

Quantifying the timescales over which exogenous and endogenous conditions affect soil respiration

Greg A. Barron-Gafford^{1,2}, Jessica M. Cable³, Lisa Patrick Bentley⁴, Russell L. Scott⁵, Travis E. Huxman^{6,7}, G. Darrel Jenerette⁸ and Kiona Ogle⁹

¹School of Geography & Development, University of Arizona, Tucson, AZ 85721, USA; ²B2 Earthscience, Biosphere 2, University of Arizona, Tucson, AZ 85721, USA; ³International Arctic Research Center, University of Alaska Fairbanks, Fairbanks, AK 99775, USA; ⁴Environmental Change Institute, University of Oxford, Oxford University Centre for the Environment, South Parks Road, Oxford, OX1 3QY, UK; ⁵Southwest Watershed Research Center, USDA-ARS, Tucson, AZ 85719, USA; ⁶Ecology and Evolutionary Biology, University of California, Irvine, CA 92697, USA; ⁷Center for Environmental Biology, University of California, Irvine, CA 92697, USA; ⁸Department of Botany and Plant Sciences, University of California Riverside, Riverside, CA, USA; ⁹School of Life Sciences, Arizona State University, Tempe, AZ, USA

Summary

Author for correspondence:

Greg A. Barron-Gafford

Tel: +1 520 548 0388

Email: gregbg@email.arizona.edu

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• Understanding how exogenous and endogenous factors and above-ground–below-ground linkages modulate carbon dynamics is difficult because of the influences of antecedent conditions. For example, there are variable lags between above-ground assimilation and below-ground efflux, and the duration of antecedent periods are often arbitrarily assigned. Nonetheless, developing models linking above- and below-ground processes is crucial for estimating current and future carbon dynamics.

• We collected data on leaf-level photosynthesis (A_{sat}) and soil respiration (R_{soil}) in different microhabitats (under shrubs vs under bunchgrasses) in the Sonoran Desert. We evaluated timescales over which endogenous and exogenous factors control R_{soil} by analyzing data in the context of a semimechanistic temperature–response model of R_{soil} that incorporated effects of antecedent exogenous (soil water) and endogenous (A_{sat}) conditions.

• For both microhabitats, antecedent soil water and A_{sat} significantly affected R_{soil} , but R_{soil} under shrubs was more sensitive to A_{sat} than that under bunchgrasses. Photosynthetic rates 1 and 3 d before the R_{soil} measurement were most important in determining current-day R_{soil} under bunchgrasses and shrubs, respectively, indicating a significant lag effect.

• Endogenous and exogenous controls are critical drivers of R_{soil} , but the relative importance and the timescale over which each factor affects R_{soil} depends on above-ground vegetation and ecosystem structure characteristics.

Introduction

Soil respiration (R_{soil}) represents a substantial source of CO_2 to the atmosphere, sometimes in excess of 70% of total ecosystem respiratory efflux (Janssens *et al.*, 2001; Law *et al.*, 2001; Barron-Gafford *et al.*, 2011). R_{soil} can also be a variable carbon flux, making its quantification important for improving our ability to predict ecosystem carbon dynamics. Of special interest is the influence of biotic (e.g. above-ground plant function) and abiotic (e.g. environmental) drivers on R_{soil} . Over the last decade, substantial progress has been made in modeling R_{soil} by moving beyond simple temperature response functions (see Lloyd & Taylor, 1994; Davidson *et al.*, 2006, 2012) to developing frameworks and models for water-limited semiarid systems (Huxman *et al.*, 2004; Cable *et al.*, 2008; Lellei-Kovács *et al.*, 2011), including multiple vegetative cover types or soil microhabitats (Cable *et al.*, 2009; Zhang *et al.*, 2009; Jin *et al.*, 2010), and incorporating antecedent environmental effects (Zhou *et al.*, 2011; Cable *et al.*, 2012).

Despite this progress, there are still significant challenges in mechanistically understanding carbon efflux processes in soils. For example, little has been done to explicitly describe how R_{soil} is influenced by the combined effects of leaf-level plant physiological activity and antecedent environmental conditions, as has been called for in the literature (Vargas *et al.*, 2011). Such processes are hypothesized to be responsible for current modeling challenges that limit our predictive abilities on fine timescales (Barron-Gafford *et al.*, 2011). Quantifying the effect of endogenous (e.g. physiological processes such as photosynthetic carbon fixation) and exogenous (e.g. environmental features that influence metabolic processes driving carbon utilization) factors has the potential to greatly advance our theory on underlying sensitivities of R_{soil} to different global change drivers and may improve our ability to quantify and predict ecosystem carbon balance in natural settings.

Dependence of R_{soil} on above-ground plant carbon fixation has been hypothesized as a source of within-day variation in R_{soil} (Högberg *et al.*, 2001, 2009; Tang *et al.*, 2005; Baldocchi *et al.*,

2006; Gaumont-Guay *et al.*, 2006; Carbone & Trumbore, 2007; Barron-Gafford *et al.*, 2011; Carbone *et al.*, 2011; Niu *et al.*, 2011). In particular, the hysteretic relationship of R_{soil} with temperature may be the result of abiotic forcings (Phillips *et al.*, 2010), but it may also be tied to subdaily lags in recently fixed carbohydrate transport from the leaves to the roots. It has been hypothesized that a stimulation of rhizosphere respiration from late-afternoon root exudation of recent photosynthates induces a higher R_{soil} than early-morning rates occurring at a similar temperature (Barron-Gafford *et al.*, 2011). Understanding the physiological dynamics of such a time-lag would be a powerful tool to assist in the prediction of rhizosphere carbon processes. We might expect this antecedent effect to be a function of the type and size of vegetation (e.g. grass, shrub, etc.), wherein large woody plants tend to have longer phloem transport times than herbaceous plants (Carbone & Trumbore, 2007; Vargas *et al.*, 2011). Thus, the vegetative composition of an ecosystem may be important in determining the period over which antecedent (prior) plant carbon gain is important for R_{soil} .

Shifts in the distribution of vegetation is a widespread feature of global change, and understanding how these community-level changes affect ecosystem processes has been a goal of modern ecology for some time. For example, many regions of North America have experienced widespread changes in the relationship between grass and shrub life forms (Goodale & Davidson, 2002). In the context of R_{soil} , the distribution and dominance of woody plants relative to grasses may determine not only the importance of endogenous and exogenous effects on R_{soil} , but also the time-scales over which these effects are important for R_{soil} . Increased woody plant cover affects canopy structure and influences ecosystem processes as a result of changes in trait composition, such as vertical root distribution (Schenk & Jackson, 2002) and maximum rooting depth (Canadell *et al.*, 1996; Hultine *et al.*, 2006). Such traits are related to plant photosynthetic capacity and plant-specific responses to environmental stress (Potts *et al.*, 2006; Barron-Gafford *et al.*, 2012), both endogenous factors likely to influence below-ground processes such as R_{soil} . Additionally, woody plants shade and cool the soil (Martens *et al.*, 2000; McLain *et al.*, 2008; Villegas *et al.*, 2010b), which can extend periods of elevated surface soil moisture as a result of reduced soil evaporation (Scholes & Archer, 2007; Breshears *et al.*, 2009; Villegas *et al.*, 2010a,b). Moisture and temperature are major exogenous drivers of R_{soil} , but how they differentially affect extant and antecedent conditions across various microhabitats and their combined influence on R_{soil} are poorly understood (Cable *et al.*, 2009; Barron-Gafford *et al.*, 2011).

How exogenous and endogenous conditions modulate ecosystem carbon dynamics in the context of mixed vegetation ecosystems is difficult to assess because of the potential, but hidden, role that antecedent conditions may play in driving current fluxes. Therefore, the objectives of this study were as follows: to quantify the response of R_{soil} to current and previous temperature, soil water content, and leaf-level carbon gain in a grass–shrub mixed ecosystem; and to determine the critical time periods over which antecedent exogenous (soil water) and endogenous (photosynthesis) factors influence R_{soil} rates. We

accomplished this by integrating datasets of above-ground plant carbon gain and R_{soil} collected at different spatial and temporal resolutions. The datasets were used to inform a simple model of leaf-level photosynthesis, which was coupled to a semimechanistic model of R_{soil} . The coupled model performed well across a number of vegetation microhabitat settings and provided us the means to evaluate the relative roles of endogenous and exogenous factors in controlling R_{soil} in a semiarid shrubland.

Materials and Methods

Site information

The study site is located in the Santa Rita Experimental Range (31.8214°N, 110.8661°W, elevation: 1116 m a.s.l.) south of Tucson, AZ, USA. The site was historically a grassland, but is now dominated by velvet mesquite (*Prosopis velutina* Woot.), which covers *c.* 35% of the *c.* 2800 m² study site. Much of the intercanopy space consists of a mosaic of bunchgrasses (predominantly *Eragrostis lehmanniana* Nees, but also including *Digitaria californica* Benth and *Bouteloua eriopoda*). Soils here are a deep sandy loam (Scott *et al.*, 2009), and the mean depth to groundwater at the upland site exceeds 100 m (Barron-Gafford *et al.*, 2013). Mean annual precipitation is 375 mm, with *c.* 50% falling in July–September as part of the North American monsoon (Fig. 1c).

An eddy covariance tower was installed at the site in 2004 to continuously monitor ecosystem-scale carbon, water, and energy exchange, as well as all associated meteorological variables (Scott *et al.*, 2009). Thirty-minute measurements of soil moisture (CS616, Campbell Scientific, Logan, UT, USA) and soil temperature (T108, Campbell Scientific) were made at 5, 10, and 50 cm depths, under both mesquite and *E. lehmanniana* bunchgrass microhabitats (Scott *et al.*, 2009). Thirty-minute measurements of incoming photosynthetically active radiation (PAR; LI-190, Li-Cor, Lincoln, NE, USA), air temperature and relative humidity (HMP35D, Vaisala, Helsinki, Finland) were made 8 m above ground.

Manual soil respiration measurements

To evaluate exogenous (soil moisture and temperature) and endogenous (photosynthetic gain) drivers of soil respiration (R_{soil}), we measured R_{soil} throughout an entire growing season, at nearly biweekly intervals for a total of 27 d of measurement in 2007. R_{soil} was measured within *P. velutina* (hereafter, ‘mesquite’) and *E. lehmanniana* (‘bunchgrass’) microhabitats using a custom chamber and permanently installed soil collars (diameter = 10.2 cm; depth = 5 cm). As described in Barron-Gafford *et al.* (2011), collars were installed every 10 m along 50 m transects, whereby we identified the closest *P. velutina* and *E. lehmanniana* individual and placed a collar halfway between the base of the plant and the canopy dripline. Transects ran west and south from the eddy covariance tower, yielding a total of 20 collars (five collars per transect × two transects per microhabitat type × two microhabitat types).

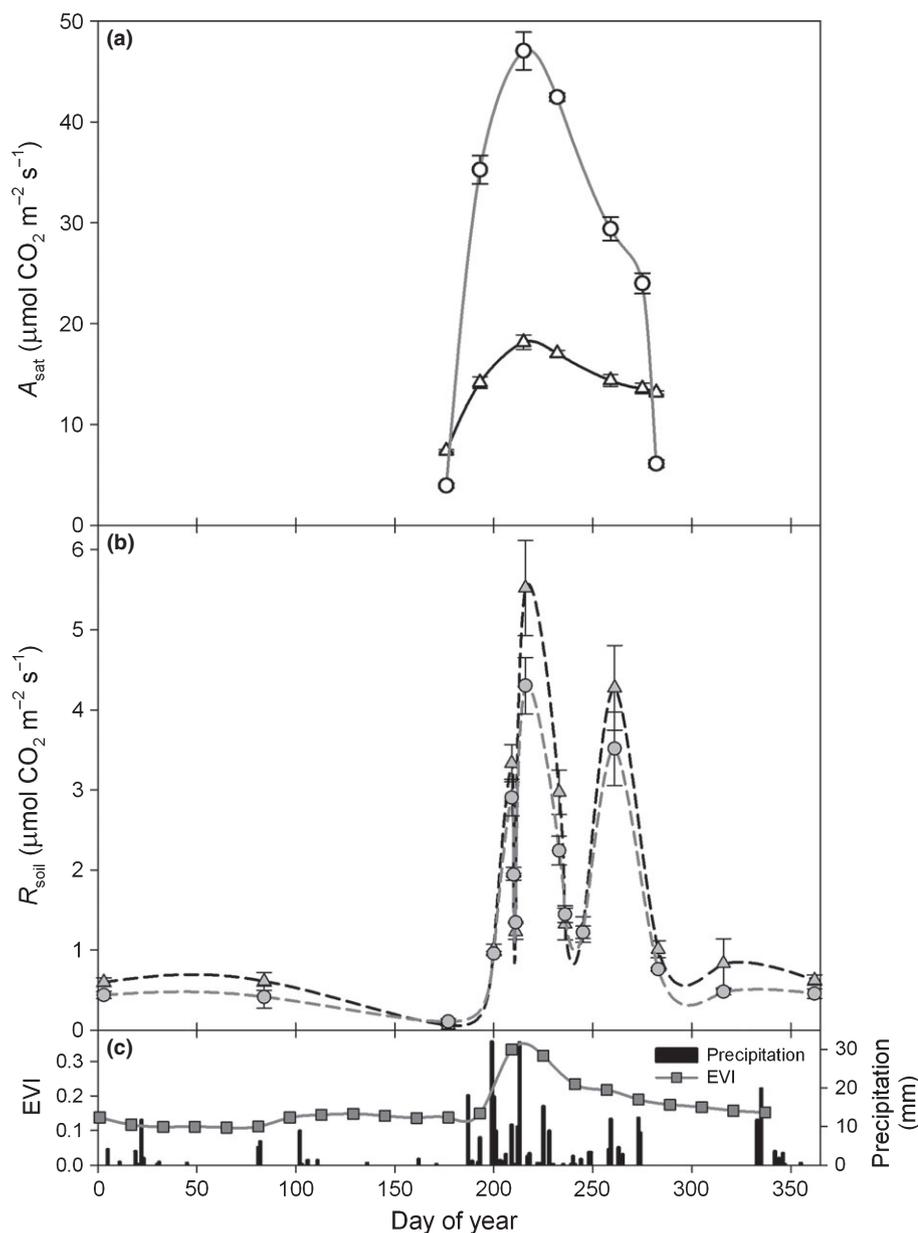


Fig. 1 (a, b) Time series of light-saturated photosynthesis (A_{sat}) (a) and soil respiration rates (R_{soil}) (b). Data are shown for two microhabitats (mesquite, triangles/black line; bunchgrass, circles/gray line) collected across 7 d spanning all seasonal periods, as illustrated by precipitation (black bars) and observed enhanced vegetation index (EVI, squares) (c), which represents the 'greenness' of the site. Each point represents the mean (± 1 SE) of 10 individual measurements, although the individual measurements ($N = 30$ for A_{sat} , $N = 144$ for R_{soil}) were used in the Bayesian analysis. A simple spline curve connects the points in time. Using the individual observations in our analysis was required to estimate the spatial effects and to link the individual measurements to the collar-level covariates.

To measure R_{soil} , we used a 3 l opaque PVC soil chamber connected to a portable CO_2 gas analyzer (LI-840, Li-Cor Biosciences) interfaced with a laptop for data collection and storage, as described by Cable *et al.* (2008) and Barron-Gafford *et al.* (2011). The accumulation of CO_2 in the chamber over time followed a straight line, and we fitted a linear regression of CO_2 vs time to obtain the rate of change (slope of line: ppm s^{-1}). We converted the slope of this line to a flux density with volume/area corrections (Percy *et al.*, 1990), providing a measurement of R_{soil} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), as has been described for this measurement system (Cable *et al.*, 2009; Barron-Gafford *et al.*, 2011). Associated with each R_{soil} measurement, soil moisture integrated over 0–12 cm was measured in the collar using a handheld water content sensor (HydroSense system, Campbell Scientific Inc.), and soil temperature from 0 to 10 cm was measured using a temperature probe (Temp-100, Oakton Instruments,

Vernon Hills, IL, USA). Near-surface air and surface soil temperature were also measured using thermocouples installed within the soil chamber. These measurements were repeated across 14 d, spanning all seasons (DOY 10, 24, 35, 47, 61, 84, 96, 113, 132, 145, 160, 177, 189, 200, 209, 210, 211, 216, 233, 236, 245, 261, 283, 301, 316, 330, 362; Fig. 1b).

Leaf-level measurements of photosynthetic activity

Light-saturated photosynthetic CO_2 assimilation (A_{sat}) was measured on five *P. velutina* and five *E. lehmanniana* individuals at the site using a portable gas-exchange system (LI-6400; Li-Cor), which allows the user to create a stable microenvironment that mimics ambient conditions outside the cuvette (LI-6400 manual; Li-Cor Biosciences, 2013). Within each species, individual plants were of similar size and located along the R_{soil} transects described

earlier. As described by Barron-Gafford *et al.* (2012), A_{sat} measurements were made mid-morning to midday (10:00–13:00 h local time) at a constant irradiance of $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$, as delivered by the LI-6400 red-blue light source (LI-6400-02b). Once clamped into the chamber, the leaf was acclimated to a CO_2 setpoint of 375 ppm, while exposed to ambient temperature and relative humidity at a constant flow rate of $500 \mu\text{mol s}^{-1}$. Leaves placed into the cuvette were allowed to acclimate and stabilize for a minimum of 10 min before gas exchange measurements. All measures were conducted on intact leaves on the southern side of the plant, midway up the canopy. A_{sat} measurements were repeated during multiple periods throughout the growing season (pre-monsoon, during the monsoon, and post-monsoon) to capture a spectrum of physiological activity, across a range of temperature, precipitation, and soil moisture conditions. Conducting measurements across this range of states was critical to capturing phenological patterns of plant and soil activity. In total, A_{sat} was measured on seven individual days in 2007 (DOY 176, 193, 215, 232, 259, 275, 282) for a total of 70 measurements (Fig. 1a).

Data analysis framework

We combined our measurements of R_{soil} , A_{sat} , and associated environmental drivers to infer endogenous (A_{sat}) and exogenous influences on R_{soil} . We achieved this by way of a Bayesian modeling framework (Wikle, 2003; Clark, 2005; Clark & Gelfand, 2006; Xie & Carlin, 2006) that integrates these datasets that are misaligned in space and time, propagates uncertainty in A_{sat} to R_{soil} , and yields estimates and associated uncertainties for parameters describing endogenous and exogenous influences on R_{soil} . Our Bayesian framework comprised three primary components: a data model that describes the likelihoods of the observed A_{sat} and R_{soil} ; a process model that includes a simple linear model for A_{sat} and a nonlinear model for R_{soil} that incorporates spatial and temporal random effects; and a parameter model that specifies prior distributions for process model parameters and all variance terms. Together, these components were used to generate posterior distributions of parameters that modulate rates and responses of A_{sat} and R_{soil} . That is, the parameters describe the effects of current environmental conditions, past environmental conditions, and the linkages between above-ground carbon gain and below-ground carbon efflux.

Data and process models for A_{sat} and R_{soil}

For the data models, we assumed that each A_{sat} observation is normally distributed with mean μA_{sat} and a variance that we estimated. Thus, for observation i ($i = 1, 2, \dots, 70$) and microhabitat m (mesquite or bunchgrass) associated with i , the process model for μA_{sat} is given by the linear regression:

$$\mu A_{\text{sat}\{i\}} = c_{1\{m\}} + c_{2\{m\}} T_{\text{air max}\{i\}} + c_{3\{m\}} \text{VPD}_{\text{max}\{i\}} + c_{4\{m\}} \text{SWC}_{\{i\}} \quad \text{Eqn 1}$$

where $T_{\text{air max}}$, VPD_{max} , SWC , μA_{sat} represent the daily maximum air temperature ($^{\circ}\text{C}$), maximum vapor pressure deficit

(kPa), and soil water content at 5 cm (v/v) on each measurement day, respectively. Previous analyses suggest that near-surface soil moisture (5 cm) is an appropriate correlate for seasonal dynamics of photosynthetic function within this well drained, sandy soil (Barron-Gafford *et al.*, 2012). The main effects of these environmental drivers are captured by c_2 , c_3 , and c_4 ; all c parameters vary by m to allow for microhabitat differences in the sensitivity to each environmental driver. Using these parameter estimates and the environmental data from the site's eddy covariance station, we generated daily estimates or predictions of A_{sat} , which we refer to as A_{pred} . Therefore, A_{pred} associated with each day of year d ($d = 1, 2, \dots, 365$) and microhabitat m (mesquite or bunchgrass) is given by:

$$A_{\text{pred}\{d,m\}} = (c_{1\{m\}} + c_{2\{m\}} T_{\text{air max}\{d\}} + c_{3\{m\}} \text{VPD}_{\text{max}\{d\}} + c_{4\{m\}} \text{SWC}_{\{d\}}) \text{EVI}_{\{d\}} \quad \text{Eqn 2}$$

where $T_{\text{air max}}$, VPD_{max} , and SWC were computed from the eddy covariance station data. To account for the development of seasonal vegetation cover, we rescaled the mean growing season A_{sat} (i.e. as given by Eqn 1 for μA_{sat}) by the MODIS enhanced vegetation index (EVI) estimated for the site for 2007 (Scott *et al.*, 2009) to obtain A_{pred} . It is important to note that this simple model for predicting photosynthesis is not meant to replace more mechanistic, higher-order models of photosynthesis (*sensu* Farquhar *et al.*, 1980; von Caemmerer, 2000) or develop a model of plant function that is more specific to this system. Rather, efforts were focused on linking above-ground uptake and below-ground processes, and the models described in Eqns 1 and 2 yield an appropriate estimate of that photosynthetic uptake.

Next, we assumed that each observation of $\log_e(R_{\text{soil}})$ is normally distributed with mean μLR (natural log scale) and a variance that we estimated (Cable *et al.*, 2008, 2011). The process model for μLR is based on an Arrhenius-type function described by Lloyd & Taylor (1994) that was modified by Cable *et al.* (2008) to incorporate collar random effects (ε). For each observation i ($i = 1, 2, \dots, 144$) and collar c ($c = 1, 2, \dots, 20$ collars) associated with i :

$$\mu LR_{\{i\}} = LR_{\text{b}\{i\}} + E_{O_{\{i\}}} \left(\frac{1}{298.15 - T_{O_{\{m\}}}} - \frac{1}{(T_{\{i\}} + 273.15) - T_{O_{\{m\}}}} \right) + \varepsilon_{\{c\}} \quad \text{Eqn 3}$$

where LR_{b} is the natural log of R_{b} , the 'base' R_{soil} at 25°C (298.15 K). We use 25°C because the annually averaged soil temperature across the two microhabitats was 25.1°C , and this is a standard reference temperature against which to compare with other studies (Cable *et al.*, 2011). E_{O} (Kelvin) is a temperature sensitivity parameter that is somewhat analogous to an energy of activation term, T_{O} (Kelvin) is another temperature sensitivity parameter, and T is soil temperature ($^{\circ}\text{C}$; 0–10 cm). We allowed

T_O to vary by m to account for inherent differences in the temperature sensitivity of R_{soil} between microhabitats.

Importantly, we extended the original Lloyd & Taylor function by modeling LR_b and E_O as functions of antecedent and current conditions similar to Cable *et al.* (2008). The model for LR_b incorporates the influence not only of environmental conditions (SWC and temperature) but also of photosynthetic activity (A_{sat}), essentially linking above- and below-ground carbon dynamics within a singular model of R_{soil} . In fact, A_{sat} is just a proxy for many plant attributes – such as the general metabolic state of the plant, the actual amount of fixed carbon, nitrogen status, etc. – but here we use this measure of maximum carbon assimilation potential to indicate peak capacity for each growth form, for each phenological point in time. The model for LR_b for observation i associated with microhabitat m is:

$$LR_b\{i\} = \alpha_{1\{m\}} + \alpha_{2\{m\}} AntA_{pred\{d,m\}} + \alpha_{3\{m\}} AntSWC_{\{d,m\}} + \alpha_{4\{m\}} SWC_{\{d,m\}} + \alpha_{5\{m\}} AntSWC_{\{d,m\}} SWC_{\{d,m\}}$$

Eqn 4

where $AntA_{pred}$ is the antecedent leaf-level, predicted saturated photosynthesis, which is linked to A_{pred} in Eqn 2; and SWC , $AntA_{pred}$ SWC and $AntSWC$, α_1 are current and antecedent soil water contents, respectively. The α_1 parameter represents the base rate under average soil water content (i.e. at mean centered $SWC = 0$ and $AntSWC = 0$) at a reference temperature of $25^\circ C$ and in the absence of above-ground carbon inputs ($AntA_{pred} = 0$). The endogenous effect of $AntA_{pred}$ is given by α_2 , and the exogenous effects of $AntSWC$, SWC , and their interaction are captured by α_3 , α_4 , and α_5 , respectively. All α parameters vary by m to allow for potential microhabitat differences in sensitivities to each driver. We employ a model for $E_{O\{i\}}$ that is identical to Eqn 4, but with its own set of parameters $\beta_1, \beta_2, \dots, \beta_5$ instead of $\alpha_1, \alpha_2, \dots, \alpha_5$.

Lloyd & Taylor (1994) suggest that E_O and T_O are relatively conserved across many ecosystem types, so we used semi-informative normal priors for T_O and the 'base' E_O value (i.e. $\beta_1 = E_O$ at mean centered $SWC = 0$ and $AntSWC = 0$ and at $AntA_{pred} = 0$). We chose normal priors for T_O and β_1 , with the prior means given by the Lloyd & Taylor estimates of T_O and E_O (227.13 and 308.56 K, respectively), as described in Cable *et al.* (2008, 2012). T_O was also restricted between 1 and 285 K, where 285 K was just below the minimum value of T measured throughout the study. We assigned standard, noninformative priors to all remaining parameters (i.e. c, α, β , and all variance terms).

Equations 1–4 describe our 'final model' which we compared with three alternative formulations (the A_{sat} model was the same in all four models). The first, which we refer to as the 'current effects model', modifies the models for LR_b and E_O by only expressing these quantities as functions of current endogenous and exogenous conditions (i.e. $\alpha_3 = \alpha_5 = \beta_3 = \beta_5 = 0$ and $AntA_{pred\{d,m\}}$ is replaced with $A_{pred\{d,m\}}$, Eqn 4). Thus, R_{soil} is linked to the current soil water and current photosynthesis (i.e. A_{pred} on the day of the R_{soil} measurement), and it does not

depend on antecedent soil water. The second, which we refer to as the 'day random effects model', builds from the current effects model by including temporal random effects (γ) such that Eqn 3 was modified to include the addition of $\gamma_{\{t\}}$, where t is the measurement day index ($t = 1, 2, \dots, 27$). The third, which we refer to as the 'exogenous model', retains the original Eqn 3, but it assumes that LR_b and E_O are uncoupled from endogenous, above-ground carbon gain (i.e. $\alpha_2 = \beta_2 = 0$, Eqn 4). Comparison of the four models allowed us to quantify: the amount of variation in R_{soil} that is captured by temporal effects that do not provide direct insight into the underlying factors governing R_{soil} (compare the current effects model with the day random effects model); how much of the variation captured by the temporal random effects is explained by exogenous antecedent drivers (compare the exogenous model with the day random effects model); and how much is explained by endogenous and exogenous antecedent drivers (compare the final model with the day random effects model).

Quantifying the antecedent drivers

Historically, when incorporating antecedent conditions, one predetermines the duration of the 'antecedent period' arbitrarily (e.g. 10 d, 2 wk, etc.) and whether or not d/wk into the past carry an equal or declining degree of influence. For example, one may define antecedent soil water as the mean SWC over the past 10 d (i.e. soil water on each day has equal influence). We take a different approach, which allows the data on R_{soil} to inform not only the process parameters in Eqns 3 and 4, but also the parameters describing the actual antecedent variables. In our model for R_{soil} , we work with SWC and predicted maximum photosynthesis (A_{pred}) on a daily timescale, and we defined their associated antecedent values as weighted averages of their past daily values, where the weights are unknown quantities.

Thus, we defined a stochastic model for the antecedent conditions that are relevant to the mechanistic model for R_{soil} . For variable X ($X = A_{pred}$ or SWC), and for day of year d , collar c , and microhabitat m associated with observation i in the R_{soil} dataset, the antecedent value of X is:

$$AntX_{\{d,m\}} = \sum_{k=0 \text{ or } 1}^{N_{days}} w_{X\{k,m\}} X_{\{d-k,c\}}$$

Eqn 5

where k is day into the past ($k = 0$ ('today'), 1 ('yesterday'), $2, \dots, N_{days}$). Note that the weight, w_X , quantifies the relative importance of variable X occurring k d ago for current R_{soil} , and we used different weights for A_{pred} and SWC . For $AntA_{pred}$, we summed from $k = 0$ to $k = N_{days}$ such that the current day's A_{pred} value is included; for $AntSWC$, we summed from $k = 1$ to $k = N_{days}$, as the current SWC is directly incorporated into the model for R_{soil} via the LR_b and E_O models (see Eqn 4). For each microhabitat, we assigned a noninformative Dirichlet before their vector of weights, which forces each w_X to be between 0 and 1 and for all weights to sum to 1 across the antecedent

period of N_{days} within each microhabitat type. Exploratory analyses that varied the value for N_{days} suggested that $N_{\text{days}} = 4$ is appropriate in this study. If $\text{Ant}X$ has a significant effect on R_{soil} – that is, the corresponding α (or β) parameter in Eqn 4 is significantly different from zero – then the w_X values inform us about the relative importance of SWC or A_{pred} conditions experienced on different days into the past; notably high values of a particular w_X would indicate important lag times. We computed the correlations between the posterior (Markov chain Monte Carlo (MCMC)) samples for each pair of parameters. The posterior results for the correlations between the covariate effects (e.g. α or a values and β or b values) in the R_{soil} and A_{sat} model are provided in the Supporting Information (Table S1). These results indicate that some of these effects are relatively highly correlated (e.g. $a[3]$ and $a[4]$, $b[3]$ and $b[4]$, $a[4]$ and $b[4]$), but this correlation is accounted for within the Bayesian model, and it did not cause issues with convergence of mixing of the MCMC chains.

Model implementation and model comparison

The four R_{soil} model formulations were implemented in the Bayesian statistical software package OpenBUGS (Lunn *et al.*, 2009). For all models, we ran three parallel MCMC chains for 110 000 iterations; we discarded the first 10 000 (burn-in) samples and thinned every 50th iteration to reduce both storage requirements and within-chain autocorrelation. This yielded an independent sample of 6000 values for each parameter from the joint posterior distribution (Brooks & Gelman, 1998; Gelman, 2003). We used the built-in Brooks–Gelman–Rubin diagnostic tool to evaluate convergence of the chains to the posterior distribution (Gelman, 2004). For each parameter of interest, we present its posterior mean and central 95% credible interval (CI). Regression model coefficients (e.g. c_2 – c_4 , α_2 – α_5 , β_2 – β_5 ; see Eqns 1 and 4) whose 95% CI contains 0 are generally deemed nonsignificant. This criterion that the CIs don't contain 0 is equivalent to a 'classical two-sided' test, whereas the Bayesian P -values we report in are equivalent to a 'one-sided' test. Thus, in the rare case where the 95% CI only slightly contains 0 (i.e. 0 is very close to one of the interval end-points), the Bayesian P -value is likely to indicate that this parameter is significantly different from 0. In such cases, where the CI and P -value may not 'agree perfectly', we utilize the P -value, as the Bayesian approach is generally more conservative in terms of revealing significant effects, and such 'marginal' cases may still imply important biological significance.

We used two different model indices to compare the four aforementioned models of R_{soil} . We conducted regressions of observed vs predicted R_{soil} (on the log scale) to visually and quantitatively evaluate model fit and bias, where the predicted values are the posterior means for μLR in Eqn 3. We also computed the deviance information criterion (DIC; Spiegelhalter *et al.*, 2002) for each model. DIC is a model comparison statistic that accounts for model fit while also penalizing for model complexity, which is represented as the effective number of parameter (pD). In a nonhierarchical model, pD should be approximately

equal to the countable number of parameters, but it is often less than the countable number in a hierarchical model. A lower DIC indicates a better model, and a difference of 10 or more between DIC values indicates strong support for the best model (Spiegelhalter *et al.*, 2002).

Results

Exogenous controls on leaf-level photosynthesis

In an attempt to better describe previously unexplained temporal variation in R_{soil} (Cable *et al.*, 2008), we incorporated the antecedent effects of light-saturated photosynthesis (A_{sat}) and SWC (AntSWC) to provide a mechanistic link between R_{soil} and above- and below-ground controls. Thus, three of the four R_{soil} models that we evaluated were linked to A_{sat} , although only the final model incorporated the effects of antecedent A_{sat} . Independent of the R_{soil} model, the A_{sat} model performed exceptionally well for both mesquite and bunchgrass ($r^2 = 0.94$ and 0.99 , respectively; Fig. 2), and measured and predicted A_{sat} values were well within range of those reported in the literature for these or similar species (Wan & Sosebee, 1990; De Soyza *et al.*, 1996; Potts *et al.*, 2008; Hamerlynck *et al.*, 2010; Barron-Gafford *et al.*, 2012, 2013). Given the covariance among the three parameters examined, we found that adding the singular term of maximum air temperature ($T_{\text{air max}}$) did not have a significant effect on A_{sat} in mesquite (95% CI for c_2 from Eqn 1 contained zero); however, $T_{\text{air max}}$ did have a significant positive influence on A_{sat} in bunchgrasses (Fig. 3a). Furthermore, increases in VPD (VPD_{max}) were positively correlated with A_{sat} rates in both species ($c_3 > 0$; see Eqn 1), but the influence was nearly five times greater in bunchgrasses (Fig. 3b). Increases in SWC did not significantly influence A_{sat} in mesquite microhabitats (95% CI for c_4 , Eqn 1, contained zero), but positively affected A_{sat} in bunchgrass

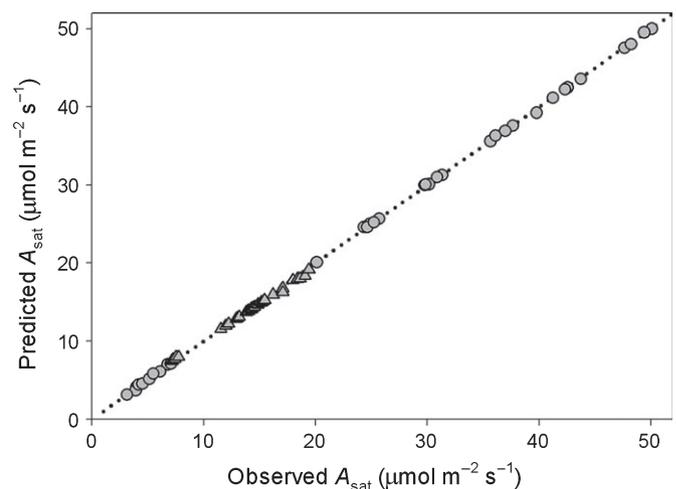


Fig. 2 Comparison of observed vs predicted light-saturated photosynthesis (A_{sat}). Data are shown for two microhabitats (mesquite, triangles; bunchgrass, circles) collected across 7 d spanning all seasonal periods; predicted values are the posterior means for μA_{sat} in Eqn 1. The diagonal dotted line is the 1 : 1 line.

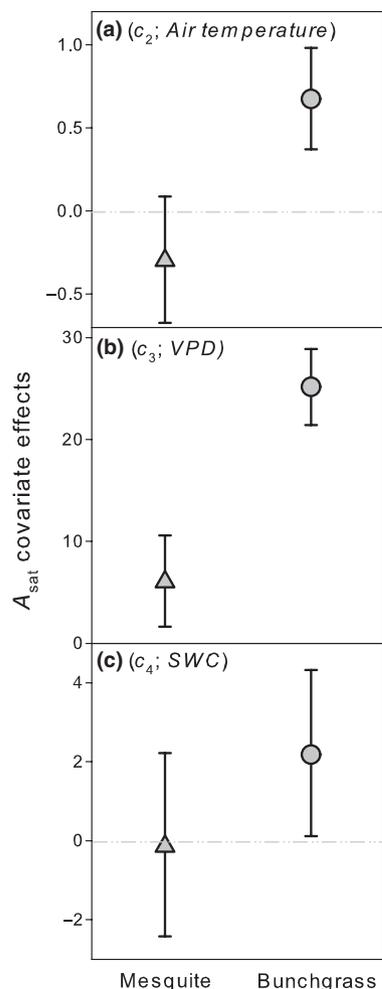


Fig. 3 The posterior means and 95% credible intervals (CIs) for the parameters (effects) in the model for light-saturated photosynthesis (A_{sat}) (see Eqn 1). Results are shown for the effects associated with: (a) air temperature (c_2); (b) vapor pressure deficit (VPD; c_3), and (c) current soil water content effect (SWC; c_4). Estimates are shown for two microhabitats (mesquite, triangles; bunchgrass, circles); CIs that overlap the dashed horizontal line at zero indicate the lack of an effect.

microhabitats ($c_4 > 0$), illustrating a greater sensitivity of photosynthesis to changes in shallow water availability within the bunchgrass (Fig. 3c).

Exogenous and endogenous controls on R_{soil}

The day random effects model fit the R_{soil} data well for both microhabitats ($r^2 = 0.94$ for both mesquite and bunchgrass; $r^2 = 0.99$ when lumped), and observed vs predicted points fell tightly around the 1:1 line (Fig. 4a). Much of this goodness-of-fit, however, was the result of the explicit incorporation of the temporal (γ) random effects into Eqn 3. The current effects model, which did not include the γ effects, notably reduced model fit and increased model bias ($r^2 = 0.55$ and 0.65 for mesquite and bunchgrass, respectively, and points do not consistently fall around the 1:1 line; Fig. 4b). That is, the poorer performance of the current effects model is

attributed to greater variation among average predicted R_{soil} rates and substantial overestimation of low fluxes (bias). Accounting for AntSWC within our exogenous model increased goodness-of-fit by 19 and 13% for mesquite and bunchgrass, respectively (Fig. 4c). Inclusion of Ant A_{pred} and AntSWC into the final model of R_{soil} , however, resulted in a more substantial increase in model fit relative to the current effects model, for both mesquite ($r^2 = 0.89$; 29% increase) and bunchgrass ($r^2 = 0.89$; 25% increase; Fig. 4d). This greatest improvement in performance suggests that the final model is capturing potential mechanisms that explain the majority of the temporal random effects associated with the day random effects model. The DIC, however, suggests that the random effects model performed the best (lowest DIC; Table 1), but this model also had the highest number of effective parameters (pD ; Table 1). Ultimately, the final model was the optimal choice because of the balance between model performance (second lowest DIC), the number of effective parameters (second lowest pD), and the amount of mechanistic insight provided (comparatively high).

Thus, we focus on the results from the final model to evaluate the influence of antecedent factors. Antecedent drivers can affect R_{soil} by influencing the base rate (LR_b , Eqns 3 and 4) and/or the temperature sensitivity (E_0 , Eqn 3). We found that higher LR_b is correlated with higher Ant A_{pred} in both microhabitats (Fig. 5a; $P < 0.0001$ for both microhabitats, Table 2). Importantly, the posterior mean for α_2 was nearly fourfold higher in mesquite than in bunchgrass microhabitats, indicating significantly greater sensitivity of LR_b to Ant A_{pred} under mesquite (i.e. 95% CIs for each α_2 do not contain the posterior mean of the other microhabitat's α_2). AntSWC positively influenced LR_b in bunchgrass microhabitats ($\alpha_3 > 0$, Fig. 5b; $P = 0.0018$, Table 2), but current-day SWC did not directly influence LR_b (Fig. 5c; 95% CI for α_4 contained zero for both microhabitats). Additionally, we detected a significant negative interaction of current-day SWC by AntSWC on LR_b , such that the strongest positive effect of AntSWC occurred when current conditions were relatively dry (Fig. 5d; $\alpha_5 < 0$ for both microhabitats; $P = 0.0092$ and 0.0052 for mesquite and bunchgrass, respectively, Table 2). Thus, during prolonged moist periods (i.e. past and current SWC are relatively high), LR_b is relatively insensitive to changes in water availability.

We found that lower E_0 is also correlated with higher Ant A_{pred} in both microhabitats (Fig. 5e; $P = 0.0007$ and 0.0260 for mesquite and bunchgrass microhabitats, respectively; Table 2). Changes in AntSWC positively influenced E_0 within the mesquite ($P = 0.0713$) but not within bunchgrass microhabitats ($P = 0.1903$, Table 2; Fig. 5f). On the contrary, increases in current SWC reduced E_0 in the bunchgrass microhabitat ($P = 0.0298$), but had no effect in the mesquite microhabitat ($P = 0.1842$, Table 2; Fig. 5g). There was a significant negative interaction effect of current-day SWC by AntSWC for both microhabitats (Fig. 5h; $P = 0.0022$ and < 0.0001 for mesquite and bunchgrass, respectively) such that the sensitivity of R_{soil} to changes in soil temperature was reduced when soil moisture had been relatively constant and/or high. Conversely, E_0 increased

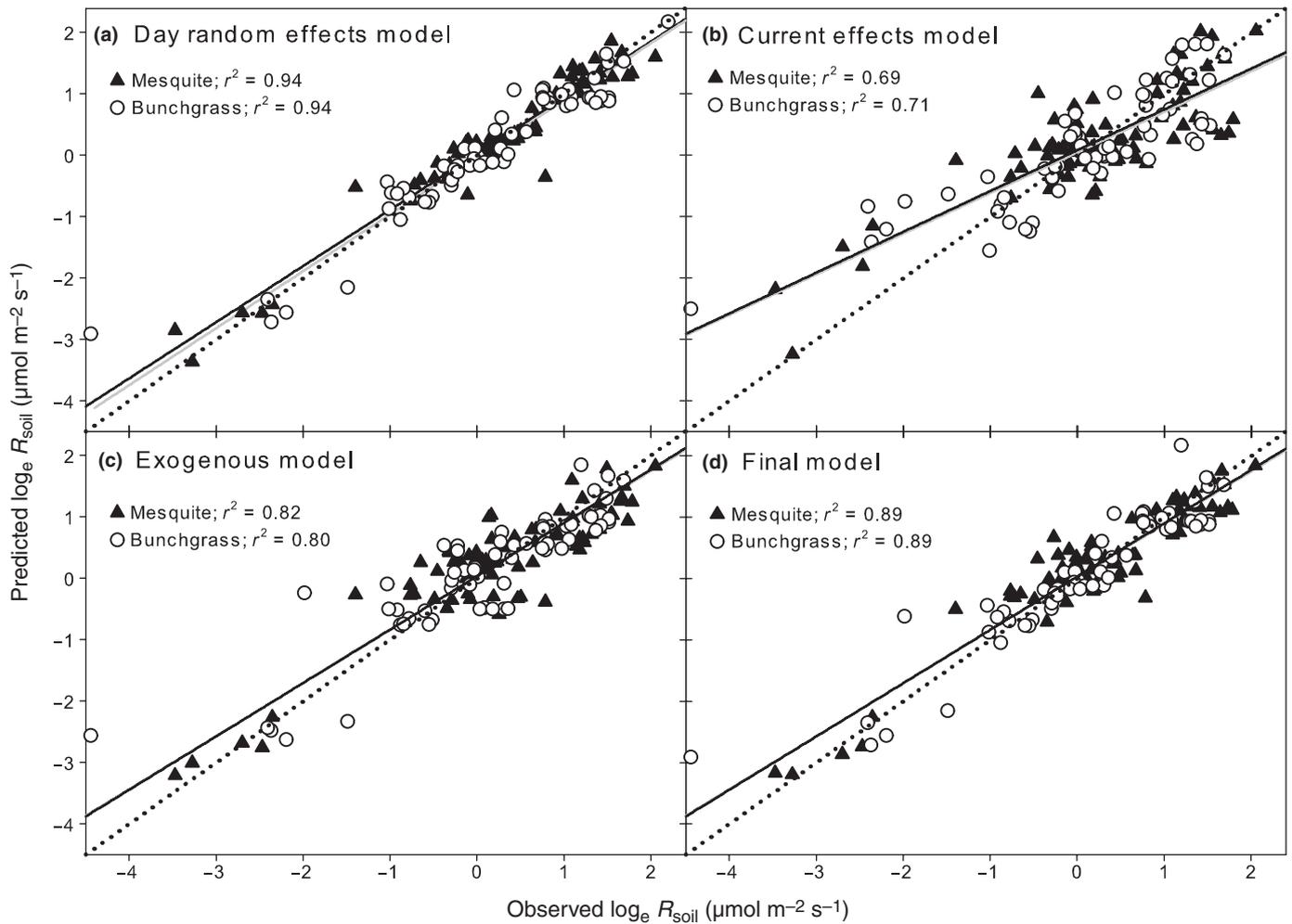


Fig. 4 Comparison of observed vs predicted natural log (\log_e) of soil respiration rates (R_{soil}) from four different models for R_{soil} : (a) the day random effects model is based on the model described in Cable *et al.* (2008), which incorporated the effects of current soil temperature, current soil water content, spatial (collar) and temporal (day of measurement) random effects, but also includes the effect of current photosynthesis (A_{pred}); (b) the current effects model is similar to the day random effects model but lacks the temporal random effects; (c) the exogenous model includes exogenous effects related to current and antecedent previous soil moisture status (AntSWC) but excludes the endogenous effect of A_{sat} ; and (d) the final model includes antecedent exogenous and endogenous factors, linking above-ground productivity and below-ground efflux by including Ant A_{pred} and AntSWC effects. The predicted values are the posterior means for μLR (mean of $\log_e R$) in Eqn 3. The gray and black lines are the regression lines for each microhabitat type; the diagonal dotted line is the 1 : 1 line.

Table 1 Model comparison indices, including the deviance information criterion (DIC), the number of effective parameters (pD , a component of DIC), and coefficients of determination (r^2) obtained from a traditional regression of the observed vs predicted R_{soil} values

Soil respiration model	DIC	pD	Observed vs predicted r^2	
			Mesquite	Bunchgrass
Day random effects model	118.9	35.3	0.939	0.935
Current effects model	323.5	26.2	0.686	0.709
Exogenous model	248.0	20.3	0.816	0.797
Final model	187.4	22.7	0.878	0.891

in response to increased moisture availability (i.e. increase in current SWC) if past conditions were relatively dry, as would occur immediately after a sizeable rain event that broke a dry spell.

Characteristics of the antecedent endogenous and exogenous drivers

The noninformative Dirichlet prior that we assigned to the microhabitat-specific weight vectors (w_X , Eqn 5) for Ant A_{pred} in the final model gave equal weight to each day over a 5 d antecedent period (prior mean = 1/5 for each daily w_X), with relatively high uncertainty (i.e. wide 95% prior predictive CIs; Fig. 6). The field data notably refined the estimates of w_X defining antecedent photosynthesis (Ant A_{pred}) in the mesquite microhabitat; that is, the posterior means for each daily w_X generally differed from the prior mean, and the posterior 95% CIs were much narrower than the prior CIs (Fig. 6a). A clear lag response to A_{sat} emerged such that A_{sat} rates 3 d before the R_{soil} measurement were most important in determining current-day R_{soil} under mesquite (Fig. 6a).

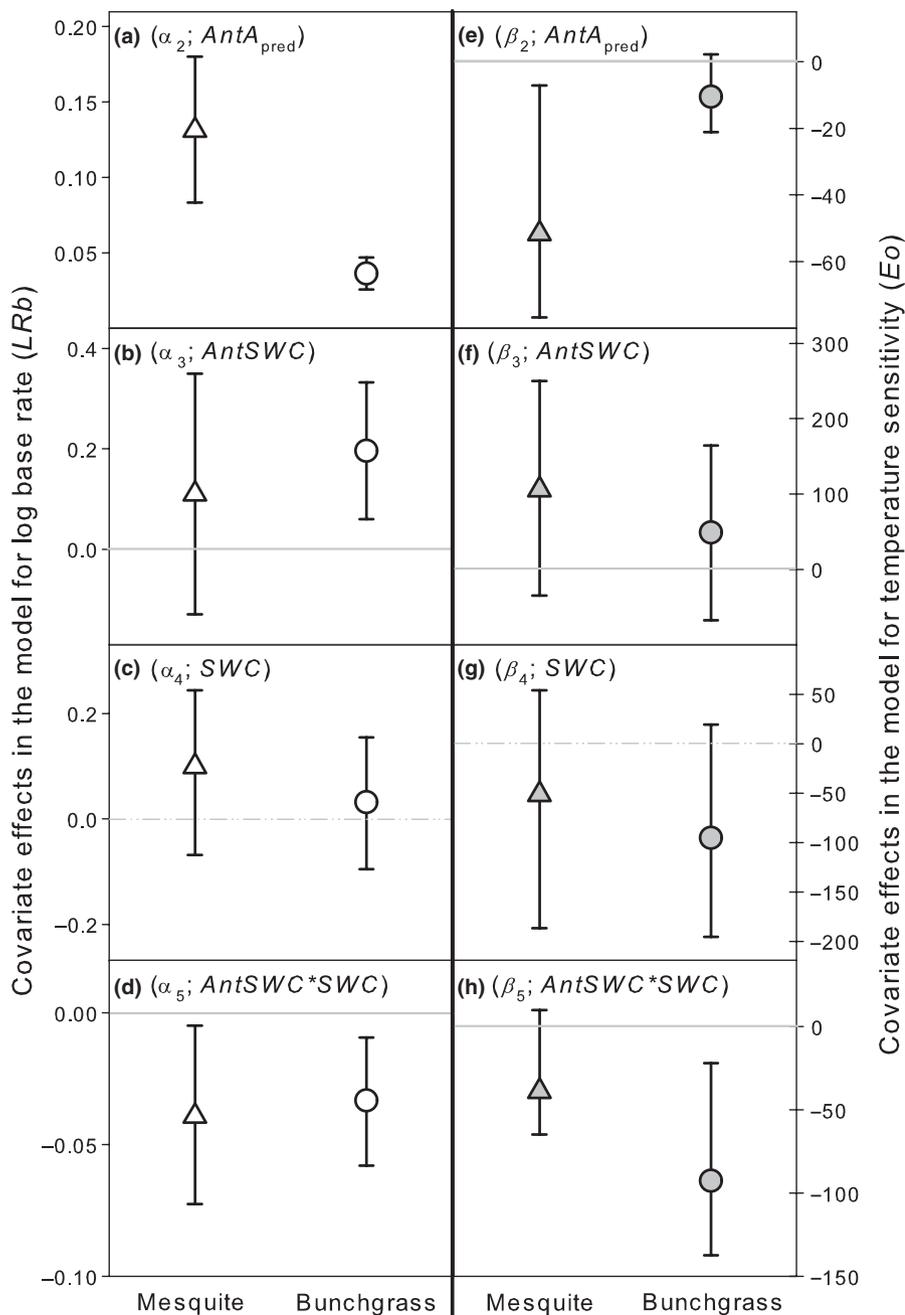


Fig. 5 Posterior means and 95% credible intervals (CIs) for the parameters (effects) in the model for the log-scale base rate (LR_b ; a–d; Eqn 4) and the temperature sensitivity (E_o ; same as Eqn 4, but with parameters indicated by β values instead of α values) (e–h) associated with the final model of R_{soil} . (a, e) The antecedent light-saturated photosynthesis ($AntA_{pred}$) effect on LR_b and E_o (α_2 and β_2 , respectively); (b) the antecedent soil water content ($AntSWC$) effect (α_3 and β_3 , respectively); (c) the current-day soil water content (SWC) effect (α_4 and β_4 , respectively); and (d) the $AntSWC \times$ current SWC effect (α_5 and β_5 , respectively). Results are shown for two microhabitats: mesquite, triangles; bunchgrass, circles.

Within the bunchgrass microhabitats, the posterior 95% CIs were wider than those for mesquite, and the means for each w_X did not differ notably from the prior means for days 0 or 2–5. Still, a shorter, 1 d lag time is likely, indicating that A_{sat} rates the day before the R_{soil} measurement were most important in determining current-day R_{soil} under bunchgrasses (Fig. 6b).

Similar analyses of the exogenous factors such as $AntSWC$ indicate that SWC conditions associated with the day before the R_{soil} measurement were most important in determining current-day R_{soil} within both microhabitats, although this 1 d lag was more pronounced under bunchgrasses (Fig. 7a,b).

Within the bunchgrass microhabitat, the posterior means for the $AntSWC$ weights were lower than the prior means for days 2–4, and the posterior 95% CIs were about two-thirds narrower than the prior CIs within both microhabitats. Given the aforementioned significant effects of current SWC , $AntSWC$, and their interaction, this indicates that the current (SWC) and previous day's soil moisture conditions ($AntSWC$ with high value of w_X for $k=1$; Eqn 5) are the most important soil moisture-related variables for predicting R_{soil} in both microhabitats. Soil moisture patterns further into the past ($k>1$, Eqn 5) appear to be relatively unimportant for predicting current R_{soil} .

Table 2 Bayesian one-sided *P*-values indicating the significance or relative importance of each exogenous and endogenous variable included in the final model; effects are ranked in order of significance (or importance) for each microhabitat within the base rate (LR_b) and temperature sensitivity (E_O) models

Log base rate (LR_b) model				Temperature sensitivity (E_O) model		
Microsite	Effect	Covariate	<i>P</i> -value	Effect	Covariate	<i>P</i> -value
Mesquite	α_2	AntA _{pred}	< 0.0001	β_2	AntA _{pred}	0.0007
	α_5	AntSWC × SWC	0.0092	β_5	AntSWC × SWC	0.0022
	α_4	SWC	0.1195	β_3	AntSWC	0.0713
	α_3	AntSWC	0.2237	β_4	SWC	0.1842
	α_2	AntA _{pred}	< 0.0001	β_5	AntSWC × SWC	< 0.0001
Bunchgrass	α_3	AntSWC	0.0018	β_2	AntA _{pred}	0.0260
	α_5	AntSWC × SWC	0.0052	β_4	SWC	0.0298
	α_4	SWC	0.3022	β_3	AntSWC	0.1903

AntA_{pred}, antecedent leaf-level, predicted saturated photosynthesis; SWC, soil water content; AntSWC, antecedent SWC.

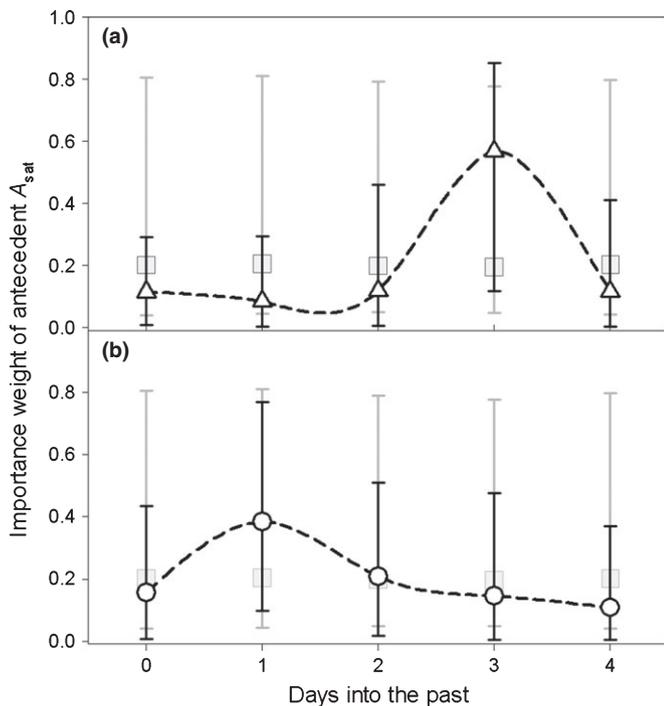


Fig. 6 Posterior means and 95% credible intervals (CIs) for the weights (w_x , Eqn 5) associated with the definition of antecedent light-saturated photosynthesis (AntA_{pred}) within mesquite (a, triangles) and bunchgrass (b, circles) microhabitats. The weights from the noninformative Dirichlet prior (gray squares, with 95% CIs) are provided for comparison with the posterior results.

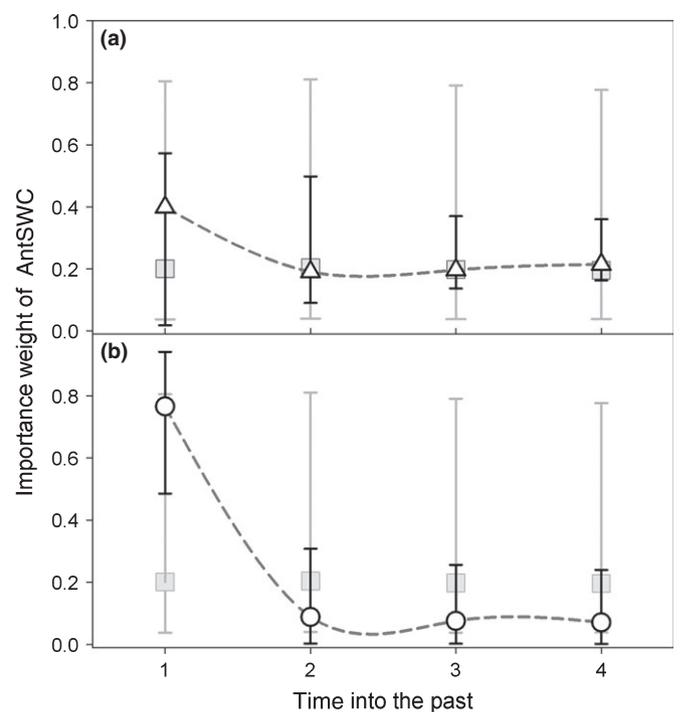


Fig. 7 Posterior means and 95% credible intervals (CIs) for the weights (w_x , Eqn 5) associated with the calculation of antecedent soil water content (AntSWC) within mesquite (a, triangles) and bunchgrass (b, circles) microhabitats. The weights from the noninformative Dirichlet prior (grey squares, with 95% CIs) are provided for comparison with the posterior results.

Discussion

Given projected concomitant changes in regional climate and vegetative cover (Seager *et al.*, 2007), it is increasingly necessary to improve predictive capacities of models that link environmentally driven and biologically mediated processes, such as soil carbon cycling and ecosystem–atmosphere exchange dynamics (Davidson *et al.*, 2006). Here, we developed a simple model for estimating soil respiration (R_{soil}) across different microhabitat types that provides an insight into the relative influence of endogenous (e.g. above-ground carbon dynamics via photosynthesis) and exogenous (e.g. temperature and soil moisture) controls on

soil respiration, while also improving our understanding of their antecedent influences. While this study was conducted within a semiarid environment, it is important to keep in mind the generality of the drivers considered in this study (air temperature, VPD, and SWC). Additionally, semiarid ecosystems make effective model systems for evaluating interactions that characterize terrestrial ecosystem dynamics globally given: that 41% of the earth’s terrestrial surface comprises drylands and that this number is predicted to grow as a result of climate change (Feng & Fu, 2013); and that the majority of the terrestrial biosphere is water-limited at some point during the year (Jenerette *et al.*, 2012).

Application of this model examining above-ground–below-ground linkages yielded four key results.

First, both endogenous and exogenous controls are critical drivers of variation in R_{soil} , but the relative importance of these two types of driver depends on characteristics tied to vegetation structure. For example, there was a positive effect of prior photosynthesis rates on base rates of R_{soil} , and R_{soil} was greatest during periods of peak above-ground carbon uptake, regardless of microhabitat type (Fig. 5). The temperature sensitivity of R_{soil} (E_{O}), however, was reduced by antecedent photosynthesis rates within both microhabitats. This finding might suggest that in periods of greater carbon input into the soils, limitations of temperature on the energy of activation of R_{soil} are less constraining. Alternatively, because plant exudates are more labile than most other substrates and E_{O} varies with substrate, the negative relationship between antecedent photosynthesis and E_{O} could reflect the higher amounts of labile soil carbon (*sensu* Davidson & Janssens, 2006). The temperature sensitivity of R_{soil} was also reduced by wetter current soil conditions in bunchgrass microhabitats, but was not affected by current or antecedent soil moisture in mesquite microhabitats. Recent studies have also found a stronger connectivity between R_{soil} and patterns of soil moisture under bunchgrasses than under mesquite shrubs, where rates of efflux are less sensitive to wetting cycles (Barron-Gafford *et al.*, 2011). Moreover, every parameter in the A_{sat} model was significantly different between microhabitat types (Fig. 3), such that the physiological responses of the deep-rooted mesquites were only minimally sensitive to changes in temperature and surface soil moisture compared with the bunchgrasses. Thus, although the plant-level physiological responses differ between these two species (Fig. 3), the R_{soil} responses among the microhabitat types are less different (Fig. 5), probably because R_{soil} represents a mixture of autotrophic and heterotrophic contributions (Cable *et al.*, 2008), and the heterotrophic responses may be similar across microhabitat types.

Secondly, the time-period over which endogenous drivers are most important for R_{soil} – that is, the antecedent effect of A_{sat} – is tied to vegetative structure and composition (Fig. 6). Under bunchgrasses, we found weak evidence for single-day lag in the time between the plant carbon uptake and the associated soil microhabitat R_{soil} . Conversely, in mesquite microhabitats, we detected a more significant and longer lag-period, such that photosynthesis rates 3 d previously were the most influential in driving current-day rates of R_{soil} (Fig. 6a). This lag period aligns with the expected amount of time that would elapse between leaf-level CO_2 assimilation by shrubs, transport of the photosynthate products to the roots, and subsequent efflux of the metabolized products from nearby soils. For example, similar carbon transport lag times in shrubs and trees have been demonstrated based on eddy covariance data (Tang *et al.*, 2005), isotopic labeling techniques (Carbone & Trumbore, 2007), estimates of stomatal conductance and photosynthetic carbon isotope discrimination (Bowling *et al.*, 2002), substrate supply and R_{soil} transfer models throughout canopy expansion (P. Y. Oikawa *et al.*, unpublished) and wavelet analysis of the synchronicity of canopy photosynthesis and R_{soil} fluxes (Vargas *et al.*, 2011).

Thirdly, the importance of antecedent exogenous drivers and the time-period over which they influence R_{soil} are also tied to vegetative structure and composition (Fig. 7). Differential rooting behavior is, again, likely to underlie dissimilarities in the influence of exogenous environmental controls, such as soil water effects on R_{soil} . Deep-rooted shrubs such as mesquite are able to access subsurface water at depths beyond the reach of the more shallow-rooted bunchgrasses (De Deyn *et al.*, 2008; Scott *et al.*, 2006; Williams *et al.*, 2006). Thus, bunchgrasses are more reliant on shallow soil water, which reflects recent precipitation inputs, yielding a relatively short antecedent period of influence. Furthermore, patterns of root exudation are driven by above- and below-ground plant activity associated with photosynthesis and nutrient uptake, respectively (Bardgett *et al.*, 2005). Given that the phenology of productivity by the deep-rooted shrubs is comparatively less coupled to precipitation (Scott *et al.*, 2006), so too are patterns of R_{soil} within these microhabitats. These findings underscore how a transformation in ecosystem structure (e.g. woody plant expansion) across semiarid regions will probably lead to a change in their functioning in terms of processes important to climate feedbacks, such as the magnitude and timing of ecosystem carbon fluxes (Goodale & Davidson, 2002).

Finally, in order to forecast ecosystem carbon balance under current and future climate regimes, we need a reliable means of estimating the dominant carbon fluxes, and our modeling approach highlights important components that should be considered. Recent models have been fairly successful at capturing the variability in observed R_{soil} rates, especially in semiarid, pulse-driven systems (Cable *et al.*, 2008, 2009, 2012; Chatterjee & Jenerette, 2011; Lellei-Kovács *et al.*, 2011). Some of these improvements have stemmed from a better quantification of microhabitat-specific sensitivities to abiotic drivers or the relative importance of moisture at different depths within the soil profile. However, a notable amount of variation in R_{soil} has been attributed to random, unexplainable temporal and/or spatial effects (e.g. Cable *et al.*, 2008). We showed that the inclusion of antecedent photosynthesis and soil water effects into a model of R_{soil} greatly improved model performance, and these antecedent effects accounted for most of the variation previously captured by the temporal random effects. The importance of incorporating endogenous influences into models of R_{soil} is not surprising, given that several recent studies have highlighted the potential importance of photosynthetic inputs for understanding the magnitude of R_{soil} (Tang *et al.*, 2005; Kuzyakov & Gavrichkova, 2010; Mencuccini & Holtta, 2010; Vargas *et al.*, 2011).

As noted by Davidson *et al.* (2006) and Gaumont-Guay *et al.* (2006), we need to move beyond simple correlations between R_{soil} and temperature to better quantify the primary driving effects of temperature, soil water, and carbon substrate supply on R_{soil} . Given that we now have > 500 eddy covariance sites worldwide recording environmental forcing variables (<http://daac.ornl.gov/FLUXNET/fluxnet.shtml>) and that the regional climate modeling community is prepared to integrate growth-form and spatially explicit models of R_{soil} (Collins *et al.*, 2008; Shen *et al.*, 2008; Zhang *et al.*, 2009), we are poised to make significant advances in forecasting soil and ecosystem carbon balance

through mechanistic models of above-ground–below-ground linkages (Luo *et al.*, 2011). In this regard, this work illustrates the importance of the inclusion of a substrate supply-like term (antecedent photosynthesis) within a simple model of R_{soil} that involves important environmental features, thereby improving soil CO_2 efflux estimates for semiarid systems. Such integration of biological and physical features in developing predictive capacity in ecology has been an important grand challenge.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1 The posterior results for the correlations between the covariate effects (e.g., α or a values and β or b values) in the R_{soil} and A_{sat} models

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