

## Article

# Evaluation of the ECOSSE-Model for Estimating Soil Respiration from Eight European Permanent Grassland Sites

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**Abstract:** This study used the ECOSSE model (v. 5.0.1) to simulate soil respiration (Rs) fluxes estimated from ecosystem respiration ( $R_{eco}$ ) for eight European permanent grassland (PG) sites with varying grass species, soils, and management. The main aim was to evaluate the strengths and weaknesses of the model in estimating Rs from grasslands, and to gain a better understanding of the terrestrial carbon cycle and how Rs is affected by natural and anthropogenic drivers. Results revealed that the current version of the ECOSSE model may not be reliable for estimating daily Rs fluxes, particularly in dry sites. However, it could still be a valuable tool for predicting cumulative Rs from PG. Additionally, the model demonstrated accurate simulation of Rs in response to grass cutting and slurry application practices. The sensitivity analyses and attribution tests revealed that increased soil organic carbon (SOC), soil pH, temperature, reduced precipitation, and lower water table (WT) depth could lead to increased Rs from soils. The variability of Rs fluxes across sites and years was attributed to climate, weather, soil properties, and management practices. The study suggests the need for additional development and application of the ECOSSE model, specifically in dry and low input sites, to evaluate the impacts of various land management interventions on carbon sequestration and emissions in PG.

**Keywords:** ECOSSE model; Permanent grasslands; Soil respiration; European grasslands

## 1. Introduction

Atmospheric carbon dioxide (CO<sub>2</sub>) concentration has been increasing since the beginning of industrialization (1). In 2021, the concentration of CO<sub>2</sub> in the atmosphere set a record of about 415 ppm, and it is predicted to reach 800 ppm by the end of this century (2). Beside respiration and fires which are significantly increasing atmospheric CO<sub>2</sub> emissions, human activities, including agricultural production, are not only increasing the CO<sub>2</sub> but also the concentration of other greenhouse gases (GHGs), such as methane (CH<sub>4</sub>) and nitrous oxide (N<sub>2</sub>O) (1). Moreover, Caldeira and Wickett (3) reported that man-made CO<sub>2</sub> emissions are contributing to acidification of open oceans however, direct pH measurements and experience in this area are still limited (4,5). Interaction between management practices, climate, and soil properties influence soil carbon stocks. For example, intensive management of permanent grasslands (PG) to support ruminant livestock production alters GHG emissions from EU-grasslands and can reduce their ability to act as C sinks (6). Further, in 2017, the livestock sector was responsible for 81–86% of the total agriculture GHG emissions in the EU-28 (7).

In Europe (EU-27 plus the UK and Switzerland), PG cover approximately 34% of the **agricultural area** and represent a source for many ecosystem services, for example climate regulation and carbon sequestration, cultural values, and high-quality animal feed (6, 8, 9, 10, 11). In terms of total area, the countries with the largest grassland area found are the United Kingdom (11 million ha), France (7.6 million ha), Germany (4.8 million ha) and Italy (4.5 million ha) (12). PG potentially contribute to mitigation of climate change by assimilating atmospheric CO<sub>2</sub> and sequestering it

in the soil depending on climate, soil, and management (13). Improved grassland management by improving grass and herb species, irrigation, liming and fertilisation can increase the annual soil organic carbon (SOC) stocks by 10% (14, 15).

Soils are the largest C pool in terrestrial ecosystems, containing more than two thirds of the total C. However, soil respiration (i.e., total CO<sub>2</sub> effluxes from the soil surface which consists of autotrophic root and heterotrophic respiration from decomposition of litter roots and soil organic matter (SOM)) is a critical component of the global carbon cycle and greatly contributes to the atmospheric CO<sub>2</sub> concentration (16). The decomposition of litter, roots, and SOM results in Rs fluxes (18). In a global meta-analysis, Wang and Fang (17) quantified annual soil CO<sub>2</sub> efflux from temperate and tropical natural grasslands as  $389.8 \pm 45.5$  and  $601.3 \pm 45.6$  g C m<sup>-2</sup>, respectively. Previous studies have found that increases in Rs are due to increasing soil temperature (19, 20,21). Higher temperature also increases the long-term soil C decomposition and impacts CO<sub>2</sub> emissions from the soil to the atmosphere (22, 23). Further, elevated CO<sub>2</sub> concentrations in the atmosphere, due to anthropogenic emissions and the positive feedback loops resulting from global warming, increases both the below and above ground biomass production and thereby, although uncertain due to high photosynthesis also, can increase CO<sub>2</sub> fluxes from soils (17, 24).

The Model to Estimate Carbon in Organic Soils-Sequestration and Emissions (ECOSSE) was created to simulate C and nitrogen (N) cycling and GHG fluxes from soils. The principles of two mother models, RothC (25, 26, 27) and SUNDIAL (28, 29) were used for this purpose. The ECOSSE uses a pool-type approach of humus (HUM), inert organic matter (IOM), biomass (BIO), resistant plant material (RPM) and decomposable plant material (DPM) (30). Material moves between these pools during the decomposition process according to first-order rate equations, characterised by a decay rate constant for each pool. The exchange between pools is controlled by temperature, moisture, crop cover and soil pH. The soil pH affects aerobic SOC decomposition according to equation 1 (31):

$$m_{pH} = m_{pH,min} + (1 - m_{pH,min}) \left( \frac{pH - pH_{min}}{pH_{max} - pH_{min}} \right) \quad (1)$$

The values of  $m_{pH,min}$ ,  $pH_{min}$  and  $pH_{max}$  can be set for each site, but by default are set at  $m_{pH,min} = 0.2$ ,  $pH_{min} = 1$  and  $pH_{max} = 4.5$ .

The work by Jenkinson (25) on the impact of plant cover on the decomposition of <sup>14</sup>C labelled ryegrass is relevant to the modelling of soil organic matter (SOM) decomposition in ECOSSE. In ECOSSE, the rate of SOM decomposition is slowed using a crop cover rate modifier ( $m_c$ ) of 0.6 if plants are actively growing, and 1 if the soil is bare. The active SOC pools implicitly encompass different qualities of SOC (e.g., lignin quantity, etc.) through their different intrinsic decomposition rates and stable C:N ratios, with N being either mineralised or immobilised to maintain that ratio. Variation in the quality of plant inputs to the soil is expressed through land-use types having different DPM-RPM ratios, e.g., grassland has a DPM:RPM ratio of 1.44, whereas forestry has a DPM:RPM ratio of 0.25 to account for its more recalcitrant plant material. Also, the plant inputs from other land-use types have different C:N ratios (27). Clay content of the soil impacts aerobic decomposition by altering the partitioning between CO<sub>2</sub> evolved and BIO+HUM formed during decomposition (25, 28). Clay content is used to determine the efficiency of decomposition ( $E$ ) under non-N-limiting conditions. The objectives of this research were to (1) evaluate the ECOSSE model to understand its strengths and weakness for estimating Rs from eight European permanent grasslands with their respective climate, grass type and management, and to (2) obtain a better understanding of the terrestrial C cycle and attribution of Rs to variability in natural and anthropogenic (climate and management) drivers in the European PG ecosystem.

## 2. Materials and Methods

### 2.1. The study sites

In this study, Rs fluxes from eight European permanent grassland sites were investigated. The sites cover seven countries and have different soils, climatic conditions, and management. Average annual temperatures and precipitation ranged from 4 to 10.2 °C and from 622 to 1365 mm, respectively. Site information with geographic coordinates, climatic conditions, grassland type and management are given in Table 1. The soil types at the sites varied from sandy loam to clay soils. Initial SOC contents were either measured or estimated using soil % C, bulk density, and sampling depth at the site. Details of soil properties, water table depth and SOC can be found in Table 2.

## 2.2. CO<sub>2</sub> Flux measurements

Measurements of net ecosystem exchange (NEE) at each site were made by Eddy Covariance (EC) using either open or closed path infra-red gas analysers (32, 33). Then ecosystem respiration ( $R_{eco}$ ) of CO<sub>2</sub> fluxes were calculated from the NEE data and made available by Super-G, GHG-Europe and Carbo-Europe projects, and the Flux-net website. Full descriptions of the sites, EC data corrections, quality control, footprint, gap filling procedures and calculations of  $R_{eco}$  can be found in the literature: Easter Bush in Jones et al. (34), Alp Weissenstein in Hiller et al. (35), Neustift in Wohlfahrt et al. (36), Chamau in Fuchs et al. (37), Matra in Pinter et al. (38), Grünschaige in Hirl et al. (39), Borova in Cuhel et al. (40) and Amperlo in Balzarolo et al. (41). Meteorological data (average daily air temperature and precipitation) over the period 2002 to 2018 were collected from the investigated sites to be used as inputs to the model. Measurement durations differed among sites and ranged from 3 to 11 years. To estimate  $R_s$  from  $R_{eco}$ , the approach (equation 2) of Hardie et al. (42) and Abdalla et al. (19) was applied.

$$R_s = R_s \text{ (from surface soils)} + R_s \text{ (below water table soils)} = 46\text{-}59\% \text{ of } R_{eco} \quad (2)$$

Where  $R_s$  is suggested to be 46% of  $R_{eco}$  during the summer (June-August), 59% during the winter (December-February) and mean value (52.5 % of  $R_{eco}$ ) during the rest of the year (March-May and September-November). More details about the estimation can be found in Hardie et al. (42) and Abdalla et al. (19).

## 2.3. The ECOSSE model

The ECOSSE model (v. 5.0.1) was applied to simulate  $R_s$  from grassland soils at all sites. Then the outputs of the model were compared to the estimated  $R_s$  values. ECOSSE is a process-based model that uses a pool-type approach, and all major processes of C and N turnover in the soil are included and described using simple equations driven by readily available input parameters. The model can be applied for all types of soils and ecosystems at site, national or global scales. To run the model, data of climate, soil characteristics, vegetation biomass inputs and management practices of each site are required (Tables 1 and 2). ECOSSE uses the water-module of the SUNDIAL model (43), where water moves through the soil pores by 'piston flow'. The 5-cm-layer soil profiles in ECOSSE gradually fill with water until saturation, then water either drains to the layer below or evaporates from the topmost layer. The model estimates the addition or loss of C and N using their amounts in the above and below-ground biomass. The model can also estimate the amount of organic matter (OM) input from the vegetation biomass if information on grass is not provided. The total SOC estimated by a steady-state (10,000 year) run using default biomass inputs is compared to the total observed SOC, and a revised estimate is made of the OM inputs so that simulated steady-state SOC matches the observed values. Plant material is divided into resistant and decomposable material based on ratio of 1.44 (as used in the RothC model) for DPM: RPM. Daily potential evapotranspiration was calculated using the Thornthwaite equation (44). More details about the ECOSSE approach can be found in (31).

**Table 1.** Site characteristics and data acquisition. MAT is mean annual air temperature; MAP is mean annual precipitation.

Site/ location	Coordinates	MAT (°C)	MAP (mm)	Type of grassland	Site management	Soil type	Investigated years
Easter Bush/ UK*	55° 52' N, 03° 02' W	9.0	947	Lolium perenne/ clover	Fertilised, grazed, cut	Sandy clay loam	2002-2010
Alp Weissenstein/ CH	46° 34' N, 09° 47' E	4.0	918	Mixed grasslands	Extensively grazed	Sandy loam	2016-2018
Neustift/ AT	47° 12' N, 11° 32' E	6.5	852	Mixed grasslands	Grazed, cut, manure	Sandy loam	2002-2012
Chamau/ CH	47° 12' N, 08° 24' E	9.1	1151	Ryegrass/ clover	Cut, grazed, fertilised	Sandy loam to silty loam	2005-2018
Matra/ HU	47° 52' N, 19° 56' E	10.2	622	Mixed grasslands	Cut	Clay soil	2007-2008
Grünschaige/ DE	48° 23' N, 11° 50' E	9.0	775	Ryegrass/ clover	Grazed, manure	Silt loam	2002-2012
Borova/ CZ	48° 52' N, 14° 13' E	7.0	650	Ryegrass/ clover	Extensively grazed, fertilised	Sandy loam	2002-2004
Amperlo/ IT	41° 90' N, 13° 22' E	10.0	1365	Mixed grasslands	Grazed	Clay soil	2002-2008

\*UK= United Kingdom; CH= Switzerland; AT= Austria; HU= Hungary; DE= Germany; CZ= Czech Republic; IT= Italy.

**Table 2.** Soil property at 0-50 cm for the ECOSSE-model input data.

Site/ location	Bulk density (g cm <sup>-3</sup> )	Soil pH	Clay (%)	Water table depth (cm)	Measured/ estimated SOC (t ha <sup>-1</sup> )
Easter Bush/ UK	1.3	5.1	23	85	120
Alp Weissenstein/ CH	1.1	6.4	20	125	32.5
Neustift/ AT	0.7	5.5	5.5	125	43.9
Chamau/ CH	1.1	5.0	20	125	36.7
Matra/ HU	1.3	5.4	35	400	19.5
Grünschaige/ DE	1.1	6.4	26	125	31.3
Borova/ CZ	1.1	7.8	6.0	25	27.9
Amperlo/ IT	1.1	6.6	56	125	54.2

\*UK= United Kingdom; CH= Switzerland; AT= Austria; HU= Hungary; DE= Germany; CZ= Czech Republic; IT= Italy; SOC= soil organic carbon.

**Table 3.** Statistical analysis of soil respiration (Rs) estimated from ecosystem respiration (R<sub>eco</sub>) and ECOSSE-simulated Rs fluxes from the eight grasslands investigated sites.

Site/location	Years of measurements	Cumulative annual estimated Rs (g C m <sup>-2</sup> )	Cumulative annual simulated Rs (g C m <sup>-2</sup> )	Mean daily estimated Rs (g C m <sup>-2</sup> )	Mean daily simulated Rs (g C m <sup>-2</sup> )	RD (%)	RMSE (g C m <sup>-2</sup> d <sup>-1</sup> )	d	R <sup>2</sup> -range
Easter Bush/ UK	9	770	490	2.11	1.35	-36	1.56	0.86	0.15-0.63
Alp Weissenstein/ CH	3	460	260	1.25	0.72	-42	0.91	0.87	0.43-0.62
Neustift/ AT	11	1120	490	3.07	1.34	-56	2.51	0.28	0.20-0.53
Chamau/ CH	14	810	430	2.92	1.55	-47	3.30	0.55	0.21-0.53
Matra/ HU	2	350	530	0.95	1.45	51	1.28	0.67	0.01-0.29
Grünschwaiqe/ DE	11	530	550	1.60	1.58	4	1.28	0.54	0.10-0.53
Borova/ CZ	3	483	394	1.32	1.08	-18	1.05	0.87	0.0-0.25*
Amperlo/ IT	7	450	560	1.55	1.95	24	1.35	0.55	0.14-0.44

\*UK= United Kingdom; CH= Switzerland; AT= Austria; HU= Hungary; DE= Germany; CZ= Czech Republic; IT= Italy. RD is relative deviation between cumulative annual estimated Rs from R<sub>eco</sub> and cumulative annual simulated Rs; RMSE is root mean square error; d is index of agreement between ECOSSE-simulated Rs and estimated Rs from R<sub>eco</sub>; R<sup>2</sup> is the coefficient of determination; R<sup>2</sup> range is the minimum and maximum R<sup>2</sup> values for the investigated years at each site. \*Only few data were available in the first year.

2.4. Model sensitivity and attribution

To investigate the impacts of anthropogenic management and natural drivers on Rs, sensitivity and attribution tests were carried out for each site. Here, only one input parameter was altered at a time, whilst all others were kept constant (19, 45). Simulations were run to assess the impacts on Rs by changes in climate variables: mean temperature (increasing/ decreasing the daily mean temperature by 3°C); from here onward named as: Temp+3 and Temp-3) and precipitation (altering the daily precipitation by +30 and -30 %) (named as: Rain+30% and Rain-30%). Simulations were also run to assess how Rs was affected by changes in soil physical properties, i.e., SOC, pH and water table (WT; i.e., WT depth). SOC (named as: SOC+30% and SOC-30%) and pH (named as: pH+30% and pH-30%) were altered by +30 and -30 %, whilst WT was lowered by 30 cm (named as: WT+30).

2.5. ECOSSE evaluation

Multi-criteria evaluations of the ECOSSE model were applied to identify how well it predicted the estimated Rs. Comparisons of simulated Rs with estimated Rs were undertaken for each site separately. Analysis was carried out to detect the coincidence and association between simulated and estimated values, following the methods described in (45) and (46). Model accuracy and performance were evaluated by calculating the relative deviation (RD; equation 3) between annual simulated Rs and annual estimated Rs, the coefficient of determination (R<sup>2</sup>) to measure the closeness between daily simulated and estimated Rs values, the root mean square error (RMSE; equation 4) to measure total error, and the index of agreement (d; equation 5) to measure the ratio of the mean square error and the potential error. The index of agreement value of 1 indicates a perfect match, and 0 indicates no agreement at all. Annual cumulative Rs for model outputs were calculated as the sum of simulated daily fluxes (47).

$$RD = (Mi - Si)/Mi$$
(3)

$$RMSE = \sqrt{[\sum(Si - Mi)^2 / n]}$$
(4)

$$d = 1 - \sum (Si - Mi)^2 / \sum [(Si - X) + Mi - X]^2$$
(5)

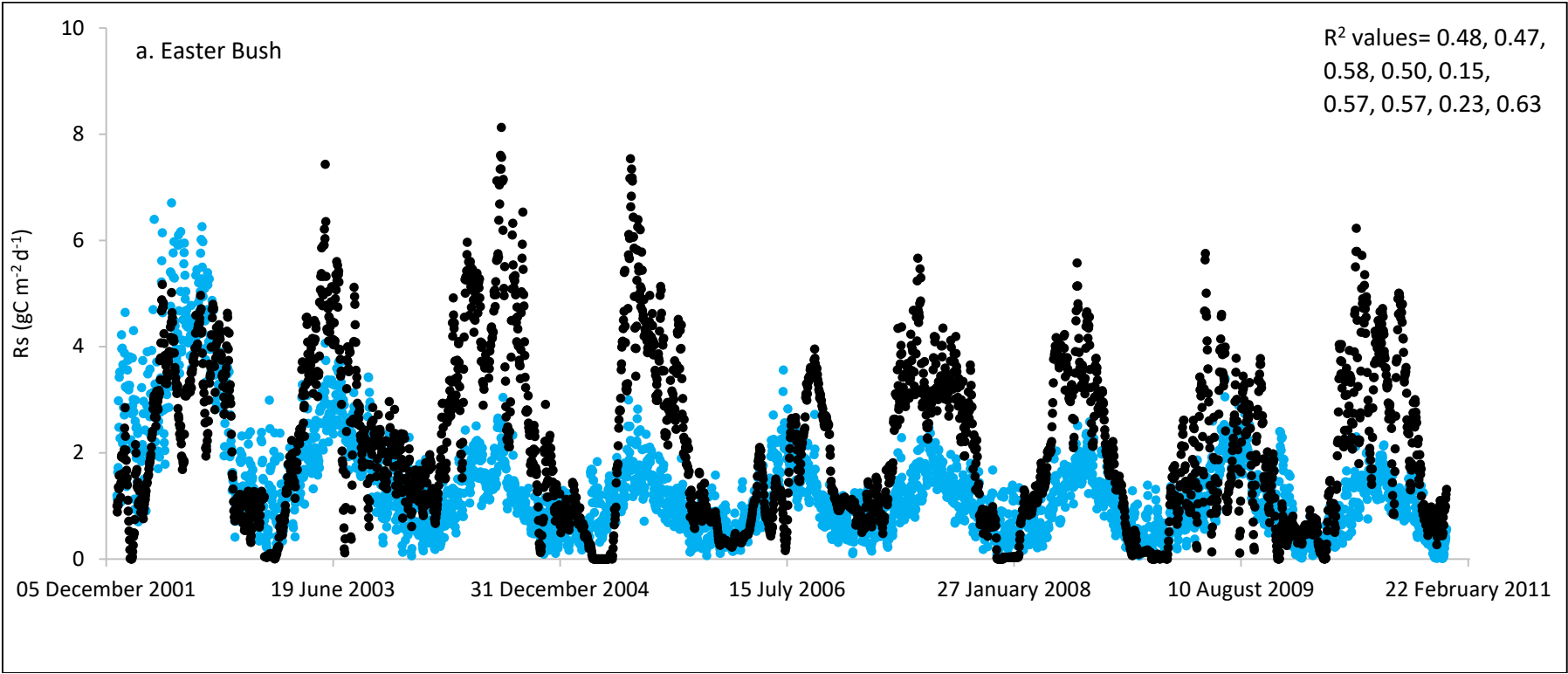
where  $M_i$  is the  $R_s$ -value estimated from  $R_{eco}$  and  $S_i$  is the  $R_s$ -value simulated by the ECOSSE model.  $N$  is the number of investigated days and  $\bar{X}$  is the mean of estimated  $R_s$  values.

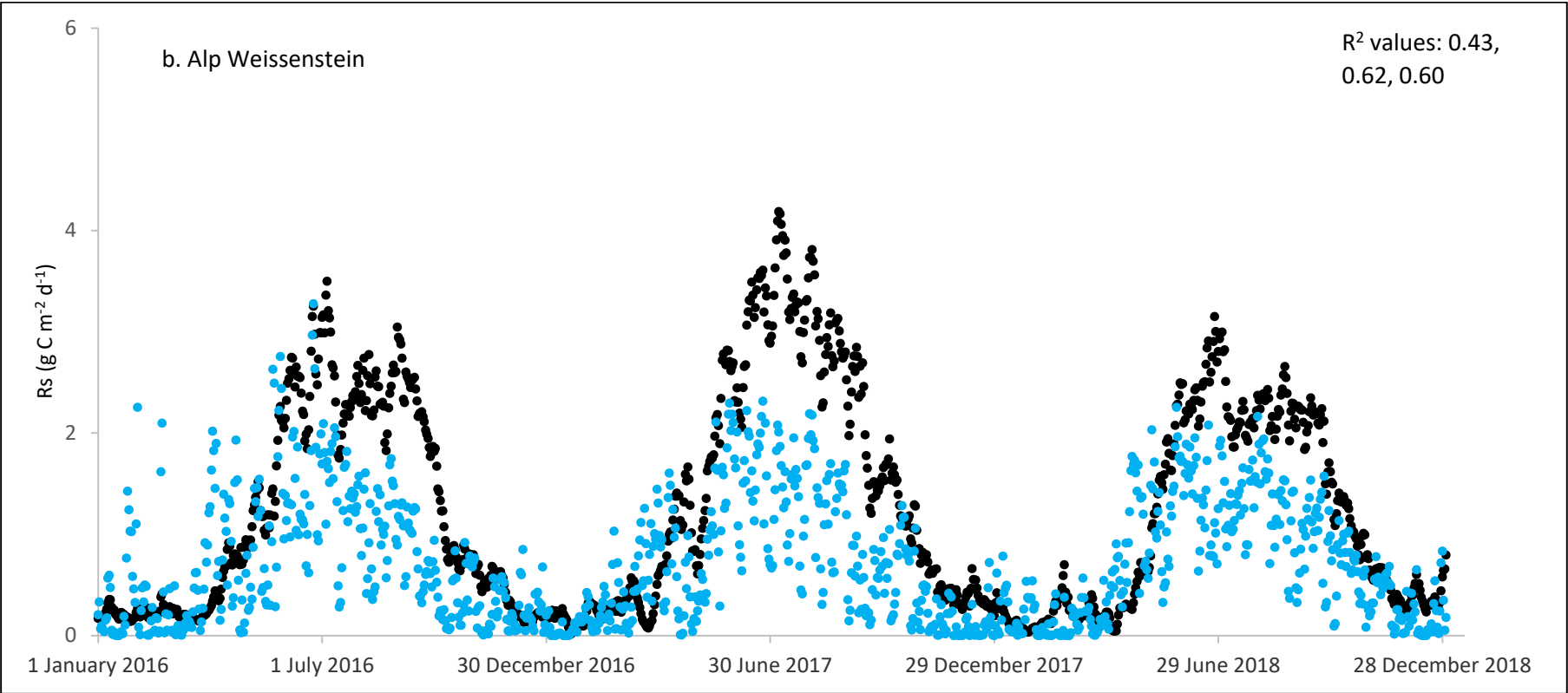
### 3. Results and discussion

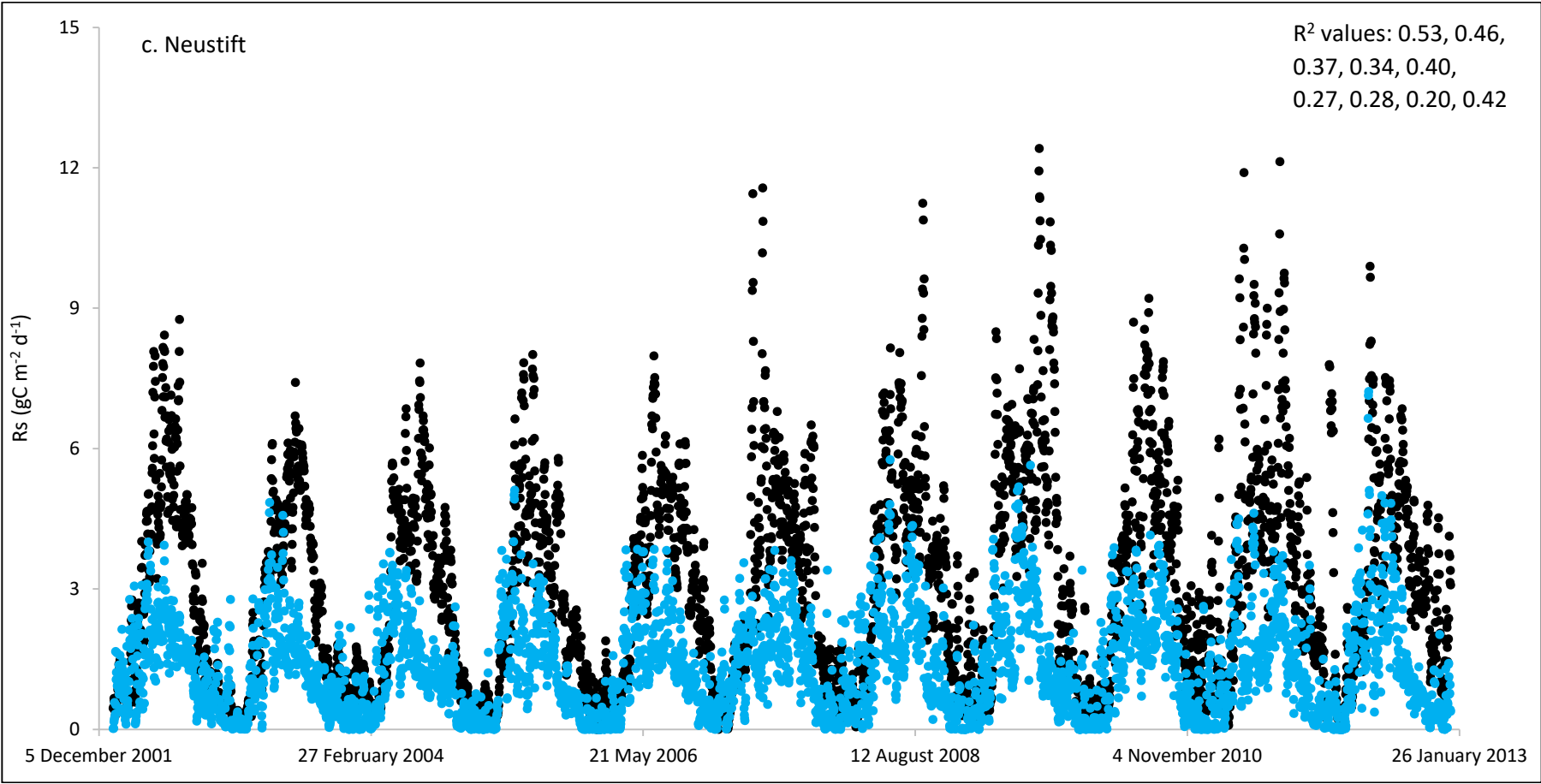
#### 3.1. Estimated soil respiration ( $R_s$ ) from $R_{eco}$

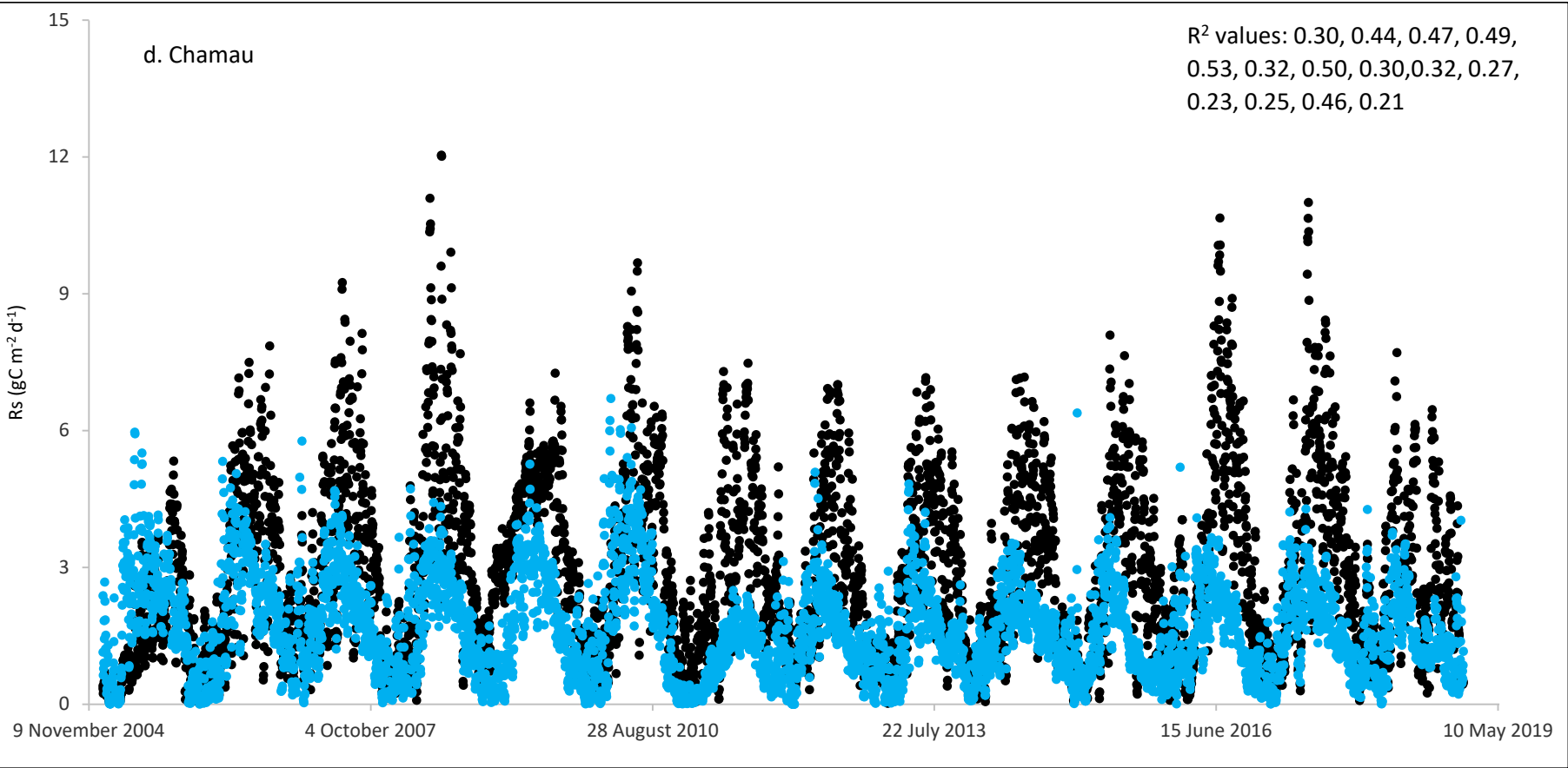
In this study, we estimated soil respiration ( $R_s$ ) from  $R_{eco}$  data using the approach of Hardie et al. (42) and Abdalla et al. (19). To the best of our knowledge, this is the only available method, at the time of this study, to estimate  $R_s$  from the  $R_{eco}$ . The long-term MAT and MAP values and soil properties were varied among the investigated sites (Tables 1 and 2). Variabilities were also clear in the average daily temperature and precipitation values at the sites as shown in Fig. S1. In Europe, climate variability especially in the summer is expected to increase with more frequent heat waves and droughts (48). The estimated daily and annual  $R_s$  flux values were also substantially variable, among sites and between years at the same site (Fig. 1 and Table 3). Peak values of estimated  $R_s$  were observed during late summer and autumn whereas lower values were observed during the wintertime (Figs. 1 and S1). The lowest average daily estimated  $R_s$  value of  $0.95 \text{ g C m}^{-2}$  found for Matra in Hungary (dry site) whilst the highest daily value of  $3.1 \text{ g C m}^{-2}$  was derived for Neustift in Austria which was intensively managed. The low  $R_s$  efflux from Matra estimated in this study, could be due to the site being dry with low input and no animal grazing. Soil moisture content has strong positive relationship with  $R_s$  however, as it continues to increase and reaches high levels, anaerobic conditions can develop, which can depress aerobic microbial activity and lead to a decrease in soil  $R_s$ . This is because, under anaerobic conditions, microbes switch to alternative metabolic pathways that do not produce  $\text{CO}_2$  (49, 50). Additionally, Frank et al. (51) found high  $R_s$  efflux from a grazed mixed-grass prairie compared to a non-grazed mixed-grass prairie due to addition of N and C by the grazing animals.

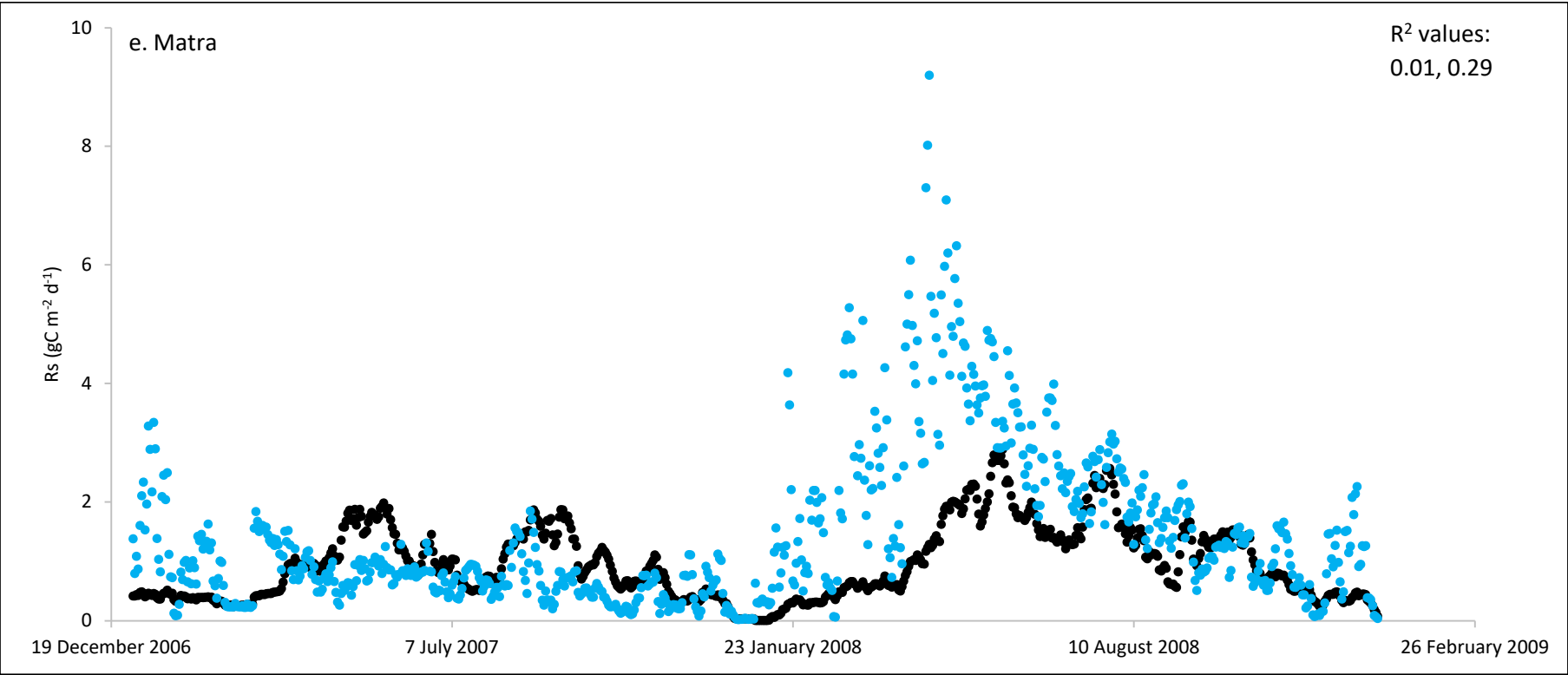
Cumulative monthly  $R_s$  values were also followed the seasonal patterns of temperature with the highest monthly average  $R_s$  rates in June, July and August and the lowest rates in January, February, November, and December (Fig. S2). For all sites, positive regression relationships between daily estimated  $R_s$  and daily temperature were found with regression- $R$  values at the different sites range from 0.24 to 0.66 (Fig. 2). However, in this study, correlation of  $R_s$  with precipitation was weak and inconsistent (data not shown). Solomon et al. (52) found that the variations in both temperature and precipitation rates significantly influenced local and regional  $R_s$  fluxes from soils. The average annual estimated  $R_s$  from the sites ranges from 350 to  $1120 \text{ g C m}^{-2}$  which fall within the annual range of 58 to  $1988 \text{ g C m}^{-2}$  measured by Bahn et al. (53) from 20 EU-grassland sites. Additionally, in a global meta-analysis conducted by Wang and Fang (17), they quantified the annual  $R_s$  efflux from natural grasslands in temperate and tropical regions. Their results showed that the annual  $R_s$  was  $389.8 \pm 45.5 \text{ g C m}^{-2}$  for temperate natural grasslands and  $601.3 \pm 45.6 \text{ g C m}^{-2}$  for tropical natural grasslands. Though, to fully understand the C-cycling and assess the response of  $R_s$  flux to climate drivers, impacts of management in grassland is considered. Management practices influence soil microbial communities and their diversity (54) and these in turn affect  $R_s$  (55). Although inconsistent, the daily  $R_s$  fluxes at Easter Bush and Chamau sites (i.e., sites where detailed management data were available), decreased after grass cutting and increased after slurry application (Table 4). Cutting of grass affects C cycling and decreases  $R_s$  fluxes by decreasing root biomass (53). The carbon and other nutrients in slurry increase productivity and microbial biomass and thereby,  $R_s$  fluxes from soils (56). High WT can decrease  $R_s$  due to creation of anaerobic conditions which are unfavourable for oxidation of SOM, plant debris, and aerobic respiration (57). Generally, in this study fluxes of  $R_s$  can be explained by the interaction between the above-ground microclimate and belowground metrics. Previous studies using data sets from the investigated sites in this study reported that the  $\text{CO}_2$  fluxes were mainly controlled by a set of variables including climate, soil, biomass, and management (e.g., 34, 35, 36).

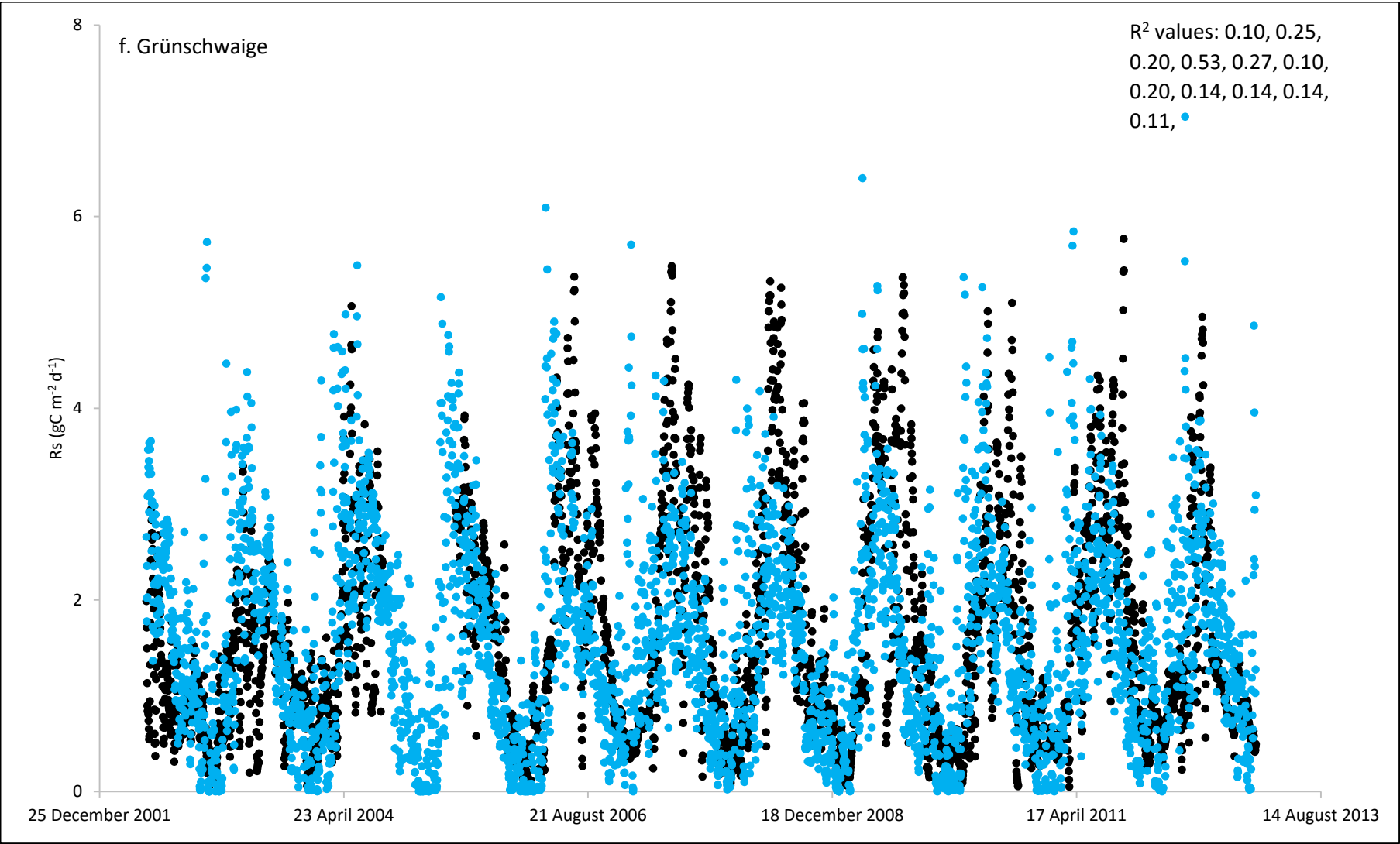


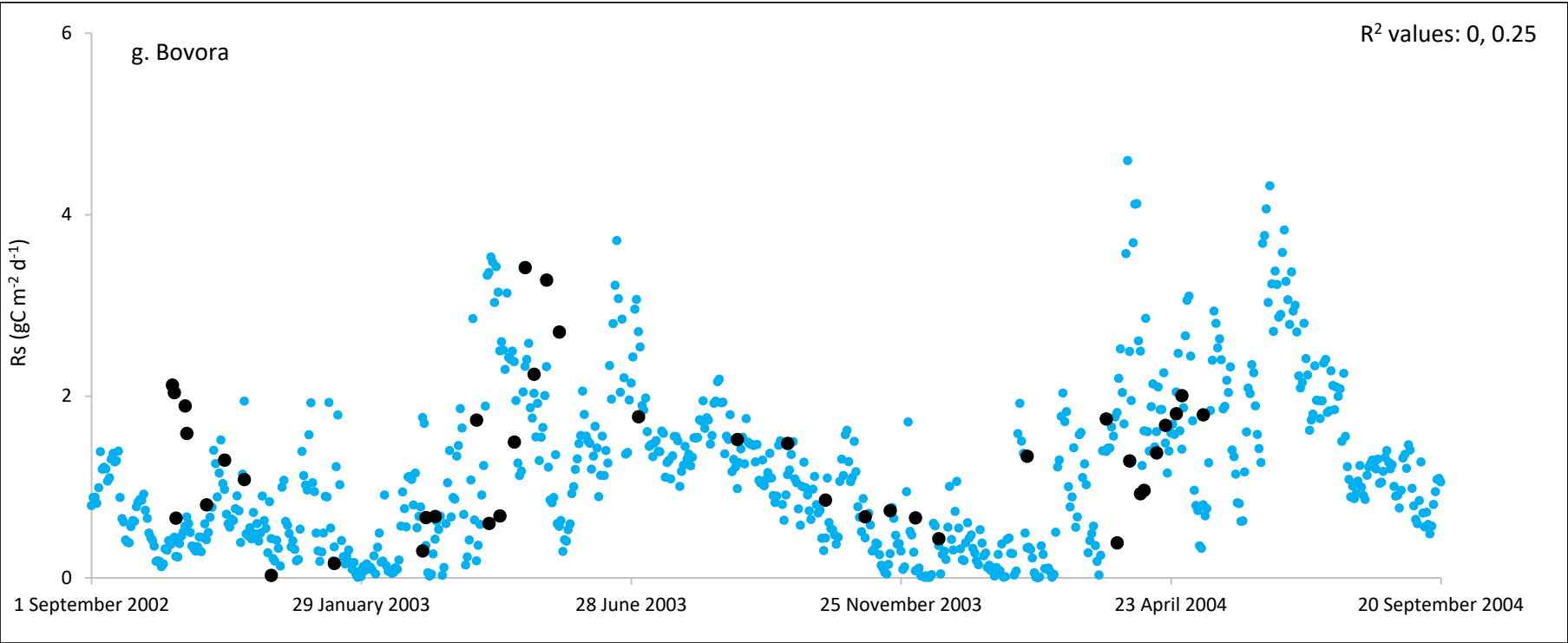


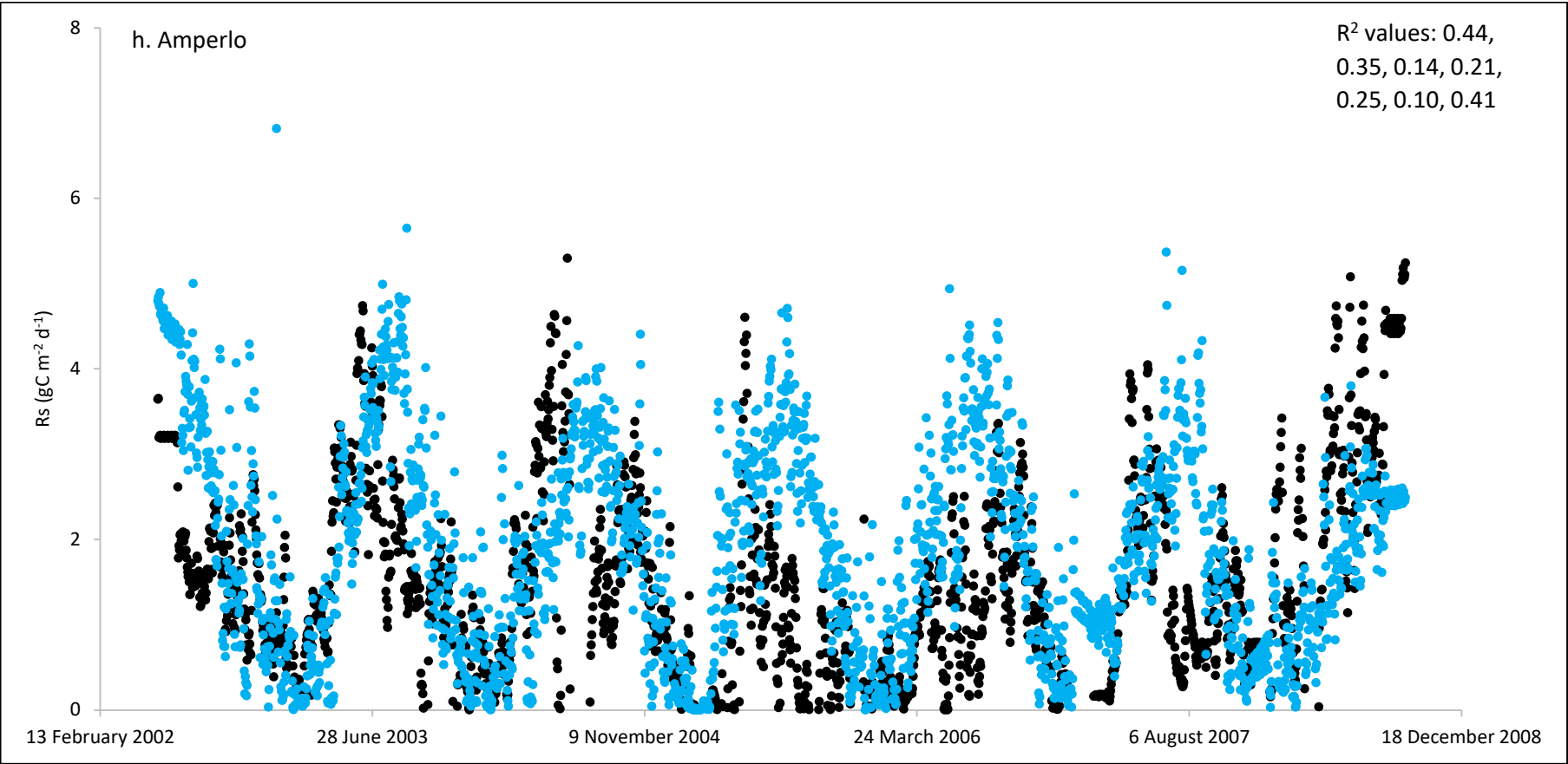




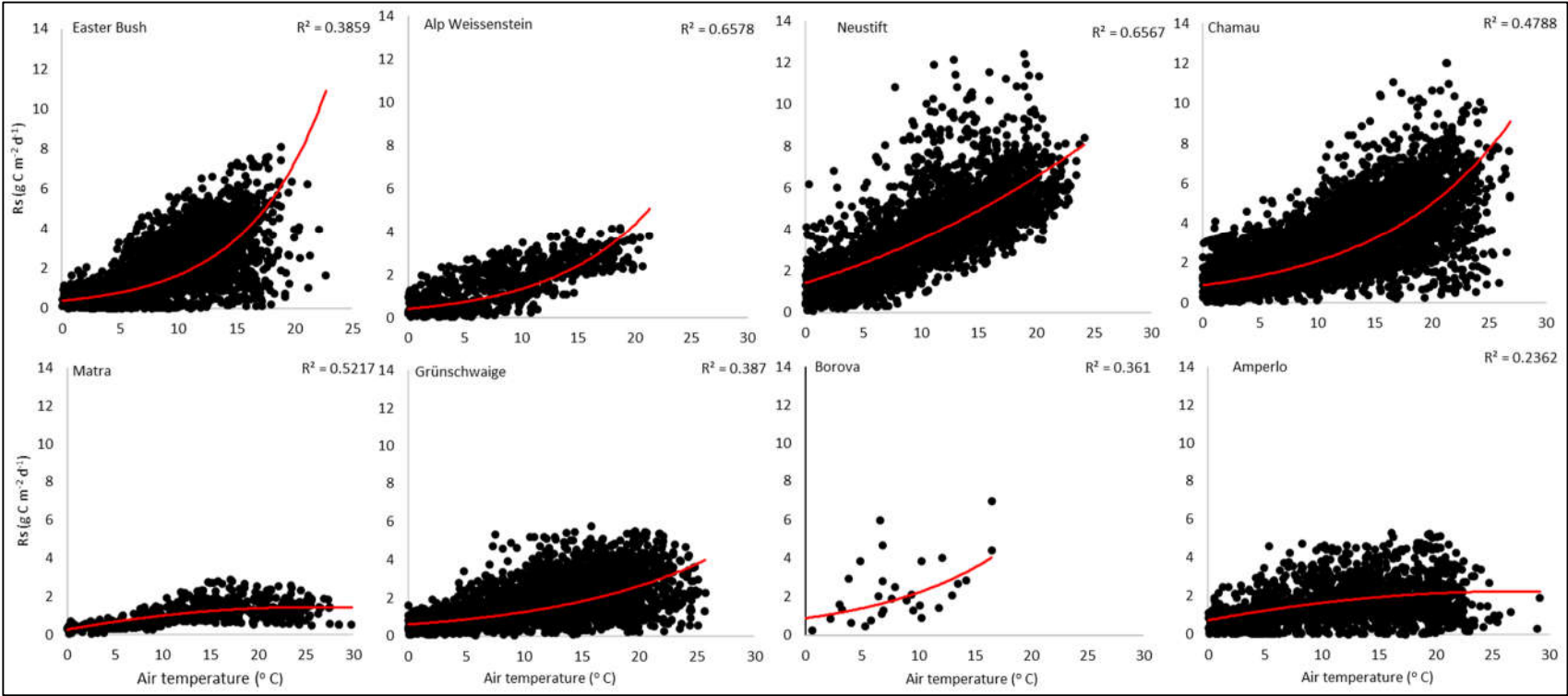








**Figure 1.** Comparisons between soil respiration ( $R_s$ ) estimated from ecosystem respiration (black closed circle) and ECOSSE-simulated  $R_s$  fluxes (open circle) at (a) Easter Bush, (b) Alp Weissenstein, (c) Neustift, (d) Chamau, (e) Matra, (f) Grünschaige, (g) Borova and (h) Amperlo grassland sites. Grass cutting at Easter Bush, Neustift, Chamau and Matra took place in the period March-August each year.  $R^2$  values are the coefficient of determination between estimated and simulated  $R_s$  for the years at each site chronologically.



**Figure 2.** Regression relationships between average daily air temperature (°C) and the daily soil respiration fluxes ( $R_s$ ;  $\text{g C m}^{-2} \text{d}^{-1}$ ) estimated from ecosystem respiration ( $R_{\text{eco}}$ ) at the investigated sites.

**Table 4.** Comparisons between estimated and simulated Rs values at Easter Bush (2002-2004) and Chamau (2005-2006) sites, two days following grass cut and slurry applications application (i.e., values compared were from day two after management).

Site name	Management	Date	Estimated Rs (% change)	Simulated Rs (% change)
Easter Bush	Grass cut	1/6/2002	-21	-10
		5/8/2002	-12	-13
		29/5/2003	20	25
	Slurry application	28/9/2004	15	15
		27/4/2005	33	0
Chamau	Grass cut	1/5/2005	-36	-32
		28/6/2005	-44	-31
		27/7/2005	17	8
		31/8/2005	-10	-14
		4/7/2006	-56	-24
		23/7/2006	-2	2
		1/9/2006	90	55
	Slurry application	10/5/2005	84	67
		2/6/2005	46	31
		3/8/2005	13	10
		5/12/2005	-29	27
		24/3/2006	58	>100
		5/5/2006	-43	-1
		13/6/2006	>100	3
		6/7/2006	38	16
		2/8/2006	-16	-19

**Table 5.** ECOSSE-sensitivity and attribution response of the soil respiration (Rs) fluxes to changes in soil properties and climate input factors at the investigated sites. Temp+3 or Temp-3 means the original daily temperature plus or minus 3 °C; Rain+30 or Rain-30 means the original precipitation minus or plus 30%; SOC+30% or SOC-30% means the original SOC minus or plus 30%; pH+30% or pH-30% means the original pH minus or plus 30%; WT+30cm means the original water table depth plus 30cm depth. Changes (%) were calculated in comparison to the model-output using the original measured input data. Matra was not included as the response to changes parameters at this site was minor.

Site/ location	Temp+3	Temp-3	Rain+30%	Rain-30%	SOC+30%	SOC-30%	pH+30%	pH-30%	WT+30cm
Easter Bush/ UK	20.1	-23.0	-0.6	0.0	4.3	-0.8	0.4	-2.2	0.0
Alp Weissenstein/ CH	25.5	-22.4	-17.7	10.9	2.2	-2.6	0.0	-6.3	11.3
Neustift/ AT	21.6	-19.1	-10.1	1.6	7.4	-2.5	0.0	-5.1	14.1
Chamau/ CH	21.4	-19.2	-5.5	0.0	3.1	-2.5	0.0	-11.1	4.7
Matra/ HU	16.0	-11.3	-6.0	-5.8	4.5	1.9	11.2	-2.5	0.0
Grünschaige/ DE	21.8	-20.1	-1.4	0.0	2.1	-2.2	0.0	-11.5	4.8
Borova/ CZ	22.4	-21.5	-1.2	1.6	0.6	-0.6	0.0	-6.4	16.2
Amperlo/ IT	24.4	-22.1	-7.2	5.7	15.6	-2.2	5.7	-15.7	8.1

### 3.2. Model sensitivity and attribution

ECOSSE attribution analysis to input factors showed similar responses in all grassland sites except for Matra where, the responses to changes of two input parameters were different i.e., decreasing rainfall (Rain-30%) decreased Rs and decreasing SOC (SOC-30%) increased Rs fluxes (Table 5). This site was a dry and low input site with low daily and annual cumulative Rs fluxes. In agreement with other studies, which suggest that soil drying reduces Rs due to soil moisture deficit which limits microbial activities (58). Overall, Rs values increased with increasing mean daily air temperature, depth to WT, SOC and soil pH, but decreased with increasing daily precipitation (Table 5). Across all sites, increases in Rs fluxes, range from 16 to 25 % and from 2 to 16 %, were calculated when daily mean temperature increased by 3°C and SOC increased by 30 %, respectively. Decreasing temperature by 3°C, compared to the original temperature, and SOC by 30% decreased the Rs flux by 11 to 23% and by 1 to 3%, respectively. Increasing the daily precipitation by 30%, compared to original precipitation, decreased Rs by 1 to 18%, whilst decreasing the precipitation by 30% increased the flux by up to 11%. Lowering WT by 30 cm increased Rs by up to 16% whilst a 30% higher pH increased the flux by up to 11%, and a 30% lower pH decreased the flux by up to 16% (Table 5). Previous studies reported that increasing temperature increased Rs rates (17, 59). The decomposition process of plant materials is dependent on temperature (60, 61), and consequently, the rate of Rs. Higher soil moisture creates unfavourable condition for decomposition of SOM (57). Moreover, decreasing soil pH inhibits microbial utilization of substrates and thereby, decreases Rs (62).

### 3.3. ECOSSE simulations

Evaluation of the ECOSSE model is shown in Table 3 where the estimated Rs fluxes from these grassland sites were compared to the model's outputs. As shown in Fig. 1, on many occasions, the ECOSSE model was able to capture the seasonal trends, peak values, and timings of estimated Rs fluxes correctly however, the model often over or under-estimated their values during warm weather condition in spring and summer (Fig. 1). The daily estimated and simulated Rs ranged from 0.95 to 3.1 and from 0.72 to 1.58 gCO<sub>2</sub>-C m<sup>-2</sup>, respectively. Summer Rs values ranged from 2.8 to 3.9 gCO<sub>2</sub>-C m<sup>-2</sup> were reported for a temperate grassland in Germany (63). Differences between estimated and simulated daily Rs were investigated by calculating RMSE and d. The model generally

underestimated the flux with RMSE values ranged from 0.91 to 3.30 g C m<sup>-2</sup> day<sup>-1</sup> (Table 3), and  $d$  values ranged from 0.28 to 0.87. The  $R^2$  between estimated and simulated daily  $R_s$  values were variable between sites (0.25, 0.52, 0.35, 0.33, 0.22, 0.15, 0.10 and 0.17 for Easter Bush, Alp Weissenstein, Neustift, Chamau, Matra, Grünschwaike, Borova and Amperlo, respectively) and years within the same site with the highest value of 0.63 found in Easter Bush (Table 3). Great variabilities in the model fit among the years for each site can be seen from the  $R^2$  range values between the daily estimated and simulated  $R_s$  fluxes. Both estimated and simulated  $R_s$  responded to seasonal temperature, precipitation, and management, which have strong impacts on  $R_s$  (Figs. 1, 2, S1 and S2). These variables impact plant photosynthetic capability, plant growth and accumulation of litter which impacts C supply to soil decomposers (64). As shown in Table 4, on most occasions, both daily estimated and simulated  $R_s$  values from Easter Bush and Chamau sites, were decreased after grass cutting and increased after slurry application. Here, although inconsistent, the model was able to predict estimated  $R_s$  following field management. ECOSSE was also able to predict annual cumulative estimated  $R_s$  at most of the sites with an overall RD value (between annual estimated and simulated  $R_s$ ) of -11.9%. Similar model-fits and responses of cumulative  $R_s$  flux from grasslands to changes in climate and management parameters using the ECOSSE and DNDC models were reported in the literature (23, 65). The use of a simple generic method to estimate field  $R_s$  from the  $R_{eco}$  data, using of estimated SOC at some sites and factors such micronutrient deficiencies and topography which are not considered in the model may contributed to the differences in the simulation results. ECOSSE had difficulties in correctly simulating  $R_s$  values from Matra site which was dry and had low inputs such as no fertilizers, manure, or animal grazing. Moinet et al. (66) found a significantly positive correlation between  $R_s$  and soil water content in dry permanent grasslands. This strong dependence of  $R_s$  on water content can explain most of variations in  $R_s$ . additionally, in low input sites both soil and plant respiration can be reduced by the limited N input (67). Nitrogen input leads to a decrease in soil C:N ratios by reducing plant species richness, which results in an increase in  $R_s$  (63). Moreover, traditional models such as ECOSSE do not consider the proportion of legume species in the grass sward or microbial mechanisms, which can affect overall productivity and lead to an underestimation of nitrogen and carbon balance in the soil (55), and consequently, underestimate simulated  $R_s$  (37). Furthermore, these models are not sensitive to common management options used in grasslands, such as nitrification inhibitors and feed supplementation, which can affect nutrient availability. To improve our understanding of  $R_s$ , it is crucial to integrate the relationship between substrate supply and the soil biota and their responses to changes in abiotic soil conditions in the model (68). Possible refinements to the ECOSSE model could include further improving its sensitivity to grassland management practices and including microbial mechanisms.

#### 4. Conclusions

This study found that the ECOSSE model (v. 5.0.1) has limitations in accurately estimating daily soil respiration ( $R_s$ ) fluxes, especially in dry and low-input permanent grassland (PG) sites. Additionally, the model does not account for factors such as the proportion of legume species in the grass sward, animal feed supplements, and microbial mechanisms. Therefore, further development and refinement of the model are needed. However, the model is effective in estimating cumulative  $R_s$  from PG, and is sensitive to input data related to soil, climate, and management practices. The model can simulate  $R_s$  following grass cutting and slurry application management accurately. Soil respiration can be explained by above-ground microclimate, below-ground metrics, and management practices. To enhance the potential of the ECOSSE model in guiding the development of best practices in land management, future research should prioritize refining the model, collecting detailed input data, and decreasing uncertainty in measured data.

**Supplementary Materials:** Figure S1: Average daily air temperature (°C; black line) and precipitation (mm; blue line) at the experimental sites during the measurements of net ecosystem respiration; Figure S2: Relationships between estimated (blue bar) and simulated (orange bar) monthly cumulative soil respiration ( $R_s$ ) and average monthly air temperature (black line) at the investigated sites.

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