50.44	11.36	1000	6.5	Cfb	grassland	mesic	–	Epis	25	0–10	
ThüringerSchiefer17	50.44	11.34	1000	6.5	Cfb	grassland	mesic	–	Epis	28	0–10	
ThüringerSchiefer18	50.46	11.35	1000	6.5	Cfb	grassland	mesic	–	Epis	24	0–10	
TurkeyPoint	42.72	–80.37	1010	7.8	Dfb	forest	mesic	–	Epis	1	0–5	MacKay et al. (2012)
WalkerBranch_Dry	35.97	–84.28	1352	14.2	Cfa	forest	mesic	–	Cont	6	0–35	Hanson et al. (2005)
WalkerBranch_Wet	35.97	–84.28	1352	14.2	Cfa	forest	mesic	+	Cont	6	0–35	

Appendix B

Table B1. For each experiment, the percentage change in precipitation is given, along with the average of observed and predicted soil CO₂ efflux (SCE; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) for control and treatment in all experiments. “Sign. level” indicates whether the difference between treatment and control SCE measurements was significant at $p < 0.01$ (**), at $p < 0.05$ (*) or not significant (ns) according to repeated measures ANOVA. For the treatment, averages are also shown for the subset including only days where SWC_{treatment} is within the range of SWC observed in the control (common SWC subset). Averages were computed over the entire measurement period. Predictions are based on the model parameterized by the control data (model 4; see Methods and Supplement Table S3 for details). The percentage difference between predicted and observed is calculated as $100 \cdot (\text{average predicted} - \text{average observed}) / \text{average observed}$. Positive values indicate overestimates, whereas negative values indicate that predicted SCE underestimated observed SCE. The percentage change in precipitation was calculated from precipitation data, averaged for the entire duration of the experiment. Negative values indicate a reduction of precipitation, while positive numbers indicate an increase in precipitation.

Experiment	% change in precip.	OBSERVED		Sign. level	PREDICTED		% difference			
		control	treatment		control	treatment	treatment common SWC subset	control	treatment	treatment common SWC subset
Achenkirch	-15.44	2.45	2.11	ns	2.47	2.29	2.41	0.87	8.75	11.86
Aranjuez	-30.00	0.72	0.73	**	0.67	0.67	0.69	-5.77	-8.39	-7.77
Boston_dry	-51.89	3.58	3.07	**	3.64	11.34	1.91	1.72	269.39	-17.35
Boston_wet	20.00	3.58	3.29	**	3.64	3.87	3.38	1.72	17.58	-2.37
Brandbjerg	-7.64	1.60	1.46	**	1.52	1.37	1.35	-4.98	-5.84	-9.86
Caxiuana	-50.00	3.70	3.00	**	3.68	2.82	3.59	-0.45	-5.89	2.87
Clocaenog	-22.04	1.33	1.62	ns	1.21	1.42	1.39	-9.14	-12.46	-13.64
Coullissenhieb	6.68	2.65	2.02	*	2.62	2.51	2.54	-1.09	24.23	27.67
Duolun_20	-20.00	1.54	1.26	**	1.43	1.24	1.32	-7.00	-1.15	-1.66
Duolun_40	-40.00	1.54	1.07	ns	1.43	1.14	1.17	-7.00	6.47	6.71
Duolun_60	-60.00	1.54	0.84	**	1.43	0.83	1.06	-7.00	-2.07	2.82
HarvardForest	-32.55	3.05	2.25	ns	2.98	2.77	2.77	-2.14	23.19	23.19
Hohenheim_LA	-11.73	1.08	1.00	**	1.01	1.06	1.04	-6.45	6.45	4.67
Hohenheim_LALF	-11.00	1.08	0.94	ns	1.01	1.07	1.02	-6.45	13.71	10.94
Hohenheim_LF	0.85	1.08	1.13	*	1.01	1.05	1.02	-6.45	-7.75	-9.88
Kiskunsag	-21.38	0.53	0.43	**	0.50	0.47	0.48	-5.76	7.79	7.12
Mols	-23.18	2.45	1.63	ns	2.41	2.65	1.10	-1.56	63.23	21.50
Oldebroek	-19.03	0.80	0.68	**	0.77	0.57	0.61	-3.59	-15.55	-8.63
PortoConte	-16.24	2.86	2.63	ns	2.74	2.61	2.66	-4.30	-0.67	-0.17
RaMPs_Alt	13.13	9.37	8.35	ns	9.16	8.47	8.49	-2.25	1.48	1.41
RaMPs_Dry	-17.59	9.57	8.88	ns	9.29	8.98	9.04	-2.90	1.16	0.88
RaMPs_DryAlt	-17.19	9.67	7.93	ns	9.39	9.03	9.19	-2.88	13.81	13.37
Sevilleta_Wet1	26.38	0.70	0.83	*	0.69	0.67	0.68	-1.85	-18.91	-18.34
Sevilleta_Wet2	15.63	0.70	1.02	ns	0.69	0.66	0.66	-1.85	-35.37	-35.29
Solling	-28.37	1.07	1.48	ns	1.06	0.98	0.99	-0.83	-33.30	-33.29
Stubai	-31.42	4.33	2.73	**	4.26	2.36	4.35	-1.60	-13.36	25.49
SulawesiCacao	-60.09	2.83	2.81	ns	2.79	1.40	2.90	-1.39	-50.28	-8.39
SulawesiForest	-53.91	3.07	1.94	ns	3.05	1.79	2.58	-0.85	-7.69	4.34
ThuringerSchiefer1	-11.11	4.77	4.11	ns	4.67	4.11	4.14	-2.09	0.01	-1.08
ThuringerSchiefer2	-11.11	5.82	3.50	ns	5.65	4.71	5.07	-2.82	34.47	34.39
ThuringerSchiefer3	-11.11	6.10	4.89	**	5.77	4.91	5.35	-5.35	0.35	2.21
ThuringerSchiefer4	-11.11	5.81	4.70	**	5.49	4.86	5.10	-5.51	3.54	4.06
ThuringerSchiefer5	-11.11	6.28	4.36	*	6.11	5.20	5.44	-2.69	19.02	18.38
ThuringerSchiefer6	-11.11	6.36	6.24	**	6.13	4.96	5.53	-3.62	-20.57	-15.36
ThuringerSchiefer7	-11.11	8.12	6.09	**	7.86	6.44	6.73	-3.16	5.79	4.73
ThuringerSchiefer8	-11.11	5.96	6.10	ns	5.84	5.85	6.14	-2.13	-4.05	-3.87
ThuringerSchiefer9	-11.11	4.36	4.12	**	4.25	4.00	4.00	-2.50	-2.96	-2.96
ThuringerSchiefer10	-11.11	4.30	4.18	**	4.18	4.06	4.06	-2.92	-2.72	-2.72
ThuringerSchiefer11	-11.11	6.41	5.61	**	6.15	5.54	5.54	-4.04	-1.36	-1.36
ThuringerSchiefer12	-11.11	5.17	4.24	**	4.61	4.08	4.35	-10.81	-3.64	-4.11
ThuringerSchiefer13	-11.11	5.93	6.46	**	5.65	5.58	5.79	-4.64	-13.68	-14.41
ThuringerSchiefer14	-11.11	4.26	3.84	**	4.24	3.80	3.96	-0.63	-1.05	-3.01
ThuringerSchiefer15	-11.11	5.99	4.56	**	5.93	4.87	5.08	-1.00	6.91	7.03
ThuringerSchiefer16	-11.11	4.54	3.91	**	4.39	3.78	3.91	-3.29	-3.50	-3.80
ThuringerSchiefer17	-11.11	4.42	4.01	**	4.37	4.15	4.71	-1.32	3.70	5.63
ThuringerSchiefer18	-11.11	4.62	4.35	**	4.54	4.29	4.29	-1.83	-1.38	-1.38
ThuringerSchiefer19	-11.11	4.12	4.98	**	4.03	3.79	3.84	-2.32	-24.02	-26.46
Tolfa	-21.44	3.22	3.81	**	3.00	3.27	3.27	-6.87	-14.23	-14.23
Tolfa_Wet	69.00	3.05	4.90	**	2.88	3.43	3.43	-5.54	-30.00	-29.98
TurkeyPoint	-23.20	2.14	1.54	**	2.10	2.65	2.48	-1.95	72.17	62.92
WalkerBranch_Dry	-33.00	3.59	3.81	**	3.52	3.05	3.11	-2.11	-20.05	-20.29
WalkerBranch_Wet	33.00	3.68	3.62	**	3.60	3.61	3.53	-1.96	-0.23	-0.33

Appendix C

For each experiment, we either fitted model 4 to the data of the control plots using the entire data set or to a subset of the data, including only the days where $SWC_{\text{treatment}}$ is within the range of SWC observed in the control (i.e., common SWC subset). Subsequently, we tested the hypothesis that the moisture response of soil CO_2 efflux (SCE) as observed in the control can be extrapolated to predict SCE in the treatment for both the entire data set and the common SWC subset via two tests (h1 and h2; see Methods for details). Results of both tests are presented for both data sets in Appendix Table C1.

Table C1. For each experiment, we present the R^2 of the model fitted to the data of the control plots, the number of data points (N) and the median interval (in days) between two consecutive measurements of soil CO_2 efflux (I). We also show the results of the two tests that we performed to test our hypothesis. For both the entire data set and the common SWC subset, “h1” is the p value of the Lilliefors test for normality, “h2” shows the ratio of $\text{RMSE}_{\text{treatment}}$ to $\text{RMSE}_{\text{control}}$ and “H” indicates whether or not H_1 was rejected (see Fig. 2 and Methods for details). Experiments for which both the entire data set and the common SWC subset gave the same result are indicated with “yes” in the column “Robust?”. The weight (W) used in this CART analysis is given (W is calculated as $1/\text{number of experiments per site}$ that are used in CART). The results of the trend analysis on the time course of the predictability index of $\text{SCE}_{\text{treatment}}$ (P_i , runs test dichotomized around the median) are presented in the column “Trend”, with 0 indicating that no trend was detected and 1 indicating a significant trend for P_i versus time. When the rainfall manipulation was initiated more than one year before the start of SCE measurements, trend analysis is considered irrelevant. This is indicated as NA, followed by the result of the trend analysis in parentheses. Note that this table includes only results for experiments with > 10 data points and for which residuals of the control were normally distributed. Values in bold highlight the reason for rejecting H_1 .

Experiment	R^2	N	I	Entire data set			Common SWC subset			Robust?	W	Trend
				h1	h2	H	h1	h2	H			
Aranjuez	0.37	29	35	0.50	1.06	0	0.50	1.06	0	Yes	1	0
Boston_dry	0.93	11	31	0.50	4.29	1	0.50	1.12	0	No	NA	NA(0)
Boston_wet	0.93	11	31	0.50	1.74	0	0.50	1.22	0	Yes	1	NA(0)
Brandbjerg	0.60	173	16	0.08	1.30	0	0.50	1.10	0	Yes	1	0
Caxiuana	0.49	22	15	0.15	2.35	1	0.50	1.55	0	No	NA	0
Clocaenog	0.59	90	15	0.50	1.09	0	0.50	1.09	0	Yes	1	NA(0)
Coullissenhie	0.86	35	9	0.09	2.41	1	0.13	2.43	1	Yes	1	0
Duolun_20	0.53	23	8	0.04	1.06	1	0.01	1.05	1	Yes	0.33	0
Duolun_40	0.53	23	8	0.07	1.09	0	0.08	1.09	0	Yes	0.33	0
Duolun_60	0.53	23	8	0.17	1.29	0	0.32	1.26	0	Yes	0.33	0
HarvardForest	0.82	43	7	0.50	1.72	0	0.50	1.72	0	Yes	1	0
Hohenheim_LA	0.71	38	7	0.50	1.20	0	0.50	1.21	0	Yes	0.5	0
Hohenheim_LALF	0.71	38	7	0.06	1.14	0	0.02	1.13	1	No	NA	0
Hohenheim_LF	0.71	38	7	0.50	0.91	0	0.50	0.92	0	Yes	0.5	0
Kiskunsag	0.34	66	27	0.50	0.99	0	0.50	1.04	0	Yes	1	NA(0)
Mols	0.80	18	24	0.18	1.67	0	0.50	1.44	0	Yes	1	NA(0)
Oldebroek	0.73	73	15	0.03	1.36	1	0.50	1.07	0	No	NA	1
PortoConte	0.30	47	36	0.50	0.97	0	0.37	0.98	0	Yes	1	0
RaMPs_Dry	0.47	74	5	0.50	0.94	0	0.50	0.92	0	Yes	0.5	0
RaMPs_DryAlt	0.45	73	5	0.50	1.29	0	0.50	1.26	0	Yes	0.5	0
Sevilleta_Wet1	0.38	163	1	0.00	1.47	1	0.01	1.39	1	Yes	0.5	1
Sevilleta_Wet2	0.38	163	1	0.50	2.53	1	0.42	2.53	1	Yes	0.5	1
Solling	0.85	264	1	0.00	2.60	1	0.00	2.59	1	Yes	1	1
Stubai	0.66	309	1	0.00	4.92	1	0.06	2.08	1	Yes	1	1
SulawesiCacao	0.37	46	14	0.00	13.14	1	0.50	1.29	0	No	NA	1
SulawesiForest	0.39	59	14	0.50	1.73	0	0.33	0.89	0	Yes	1	1
ThuringerSchiefer1	0.72	14	22	0.11	1.28	0	0.30	1.45	0	Yes	0.07	0
ThuringerSchiefer2	0.81	13	24	0.17	1.95	0	0.03	2.38	1	No	NA	0
ThuringerSchiefer3	0.35	13	24	0.04	0.87	1	0.11	0.72	0	No	NA	0
ThuringerSchiefer4	0.59	14	22	0.50	0.85	0	0.50	0.88	0	Yes	0.07	0
ThuringerSchiefer7	0.72	14	22	0.50	1.53	0	0.50	1.47	0	Yes	0.07	0
ThuringerSchiefer8	0.75	15	24	0.33	1.57	0	0.50	1.62	0	Yes	0.07	0
ThuringerSchiefer9	0.83	15	24	0.32	1.26	0	0.32	1.26	0	Yes	0.07	0
ThuringerSchiefer10	0.76	14	22	0.34	1.12	0	0.34	1.12	0	Yes	0.07	0
ThuringerSchiefer11	0.67	13	27	0.13	1.14	0	0.13	1.14	0	Yes	0.07	0
ThuringerSchiefer12	0.52	14	23	0.50	0.88	0	0.50	0.94	0	Yes	0.07	0
ThuringerSchiefer13	0.73	14	23	0.13	1.18	0	0.20	1.37	0	Yes	0.07	0
ThuringerSchiefer14	0.86	12	26	0.22	1.13	0	0.08	1.18	0	Yes	0.07	0
ThuringerSchiefer15	0.96	14	26	0.50	1.44	0	0.50	1.47	0	Yes	0.07	0
ThuringerSchiefer16	0.73	15	24	0.14	0.95	0	0.27	0.95	0	Yes	0.07	0
ThuringerSchiefer17	0.83	14	22	0.13	1.86	0	0.38	1.62	0	Yes	0.07	0
ThuringerSchiefer18	0.83	14	22	0.50	1.18	0	0.50	1.18	0	Yes	0.07	0
TurkeyPoint	0.85	106	1	0.04	3.59	1	0.04	3.63	1	Yes	1	1
WalkerBranch_Dry	0.59	20	38	0.50	1.46	0	0.50	1.42	0	Yes	0.5	0
WalkerBranch_Wet	0.63	21	33	0.45	1.13	0	0.47	1.13	0	Yes	0.5	0

Appendix D

Table D1. List of abbreviations.

CART	classification and regression tree
H1	hypothesis that the relationship between SCE and ST and SWC observed from fluctuations over time in the control plots can be extrapolated to predict SCE in plots exposed to a different precipitation regime
MAP	mean annual precipitation
MAT	mean annual temperature
Pi	predictability index, calculated as the absolute error of predicted soil CO ₂ efflux in the treatment reduced by the absolute error of predicted soil CO ₂ efflux in the control at a specific moment (see Eq. 5). Pi values close to zero indicate that SCE _{treatment} was predicted similarly well compared to SCE _{control} , whereas values substantially below or above zero indicate the difference in predictability of SCE _{treatment} relative to SCE _{control} . Negative values indicate that the prediction of SCE _{treatment} was worse than that of SCE _{control} , and vice versa for positive values.
SCE	soil CO ₂ efflux
SCE _{control}	soil CO ₂ efflux in the control
SCE _{treatment}	soil CO ₂ efflux in the treatment
SWC	volumetric soil water content
SWC _{control}	volumetric soil water content in the control
SWC _{treatment}	volumetric soil water content in the treatment
common SWC subset	data set using only dates when SWC _{treatment} was within the range of SWC _{control}
ST	soil temperature

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