2 high plant-interspace heterogeneity Jinnan Gong¹, Ben Wang^{1,2,}, Xin Jia^{1,2,}, Wei Feng², Tianshan Zha², Seppo Kellomäki¹ and Heli 3 Peltola¹ 4 5 ¹ School of Forest Sciences, University of Eastern Finland, P.O. Box 111, 80101 Joensuu, Finland 6 ² Yanchi Research Station, School of Soil and Water Conservation, Beijing Forestry University, 7 Beijing 100083, China 8 9 Correspondence to: Jinnan Gong (jinnan.gong@uef.fi) 10 11 12 Abstract We used process-based modelling to investigate the roles of C-flux components and plant-interspace 13 14 heterogeneities in regulating soil CO₂ exchanges (F_s) in a dryland ecosystem with sparse vegetation.

Modelling the diurnal and seasonal dynamics of soil CO₂ exchange in a semiarid ecosystem with

15 To simulate the diurnal and seasonal dynamics of F_s, the modelling considered simultaneously the 16 CO₂ production, transport and surface exchanges (e.g. biocrust photosynthesis, respiration and 17 photodegradation). The model was parameterized and validated with multivariate data measured 18 during year 2013-2014 in a semiarid shrubland ecosystem in Yanchi, northwestern China. The model 19 simulation showed that, soil rewetting could enhance CO₂ dissolution and delay the emission of CO₂ 20 produced from rooting zone. In addition, an ineligible fraction of respired CO₂ might be removed 21 from soil volumes under respiration chambers by lateral water flows and root uptakes. During 22 rewetting, the lichen-crusted soil could shift temporally from net CO₂ source to sink, due to the 23 activated photosynthesis of biocrust but the restricted CO₂ emissions from subsoil. The presence of 24 plant cover could decrease the root-zone CO₂ production and biocrust C sequestration, but increase 25 the temperature sensitivities of these fluxes. On the other hand, the sensitivities of root-zone 26 emissions to water content were lower under canopy, which may be due to the advection of water 27 flows from the interspace to canopy. To conclude, the complexity and plant-interspace heterogeneities 28 of soil C processes should be carefully considered to extrapolate findings from chamber to ecosystem 29 scales, and to predict the ecosystem responses to climate change and extreme climatic events. Our 30 model can serve as a useful tool to simulate the soil CO₂ efflux dynamics in dryland ecosystems.

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32 Keyword: ecosystem modelling; heterogeneity; inorganic carbon; semiarid shrub ecosystem; biocrust

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34 1. Introduction

35 CO₂ exchange between soil and atmosphere constitutes a major C loss from terrestrial ecosystems 36 (Raich et al., 2002; Giardina et al., 2014). It also plays an important role in the feedbacks between 37 global carbon cycle and climate change (Rustad et al., 2000; Giardina et al., 2014; Karhu et al., 2014). 38 Arid and semiarid (dryland) ecosystems cover over 40% of land surface and contribute notably to 39 inter-annual variations of terrestrial C sink (Poulter et al., 2014). However, the contribution of soil 40 CO₂ flux (F_s) from those ecosystems to the global C budget is less-studied (Castillo-Monroy et al., 2011; Gao et al., 2012; Jia et al., 2014). The temperature dependency of biological CO_2 production 41 42 (i.e. autotrophic respiration and heterotrophic respiration) serves a conventional basis for F_s modelling 43 in many terrestrial ecosystems (Raich and Tufekciogul, 2000; Ryan, 2005; Song et al., 2015). Soil 44 CO₂ flux of dryland ecosystems is also widely interpreted using temperature-response functions 45 modified by other environmental constraints, e.g. soil water content, abundances of substrates and microbial activities (Curiel Yuste et al., 2007; Wang et al., 2014a, 2014b, 2015). 46

47 Although many empirical studies have explained the dynamics of soil CO₂ flux in specified spacetime, their lack of mechanistic descriptions represents a major difficulty in extrapolation under 48 changing environmental conditions (Fan et al., 2015). Soil CO2 flux is a "bulk" exchange that 49 50 comprises two main sets of processes, i.e. the CO₂ production and transport (Fang and Moncrieff, 51 1999; Fan et al., 2015). Hence, models considering only autotrophic and heterotrophic respirations 52 often fail to account for the observed Fs dynamics (Austin and Vivanco, 2006). Gas-transport processes are important mechanisms regulating the magnitudes and hysteretic features of soil CO₂ 53 54 fluxes (Ma et al., 2013). A substantial fraction of respired CO₂ may be transported to atmosphere via 55 xylem, and may not be measured by techniques like soil reparation chambers (Bloemen et al., 2013; 56 2016). During wet periods, soil CO₂ efflux could decrease significantly by water clogging of soil pores, which restricts the diffusion of O₂ and CO₂ gases (Šimunek and Suarez, 1993; Fang and 57 58 Moncrieff, 1999). In dryland soils of high salinity/alkalinity, CO₂ transport and water cycle are tightly 59 coupled, as large inorganic C fluxes can be driven solely by dissolution and infiltration of CO₂ and 60 carbonates (Buysse et al., 2013; Ma et al., 2013; Fa et al., 2014). Such inorganic processes may not 61 only introduce fluctuations to hourly or diurnal soil CO₂ effluxes (e.g. Emmerich, 2003; Xie et al., 62 2009; Buysse et al., 2013), it may also to terrestrial CO₂ sinks at much broader spatiotemporal scales 63 (Schlesinger, 2009; Li et al., 2015).

Key processes contributing to CO₂ production in dryland soils also extend beyond autotrophic and heterotrophic respirations. Although biocrust organisms (lichens, mosses, bacteria, fungi and microfauna) mainly inhabit in the top few centimetres of a soil profile, they constitute up to 70% of biomes in interspace areas (Belnap, 2003). These communities are able to uptake C from atmosphere (Belnap, 2003; Castillo-Monroy et al., 2011; Maestre et al., 2013), leading to greater concentrations of 69 organic matters in soil crust than the layer underneath (Ciais et al., 2013). Although crust organisms 70 could be inactive under stresses (e.g. drought, Green and Proctor, 2016), their photosynthetic 71 potentials could be large (Zaady et al., 2000; Lange, 2003), even comparable to temperate forests with 72 closed canopies (e.g. Zaady et al., 2000). The C uptakes of biocrusts are highly sensitive to stresses 73 like droughts, thermal extremes and excessive ultraviolet radiation (Pointing and Belnap, 2012). Such 74 variations can readily alter crusted soils between considerable CO_2 sinks and sources within a few 75 hours (e.g. Bowling et al., 2011; Feng et al., 2014). In addition, the accumulation of debris from crust 76 and canopy fuels photodegradation, which represents an important abiotic C loss in arid conditions 77 aside of biotic decompositions (e.g. Austin and Vivanco, 2006; Throop et al., 2009). Photodegradation 78 is likely to dominate the mineralization during dry daytime periods, when radiation is strong and 79 microbial activities are prohibited by low moisture content and high temperature (e.g. Gliksman et al., 80 2016). On an annual basis, photodegradation could consume more than 10% of soil organic matter 81 (SOM) at surface (e.g. Austin and Vivanco, 2006; Henry et al., 2008; Brandt et al., 2010), even for the 82 substrates (e.g. lignin) that are difficult to degrade via biotic pathways (Henry et al., 2008).

83 The influences of the multiple C processes (i.e. autotrophic and heterotrophic respirations, C 84 exchanges by biocrust organisms, inorganic C fluxes and photodegradation) on soil CO₂ exchanges 85 are highly overlapped and tightly related to water-energy conditions. In dryland ecosystems, patchy 86 vegetation and large fractions of interspace area are common features (Domingo et al., 2000), and the 87 water-thermal conditions can vary considerably from plant-covered areas to interspace within even a few meters (Rodríguez-Iturbe et al., 2001; Caylor et al., 2008; Ma et al., 2011). The water-energy 88 89 dynamics at the different surfaces are linked by multiple advection processes both above- and belowground (Gong et al., 2016). Due to the complexity of water-energy processes, there may exist possibly 90 91 high non-linearity of water-thermal responses to climatic variabilities (e.g. Phillips et al., 2011; 92 Barron-Gafford et al., 2013). This will also complicate the C responses and consequently affect the 93 relationships between CO_2 fluxes and environmental controls (e.g. Jarvis et al., 2007; Song et al., 94 2015).

Global climate change is expected to increase annual mean air temperatures considerably and alter 95 96 precipitation regimes (Donat et al., 2016). Understanding the responses of dryland ecosystems to such 97 changes requires mechanistic models that integrate the multiple biotic and abiotic processes in soil C cycling. So far, only a few models have coupled the biotic CO₂ production with the transports of gases 98 99 and heat (Šimunek and Suarez, 1993; Fang and Moncrieff, 1999; Phillips et al., 2011; Ma et al., 2013; 100 Fan et al., 2015). Nevertheless, none of those models has described the heterogeneous water-energy 101 conditions in soil-plant-atmosphere continuum (SPAC), nor the unconventional C fluxes such as C 102 uptake by biocrusts and photodegradation despite the importance of these processes to arid and 103 semiarid environments. Perhaps, models by Porada et al. (2013) and Kinast et al. (2016) represent the 104 few existing works in this sense. However, both the models focus on the patterns at the regional-scale 105 with very simplified ecosystem processes. In this study, we aim to: i) investigate the roles of soil CO_2 106 components in regulating soil CO_2 effluxes in a dryland ecosystem using a process-based modelling 107 approach, and ii) to estimate the plant-interspace differences in the componential C processes.

108

109 2. Materials and methods

110 **2.1 Model overview**

111 The process-based model was build based on a semiarid shrubland ecosystem located at the southern edge of Mu Us desert (37°42'1" N, 107°13'7" E, 1560 m above sea level, Fig. 1a), Ningxia, 112 China (see Wang et al., 2014a, 2015). The long-term mean temperature (1954–2004) is 8.1 °C, and 113 114 the mean annual precipitation is 287 mm, most of which falls from July to September (Jia et al., 2014). 115 The radiation and evaporation demand are high in this area. The annual incoming shortwave radiation is 1.4×10^5 J cm⁻² and the annual potential evaporation is 2024 mm. The vegetation is dominated by 116 scattered crowns of Artemisia ordosica (Fig. 1b). The soil is highly alkaline (pH = 8.2). Biocrust 117 (mainly lichens and algae) covers about 40% of interspace soil (Fig. 1c - 1e). The thickness of the 118 119 crust layer was 0.5 - 2.5 cm (Gong et al., 2016).

120 In the modelling, the structure of ecosystem was considered as replications of "representative land 121 units" (RLU, Fig. 1f; Gong et al., 2016), which comprises the area covered by shrubs and the surrounding soil (interspace). Vertically, the model simulates the C flows across soil profile and the 122 water-energy transport from the lower boundary of rooting zone to a reference height in the boundary 123 124 atmosphere. Horizontally, the SPAC processes at the plant-covered and interspace areas are 125 differentiated but related via advection and diffusion flows, as driven by the gradients of temperature, 126 water potential and gas concentration. The mineralization, uptake and transport of soil C and N are 127 also regulated by water-energy conditions.

Fig. 2 shows the framework of key processes and variables included in the Fs modelling. The 128 model includes a set of sub-models, which describe: (i) CO₂ dissolution, transport and efflux; (ii) 129 130 Autotrophic and heterotrophic CO_2 productions in soil profile; (iii) CO_2 uptake and emission by biocrust; (iv) Surface energy balance and soil temperature profile; and (v) Soil hydrology and water 131 132 balance. These sub-models are linked by multiple feedbacks to represent the coupling of C, water, 133 vapor and energy transportations in the ecosystem. Sub-models (iv) - (v) have been developed and 134 described in details in our previous work (Gong et al. 2016), which focused on (i) introducing the plant-interspace heterogeneity into water-energy modelling, and (ii) investigating the influences of 135 136 such heterogeneity on the ecosystem water-energy budgets for a dryland ecosystem. Gong et al. (2016) 137 also validated the model in regard to the diurnal to seasonal dynamics of radiation balance, surface 138 energy balance, soil temperature and moisture content in the footprint area of a eddy-covariance (EC) 139 site (details of measurement see Jia et al., 2014). In this work, we therefore focused on the development of sub-models (i) – (iii) and the model validation, using F_{s} data measured by multiple 140

- 141 automatic respiration chambers from crust-covered and non-crusted soils. Based on the validated
- 142 model, a series of sensitivity analysis were carried out addressing the following questions: i) how the
- soil CO_2 components regulate F_s in the studied ecosystem, and ii) how the plant-interspace
- 144 heterogeneities influence the componential C processes and F_s .
- 145

146 **2.2 Modelling approaches**

147 2.2.1 Submodel (i): CO₂ transport, dissolution and efflux

For soil fraction *x* (see Fig. 1f for RLU settings), CO₂ exchange (F_s , upward positive) was the sum of CO₂ uptake by biocrust (F_{Ct}), photodegradation (F_P) and the emission from soil under the biocrust layer (F_T):

151
$$F_{S_{\chi}} = F_{Ct_{\chi}} + F_{T_{\chi}} + F_{P_{\chi}}$$
 (1)

where F_{Ct} is the net balance between biocrust photosynthesis (P_{Ct}) and respiration (R_{Ct}), and $F_{Ct} = P_{Ct}$ $-R_{Ct}$ (see Section 2.2.3). F_T was modelled based on the mass-balance functions developed by Fang and Moncrieff (1999), which combined major transport processes in both gaseous and liquid phases. We expanded the original function from one-dimensional to two-dimensional. For soil layer (x, i) and time step t, the CO₂ concentration and C flows were calculated as follows:

157
$$\frac{\partial C_{x,i}}{\partial t} = \frac{\partial}{\partial Z} \left(F_{dg}^{\nu} + F_{ag}^{\nu} + F_{dw}^{\nu} + F_{aw}^{\nu} \right) + \frac{\partial}{\partial h} \left(F_{dg}^{h} + F_{ag}^{h} + F_{dw}^{h} + F_{aw}^{h} \right) + S_{x,i}$$
(2)

where superscripts *v* and *h* denote the vertical and horizontal directions, respectively (see also in Gong et al., 2016); *C* is the total CO₂ content; F_{dg} and F_{dw} are the CO₂ flows due to diffusion/dispersion via the gaseous and liquid phases; F_{ag} and F_{aw} are the flows in gaseous and liquid phases due to gas convection and water movement, and *S* is the net CO₂ sink of the layer. The calculation schemes of F_{dg} , F_{dw} , F_{ag} and F_{aw} have been described in detail by Fang and Moncrieff (1999). F_T is the total exchange of gaseous CO₂ between surface and topmost layer:

164
$$F_{T_{\chi}} = F_{dg_{\chi,1}}^{\nu} + F_{ag_{\chi,1}}^{\nu} + E_{\chi,1}^{S} C_{w_{\chi,1}}$$
(3)

where $E_{x,l}^{S}$ is the soil evaporation at section *x* (see Eq. (17) in Gong et al., 2016); C_{w} is the equivalent CO₂ concentrations in soil solution. For layer (*x*, *i*), C_{w} is linked to the gaseous CO₂ concentration (C_{g}):

167
$$C_{x,i} = Cg_{x,i}(V_{x,i} - \theta_{x,i}) + Cw_{x,i}\theta_{x,i}$$
 (4)

168 where V is the total porosity; and θ is soil water content.

169 C_g and C_w were further related via the dissolution-dissociation balance of CO₂ in soil solution, 170 following Fang and Moncrieff (1999) and Ma et al (2013):

171
$$CO_2(g) + H_2O(l) \rightleftharpoons H_2O(l) + CO_2(aq) \quad K_H = P_C/CO_2^{aq}$$
 (5)

172
$$CO_2(aq) + H_2O(l) \rightleftharpoons H_2CO_3$$
 $K_0 = CO_2^{aq} / [H_2CO_3]$ (6)

173
$$H_2CO_3 \rightleftharpoons [H^+] + [HCO_3^-]$$
 $K_1 = [H^+][HCO_3^-]/[H_2CO_3]$ (7)

174
$$HCO_3^- \rightleftharpoons [H^+] + [CO_3^{2-}]$$
 $K_2 = [H^+][CO_3^{2-}]/[HCO_3^{-}]$ (8)

where P_C is the partial pressure of CO₂ in pore air; K_H is Henry's Law constant; K_0 , K_1 and K_2 are the equilibrium coefficients of dissolution, the first- and the second-order dissociation reactions of carbonic acid, respectively (for details see Fang and Moncrieff, 1999). The equilibrium [H⁺] was determined by soil pH and the coefficients K_H , K_0 , K_1 and K_2 , which were functions of temperature in each soil layer (Fang and Moncrieff, 1999). *Cw* was calculated as the sum of CO₂^{aq}, H₂CO₃, HCO₃⁻ and CO₃²⁻.

181

182 2.2.2 Submodel (ii): autotrophic and heterotrophic CO₂ production along the soil profile

For soil layer (x, i), $S_{x,i}$ (Eq. 2) was calculated as the sum of autothrophic and heterotrophic CO₂ productions, and the dissolved CO₂ removed with the water uptaken by roots:

185
$$S_{x,i} = Rs_{x,i} + Ra_{x,i} - E_{x,i}Cw_{x,i}$$
 (9)

where *E* is the transpirative uptake of water (Gong et al., 2016); *Rs* is the CO₂ production by heterotrophic SOM decomposition; *Ra* is the autotrophic respiration of the rhizosphere, which comprises maintenance respiration (*Rm*) and growth respiration (*Rg*):

189
$$Ra_{x,i} = Rm_{x,i} + Rg_{x,i}$$
 (10)

190 To simulate R_s , we simplified the pool-type model of Gong et al (2013, 2014), which was 191 originated from Smith et al (2010) for simulating coupled C and N cycling in organic soils. SOM pool 192 in each soil layer was divided into debris (M_{deb} , i.e. litters from roots and biocrust), microbes (M_{mic}) 193 and humus (M_{hum}) , which are different in biochemical recalcitrance and N content. During decaying, mineralized masses transfer from M_{deb} and M_{mic} to more resistant form (i.e. M_{hum}), leading to a 194 195 decrease in labiality (e.g. Li et al., 1992). The mineralization of organic C followed first-order kinetics 196 and was constrained by multiple environmental multipliers, including temperature, water content and 197 oxygen content (Šimunek and Suarez, 1993; Fang and Moncrieff, 1999):

198
$$m_{x,i}^r = M_{x,i}^r k_r f(Ts_{x,i}) f(\theta_{x,i}) f(O_{x,i}) dt$$
(11)

where superscript *r* denotes the type of SOM pool (*r*=1 for M_{deb} , *r*=2 for M_{mic} , and *r*=3 for M_{hum}); *m* is mineralized SOM during time step *dt*; *k* is the decomposition constant; *dt* is time step; $f(T_{s_{x,i}})$, $f(\theta_{x,i})$ and $f(O_{x,i})$ are multiplier terms regarding the temperature, water content and oxygen restrictions, respectively. $f(O_{x,i})$ was calculated following Šimunek and Suarez (1993). $f(T_{s_{x,i}})$ and $f(\theta_{x,i})$ were reparameterized with respect to the site-specific conditions of plants and soil (see section 2.4.3). The 204 CO₂ production from mineralization was further regulated by the N-starvation of microbes following
205 Smith et al. (2010):

206
$$Rs_{x,i} = r_E m_{x,i}^r$$
 (12)

where r_E is the gas production rate ($r_E \epsilon$ [0, 1]), and (1- r_E) is the proportion of organic matters passed to downstream SOM pools. The evolution of each SOM pool was calculated as below:

209
$$M_{x,i}^{r} = (1 - r_E)m_{x,i}^{r-1} - m_{x,i}^{r} + A_{x,i}^{r}dt$$
(13)

where A is the SOM input rate (A=0 for M_{mic} and M_{hum}); superscript r-1 denotes the source SOM pools.

211 $Rm_{x,i}$ was calculated in a way similar to $Rs_{x,i}$ (e.g. Chen et al., 1999; Fang and Moncrieff, 1999). $Rg_{x,i}$ 212 was calculated as a fraction of photosynthetic assimilates, following Chen et al. (1999):

213
$$Rm_{x,i} = M_{x,i}^R k_R f(Ts_{x,i}) f(\theta_{x,i}) f(O_{x,i}) dt$$
(14)

$$214 Rg_{x,i} = k_g P_g f r_{x,i} (15)$$

where M^{R} is the root biomass; k_{R} is the specific respiration rate of roots; k_{g} is the fraction of 215 photosynthetic assimilate consumed by growth respiration; $fr_{x,i}$ is the mass fraction of roots in soil 216 217 layer (x, i). P_g is the photosynthesis rate of plants. P_g was estimated using a modified Farquahar's leaf 218 biochemical model (see Chen et al., 1999). This model simulates the photosynthesis based on biochemical parameters (i.e., the maximum carboxylation velocity, V_{max} , and maximum rate of 219 electron transport, J_{max}), foliage temperature (Tc) and stomatal conductance (gs). The values of V_{max} 220 221 and J_{max} were obtained from in situ measurements from the site (Jia et al., unpublished). Tc and gs 222 were given in the energy balance sub-model, which was detailed in Gong et al. (2016).

223 N content bonded in SOM is mineralized and released to soil layers simultaneously with decaying. The abundance of mineral N (i.e. NH_4^+ and NO_3^-) regulates the growth of microbial biomass and r_E 224 following Smith et al. (2010) and Gong et al. (2014). Key processes governing the dynamics of 225 mineral N pools included nitrification-denitrification (Smith et al., 2010), solvent transport with water 226 227 flows (Gong et al, 2014) and the N uptake by root system. However, the plant growth was not modelled in this work. Instead, N_{upt} was calculated using the steady-state model of Yanai (1994), 228 229 based on the transpiration rate, surface area of fine roots and the diffusion of solvents from pore space 230 to root surface:

$$231 \qquad N_{upt} = 2\pi r_o L\alpha C_o dt \tag{16}$$

where r_o is the fine root diameter; *L* is the root length, and $2\pi r_o L$ is the surface area of fine roots; α is the nutrient absorbing power, which denotes the saturation degree of solute uptake system ($\alpha \in [0,1]$); *C_o* is the concentration of solvents at the root surface, and is a function of bulk concentration of mineral N (*N_{min}*), inward radial velocity of water at root surface ($v_o = E/(2\pi r_o L)$) and saturation absorbing power α . Further details for calculating α and *C_o* can be found in the work of Yanai (1994). 237

238 2.2.3 Submodel (iii): CO₂ exchange of biocrust and photodegradation

239 Biocrusts are vertically layered systems that comprise topcrust (or, bio-rich layer) and underlying 240 subcrust (or, bio-poor layer), which are different in microstructure, microbial communities and C functioning (Garcia-Pichel et al., 2016; Raanan et al., 2016). Topcrust is usually few-millimetre thick, 241 242 which allows the penetration of light and the development of photosynthetic microbes (Garcia-Pichel et al., 2016). On the other hand, the subcrust has little photosynthetic-activity. We here focused 243 244 mainly on describing the C exchanges in the topcrust, but assumed the C processes in the subcrust were similar to those in the underneath soil. We developed the following functions to describe the C 245 fixation and mass balance in the topcrust, 246

247
$$F_{Ct} = P_{Ct} - R_{Ct}$$
 (17)

248 where P_{Ct} is the bulk photosynthesis rate; and R_{Ct} is the bulk respiration rate. P_C and R_C were further 249 modelled as follows:

$$P_{Ct} = \frac{\alpha_C A_{PAR} P_{Cm}}{\alpha_C A_{PAR} + P_{Cm}}$$
(18)

251
$$R_{Ct} = M_{Ct} k_{cr} f_{RC}(T_{Ct}) f_{RC}(\theta_{Ct})$$
 (19)

where α_C is the apparent quantum yield, P_{Cm} is the maximal rate of photosynthesis, and was a function of moisture content (θ_{Ct}) and temperature (T_{Ct}) in topcrust; A_{PAR} is the photosynthetically active radiation (PAR); M_{Ct} is the total C in the SOM of topcrust; k_{cr} is the respiration coefficient; $f(\theta_{Ct})$ and $f(T_{Ct})$ are water and temperature multipliers. Here, we assumed zero photosynthesis rate for subcrust. The heterotrophic respiration (R_{Cs}) was calculated following Eq. (11), based on the C storages ($M_{x,1}^r$), temperature and moisture content of crust layer (i.e. $Ts_{x,1}$ and $\theta_{x,1}$; see Eq. (29) and Eq. (14) in Gong et al., 2016).

259 To consider different C losses and exchanges, and to calculate the C balance in topcrust and subcrust, respectively, we considered the following matters. R_{Ct} includes the respirations from both 260 autotrophic (M_{CA}) and heterotrophic (M_{CH}) pools. When autotrophic organisms die, SOMs pass from 261 M_{CA} to M_{CH} and influence the turnover processes. A variety of topcrust organisms can reach into 262 263 subcrust (e.g. through rhizines, Aguilar et al., 2009) and export litters there. When the surface is gradually covered by deposits, topcrust organisms tend to move upward and recolonize at the new 264 265 surface (e.g. Garcia-Pichel and Pringault, 2001; Jia et al., 2008), leaving old materials buried into the subcrust (Felde et al., 2014). On the other hand, the debris left to soil surface are exposed to 266 photodegradation. Based on above, the C balance in topcrust and subcrust was calculated as following, 267 assuming the partitioning of respiration between autotrophic and heterotrophic pools was proportional 268 to their fractions: 269

270
$$M_{Ct} = M_{CA} + M_{CH}$$
 (20)

271
$$\frac{dM_{CA}}{dt} = P_{Ct} - R_{Ct} \frac{M_{CA}}{M_{Ct}} - k_m M_{CA} - k_b M_{CA}$$
(21)

272
$$\frac{dM_{CH}}{dt} = k_m M_{CA} - R_{Ct} \frac{M_{CH}}{M_{Ct}} - k_b M_{CH} - F_P$$
(22)

$$273 \qquad \frac{dM_{CS}}{dt} = k_b M_{Ct} - R_{CS} \tag{23}$$

where k_m is the rate of C transfer (e.g. mortality) from autotrophic pool to heterotrophic pool; k_b is the rate of C transfer (e.g. burying) from topcrust to subcrust; F_P is the loss of SOM due to photodegradation.

Photodegradation tends to decrease surface litter masses in a near linear fashion with the time of
exposure (Austin and Vivanco 2006; Vanderbilt et al., 2008). Considering the diurnal and seasonal
variations of radiation, F_P was calculated as a function of surface SOM mass and solar radiation:

$$280 F_{P_x} = M_{surf} k_p Rad_x (24)$$

where Rad_x is the incident shortwave radiation at surface x (Gong et al., 2016); M_{surf} is the surface litter mass; and k_p is the photodegradation coefficient.

283

284 2.3 Micrometeorological and soil CO₂ efflux measurements

285 Meteorological variables were measured every 10 seconds and aggregated to half-hourly resolution 286 during 2013-2014. The factors measured included the incoming and outgoing irradiances (PAR-LITE, 287 Kipp and Zonen, the Netherlands), PAR (PAR-LITE, Kipp and Zonen, the Netherlands), air temperature and relative humidity (HMP155A, Vaisala, Finland). Rainfall was measured with a 288 tipping bucket rain gauge (TE525WS, Campbell Scientific Inc., USA) mounted at a nearby site (1 km 289 290 away, see Wang et al., 2014a). The seasonal trends of the measured Ta and P can be found in Jia et al. (2016). No surface runoffs were observed at the site, indicating the horizontal redistribution of rainfall 291 292 was mainly through subsurface flows.

293 Continuous measurements of F_s were conducted using an automated soil respiration system (model 294 LI-8100A fitted with a LI-8150 multiplexer, LI-COR, Nebraska, USA). The system was on a fixed 295 sand dune of typical size (Wang et al., 2014a), which was located about 1.5 km south from the EC 296 tower described in Gong et al (2016). Three collars (20.3 cm in diameter and 10 cm in height, of 297 which 7 cm inserted into the soil) were installed on average at 3m spacing in March 2012. One collar 298 (C1, see Fig. 1c) was set on a bare-soil microsite with no presence of biocrust. Two other chambers 299 (C2, see Fig. 1d and C3, see Fig. 1e) were set on lichen-crusted soils. F_s was measured hourly from 300 C1 and C2 by opaque chambers, whereas by transparent chamber from C3 to include the photosynthesis and photodegradation. Litters from the shrub canopies were cleared from the collars 301 302 during weekly maintenance. Hourly Ts and θ at 10 cm depth were measured outside each chamber 303 using the 8150-203 soil temperature sensor and ECH2O soil moisture sensor (LI-COR, Nebraska, 304 USA), respectively. Root biomass was sampled near each collar (within 0.5 m) in July 2012, using a 305 soil corer (5 cm in diameter) to a depth of 25 cm. The samples were mixed and sieved sequentially 306 through 1, 0.5 and 0.25 mm meshes, and the living roots were picked by hands. The comparison of the 307 three micro-sites is shown in Table 1. Methods used in data processing and quality control have been 308 described earlier in details (see Wang et al., 2014a, 2015). The quality control led to gaps of 10 - 13% 309 in the F_s dataset.

310

311 2.4 Model set-ups

312 2.4.1 Parameterization of vegetation and soil texture

The parameterization schemes supporting the simulations of energy balance and soil hydrology in 313 314 sub-model (i) - (v) have been described previously in detail by Gong et al. (2016). As the water-315 energy budget is sensitive to vegetation (i.e. canopy size, density and leaf area) and soil hydraulic properties (see Gong et al., 2016), we hereby re-estimated these parameters for the F_s site. 316 Measurements based on four 5m×5m plots showed that the crown diameter D (86 ± 40 cm) and height 317 H (47± 20 cm) at this site were similar to those measured from the eddy-covariance (EC) footprint by 318 319 Gong et al. (2016). However, the shrub density was 50% greater, leading to higher shrub coverage (42%), shorter spacing distance L (40.2 cm) and greater foliage area. On the other hand, the subsoil at 320 the F_s site is sandy and much coarser than that at the EC footprint. Therefore, we collected 12 soil 321 322 cores from 10 cm depth, and measured saturated water content (θ_{sat}), bulk density and residual water 323 content (θ_r) from each sample. Then, the samples were saturated, and covered and drained by gravity. We measured the water content after 2-hour and 24-hour draining, which roughly represented the 324 325 matrix capillary water content (10 kPa) and field capacity (33 kPa) (Armer, 2011). The shape 326 parameters n and α_h (see Eq. (26) in Gong et al. 2016) for the water-retention function were estimated 327 from these values (Table 2).

328

329 2.4.2 Parameterization of soil C and N pools

The sizes and quality of soil C pools were parameterized based on a set of previous studies. The total SOC in the root-zone soil (i.e. 60cm depth, bulk density of 1.6 g cm⁻³) was set to 1200 g m⁻², based on the values reported from previous studies in Yanchi area (e.g. Qi et al., 2002; Chen and Duan, 2009; Zhang and Hou, 2012; Liu et al., 2015; Lai et al., 2016). The mass fraction of resistant SOM pool (M_{hum}) was set to 40 - 50 % of total SOM, following work by Lai et al. (2016). The vertical distribution of the SOM pools was described following Shi et al. (2013). At the ecosystem level, the

- aboveground biomass was linearly related to the crown projection area $(M^{S} = 0.2917 * \pi (0.5D)^{2}, \text{ see})$
- 337 Zhang et al., 2008). The total root biomass was then calculated as proportional to the aboveground
- biomass, using a root-shoot ratio of 0.47 ($M^R = 0.47M^S$, Xiao et al., 2005). The vertical profile of root
- 339 biomass was parameterized as decreasing exponentially with depth, using the depth profile reported
- 340 by Lai et al. (2016). On the horizontal direction, root biomass was set to decrease linearly with the
- 341 distance from the centre of a shrub crown (Zhang et al., 2008). The N content was parameterized
- following the measurement of Wang et al. (2015).

343 Based on the above settings, the specific decomposition rate of debris was estimated from the 344 litterbag experiment done by Lai et al. (2016), which showed a 16% decrease in the mass of fine-root litters during a 7-month period of year 2013 at the Yanchi site. The photodegradation coefficient (k_p) 345 was set to 0.23 yr⁻¹, which was the mass-loss rate reported by Austin and Vivanco (2006). M_{surf} was 346 347 set to 33% of M_{CH} in topcrust, assuming the depth of light penetration was about 2 mm and C 348 concentration was homogeneous in topcrust. The surface litter from canopy was not considered in this 349 modelling, as the plant litters were cleaned from the collars during weekly maintenance. The specific respiration rate of roots (k_R) , however, could be much greater during vegetative growing stage than 350 other periods, e.g. at the defoliation stage (Fu et al., 2002; Wang et al., 2015). Here we linked k_R to the 351 development of foliage in modelling using the approach of Curiel Yuste et al. (2004): 352

353
$$k_R = k_{R0}(1 + n_R L_l / L_{max})$$
 (25)

where k_{R0} is the "base" respiration rate (Table 2); L_l is the green leaf area, which is a function of Julian day (Gong et al., 2016); L_{max} is the maximum L_l ; n_R is the maximum percentage of variability and is set to 100%.

357

358 2.4.3 Parameterization of soil CO₂ production

Based on the empirical study of Wang et al. (2014a), the steady-state sensitivity of CO₂ production to soil temperature and water content (i.e., $f(Ts)f(\theta)$, Eq. (11)) can be described as a logistic-power function:

362
$$f(Ts)f(\theta) = f(Ts,\theta) = \{1 + exp[a(b - Ts)]\}^{-1}(\theta/\theta_{sat})^c$$
 (26)

where *a*, *b* and *c* are empirical parameters. This function represents the long-term water-thermal sensitivity of CO₂ production over the growing seasonal, yielding an apparent temperature sensitivity Q_{10} of 1.5 for the emitted CO₂ (Wang et al. 2014a). However, this could underestimate the short-term sensitivities of CO₂ production. The apparent Q_{10} could be much greater at the diurnal level than at the seasonal level (Wang et al., 2014a). In this work, we firstly calculated the "base" sensitivity using the long-term scheme (Eq. 26) with 1-day moving average of water-thermal conditions. Then the deviation of hourly sensitivity from "base" condition was adjusted by the short-term Q_{10} :

370
$$f(Ts)f(\theta) = f(Ts_{short}, \theta_{short}) + [f(Ts, \theta) - f(Ts_{short}, \theta_{short})]Q_{10}^{(Ts - Ts_{short})/10}$$
(27)

371
$$Q_{10} = max \left[Q_{10}(Ts_{short}), Q_{10}(\theta_{short}) \right]$$
 (28)

372
$$Q_{10}(Ts_{short}) = -0.42Ts_{short} + 12.4$$
 (29)

373
$$Q_{10}(\theta_{short}) = 18010\theta_{short}^{3.721} + 1.604$$
 (30)

where Ts_{short} and θ_{short} are the 1-day moving averages of Ts and θ , respectively; Q_{10} (Ts) and Q_{10} (θ) are the adjustment functions for short-term apparent Q_{10} , regarding the short-term Ts and θ .

Further non-linearity of soil respiration responses refers to the rain-pulse effect (or the "Birch 376 377 effect", Jarvis et al. 2007), that respiration pulses triggered by rewetting can be orders-of-magnitude greater than the value before rain event (Xu et al., 2004; Sponseller, 2007). Such response could be 378 379 very rapid (e.g. within 1 hour to 1 day, Rey et al. 2005) and sensitive to even minor rainfalls. It also 380 seems that the size and duration of a respiration pulse not only depend on the precipitation size, but also on the moisture conditions prior to the rainfall (Xu et al., 2004; Rey et al., 2005; Evans and 381 382 Wallenstein, 2011). As numerical descriptions on such an effect remain unavailable at the moment, 383 we simply multiplied Eq. (26) to a rain-pulse coefficient (f_{pulse}):

384
$$f_{pulse} = max[1, (\theta/\theta_{72h})^{n_p}]$$
 (31)

where is the 3-day moving average of soil moisture content; n_p is a shape parameter and was set to 2 in this study. θ_{72h} is the 72-hour moving average of θ . For tests about model sensitivities to different parameterizations of f_{pulse} , see section 2.5.3.

388

389 2.4.4 Parameterization of biocrust photosynthesis and respiration

390 In sub-model (iii), Equations (17) - (19) were parameterized based on the experiment of Feng et al. 391 (2014). In the experiment, 50 lichen (topcrust) samples of 0.5-0.7 cm thickness (100% coverage, average C content of 1048 μ mol C cm⁻³) were collected from a 20 m \times 20 m area. The samples were 392 wetted and incubated under controlled T_{Ct} (i.e. 35°C, 27°C, 20°C, 15°C, and 10°C). These samples 393 394 were divided into two groups to measure the net primary productivity (NPP) and dark respiration (Rd) 395 separately. Gas exchanges and light response curve for each crust sample were measured using LI-6400 infrared gas analyzer equipped with an LI-6400-17 chamber and an LI-6400-18 light source (LI-396 397 COR, Lincoln, NE, USA). Measurements were taken at ambient CO₂ values of 385 ± 35 ppm. Saturated topcrust samples were placed in a round tray and moved to the chamber. CO₂ exchange was 398 399 measured during the drying of samples, until the CO₂ flux diminished. During drying, θ_{Ct} was 400 measured every 20 min. For more details see Feng et al. (2014).

401 Fitting measured Rd to T_{Ct} and θ_{Ct} (see Fig. 3a) was based on Matlab[®] (2012a) curve-fitting tool. 402 The obtained multipliers in Eq. (19) are as following:

403
$$f_{RC}(T_{Ct})f_{RC}(\theta_{Ct}) = Q_{Ct} \frac{(T_{Ct}-20)}{10} \left(a_{RC} + b_{RC}\theta_{Ct} + c_{RC}\theta_{Ct}^2 \right)$$
(32)

404 where Q_{Ct} , a_{RC} , b_{RC} , c_{RC} are the fitted shape parameters (Table 2).

The parameterized Eq. (19) was then used to simulate the Rd for the NPP samples, based on the correspondent T_{Ct} and θ_{Ct} from each measurement. P_{Cm} was determined by subtracting the simulated respiration rate from the NPP measured under light-saturated conditions. Then P_{Cm} was fitted to T_{Ct} and θ_{Ct} in Matlab[®] (2012a) curve-fitting tool using following equations (Fig. 3b):

409
$$P_{Cm} = f_{Pt}(T_{Ct})f_{Pw}(\theta_{Ct}) =$$

410
$$(a_{Pt} + b_{Pt}T_{Ct} + c_{Pt}T_{Ct}^{2} + d_{Pt}T_{Ct}^{3})(-a_{Pw} + b_{Pw}\theta_{Ct} - c_{Pw}\theta_{Ct}^{2} + d_{Pw}T_{Ct}^{3})$$
(33)

411 where a_{Pt} , b_{Pt} , c_{Pt} , d_{Pt} , a_{Pw} , b_{Pw} , c_{Pw} , d_{Pw} are fitted shape parameters (Table 2).

It should be addressed that T_{Ct} and θ_{Ct} could change more rapidly than the mean conditions of the crust (i.e. $Ts_{x,1}$ and $\theta_{x,1}$). In this work, T_{Ct} was calculated from the surface temperature (T_x , see Eq. (13) in Gong et al., 2016) and $Ts_{x,1}$ by linear interpolation. The calculation of θ_{Ct} , on the other hand, depended on the drying-rewetting cycle. During drying phases, θ_{Ct} was interpolated linearly from $\theta_{x,1}$ and surface moisture content (θ_x); whereas during wetting phases, the mass balance of water input *P* and evaporation loss ($E_{x,1}^s$, see Eq. (17) in Gong et al., 2016) was considered:

418
$$T_{Ct} = \frac{T_x Z_{Ct} + T_{S_{x,1}} Z_{S_{x,1}}}{Z_{Ct} + Z_{S_{x,1}}}$$
(34)

419
$$\theta_{Ct} = max \left[\frac{\theta_{x} Z_{Ct} + \theta_{x,1} Z_{S_{x,1}}}{Z_{Ct} + Z_{S_{x,1}}}, \theta_{Ct} + \frac{P - E_{x,1}^{S}}{Z_{Ct}} \right]$$
(35)

420 where $Zs_{x,I}$ is the thickness of the biocrust; and Z_{Ct} is the thickness of the topcrust. θ_x was calculated 421 from the surface humidity and the water retention of the crust layer, using Eq. (25) – (26) by Gong et 422 al. (2016).

423

424 2.4.5 Calculation of litter input to soil and SOC transport in biocrust

The litterfall added to each soil layer $(A_{x,i}^1, \text{Eq. (13)})$ was linked to the mortality of roots, which was calculated following Asaeda and Karunaratne (2000).

427
$$A_{x,i}^{1} = k_{mo} Q_{mo}^{T_{x,i}-20} M_{x,i}^{R}$$
(36)

428 where k_{mo} is the optimal mortality rate at 20°C; Q_{mo} is the temperature sensitivity parameter (Asaeda 429 and Karunaratne, 2000). Similarly, we attributed the C transport rate (A_{Cm}) from M_{CA} to M_{CH} mainly to 430 the mortality of autotrophic organisms. We assumed that most mortality of crust organisms occurred 431 during abrupt changes in wetness, as microbial communities may adapt slow moisture changes or 432 remain inactive during drought (e.g. Roberson and Firestone, 1992; Reed et al., 2012; Coe et al., 2012; 433 Garcia-Pichel et al., 2013; Maestre et al., 2013). Here, we introduced a water-content multiplier, 434 $f_m(\theta_{Ct})$, to describe the impact of abrupt θ_{Ct} changes on k_m :

435
$$A_{Cm} = k_{mc} Q_{mo}^{T_{Ct}-20} f_m(\theta_{Ct}) M_{CA}$$
(37)

436
$$f_m(\theta_{Ct}) = max[0.01, 1 - min \ (\theta_{Ct}, \theta_{Ct7}) / max \ (\theta_{Ct}, \theta_{Ct7})]$$
(38)

437 where k_{mc} is the optimal mortality rate at 20°C; Q_{mo} is the temperature sensitivity parameter (Asaeda 438 and Karunaratne, 2000); θ_{Ct7} is the forward 7-day moving average of θ_{Ct} .

439 C transport from topcrust to subcrust was calculated as driven mainly by the sand deposition and 440 burying of topcrust SOM. Assuming the C content in topcrust was homogeneous and the thickness Z_{Ct} 441 was near-constant, the transport rate (k_b) was then proportional to the sand deposition rate:

442
$$k_b = \frac{k_{sand}}{\rho_{bulk}} \frac{1}{Z_{Ct}}$$
(39)

443 where ρ_{bulk} is the bulk density of soil; k_{sand} is the sand deposition rate in Yanchi area, which is a 444 function of wind velocity (Li and Shirato, 2003):

445

446 **2.5 Model validation and sensitivity analyses**

447 2.5.1 Simulation set-ups

In the model simulations, soil depth was set to 67.5 cm to cover the rooting zone (Gong et al., 448 449 2016), including the crust layer (2.5 cm) and sandy subsoil (65 cm, stratified into 5 cm layers). Water 450 contents measured at 70 cm depth was used as the lower boundary conditions for hydrological 451 simulations (Jia et al., 2014). The calculation of soil temperature extended to 170 cm depth with no-452 flow boundary, regarding the probably strong heat exchange at the lower boundary of rooting zone (Gong et al., 2016). Zero-flow condition was set for the lower boundary of CO₂ and O₂ gases, whereas 453 454 dissolved CO₂ was able to leach with seepage water. Based on presumed similarity of RLU structures, 455 we assumed no-flux conditions for transports of water, heat, solvents and gases at outer boundary. In 456 the simulation, we assumed instant gas transport via topcrust, whereas considered the CO_2 released by subcrust (R_{Cs}) was subject to the dissolving-transport processes. In this work, we aggregated the C 457 458 processes in subcrust with those in soil profile. The initial ratio of M_{CA} : M_{CH} was set to 2:3. The C 459 concentration of organic matters was set to 50%.

460 The model run with half-hourly meteorological variables including the incoming shortwave 461 radiation, incoming longwave radiation, PAR, *Ta*, relative humidity, wind speed and precipitation. 462 Initial temperatures and soil moisture contents for each soil layer were initialized following the work 463 by Gong et al. (2016). Surface CO_2 concentration was set to 400 ppm. The initial gaseous CO_2 464 concentration was set to increase linearly with depth (5 ppm cm⁻¹). The initial CO_2 concentration in 465 liquid form was then calculated based on Eq. (4) – Eq. (8). The initial content of mineral N content 466 was set to 40 mg/g, which was within the range of the field observations. The two-dimensional 467 transpirations of water, energy and gases along the soil profile were solved numerically using the 468 Predict–Evaluate–Correct–Evaluate (PECE) method (Butcher, 2003). In order to avoid undesired 469 numerical oscillations, the transport of water, energy and gases were calculated at 5-min sub steps.

470

471 2.5.2 Model validation

First, we validated the modelling of soil temperature and moisture content for the F_s site (Test 0). The simulated hourly soil temperature and moisture content at 10 cm depth were compared to the measured values for each collar. The validation was based on the same meteorological data as used by Gong et al. (2016), who validated the model in regard to the diurnal to seasonal dynamics of radiation balance, surface energy balance, soil temperature and moisture content at the EC site.

477 The validity of the modelled F_s was then examined in three separate tests. In Test 1, modelled F_s 478 was validated for non-crusted soils. In this case, F_T in Eq. (1) was the only term affecting F_S ($F_B=0$ 479 and $F_P = 0$), and the crust influences on C-water exchanges were excluded. The biocrust-related processes were considered in Test 2 and Test 3. Test 2 considered the dark respiration of biocrust 480 481 (R_{Ct}) , and set $F_B = R_{Ct}$ and $F_P = 0$. Test 3 considered all the flux components $(F_T, F_P \text{ and } F_B)$. In these 482 tests, different values of root biomass were assigned to the model, regarding the different collar 483 conditions (Table 1). In Test 1 – Test 3, half-hourly F_s were simulated and averaged to hourly, and compared to those measured from the collar C1 - C3, respectively. Linear regressions were used to 484 compare the modelled and measured values. The biases (ζ) of the simulated values were calculated by 485 486 subtracting the measured values from the modelled ones. Gap values in the measurements were 487 omitted in the validation and the bias analyses.

488

489 2.5.3 Simulating componential CO₂ fluxes and their parameter sensitivities

490 Using the validated model, we simulated the temporal trends of C flux components (i.e. P_{Ct} , R_{Ct} , F_P , 491 F_T , Ra and Rs) in Test 4, in order to find out how the different flux components may have contributed 492 to the total efflux (Table 3). The simulation used the same model set-ups and climatic variables as 493 Test 3. It should be noticed that, although the model was built as an abstract for ecosystem-level 494 processes, the simulation set-ups and validation were performed at a point level corresponding to 495 respiration chambers. Therefore, understanding the uncertainty sourced from parameterization could 496 be helpful for future development and applications. In Gong et al. (2016), we have studied the 497 sensitivities of modelled soil temperature and moisture content to the variations in soil texture, water 498 retention properties, vegetation parameters and plant-interspace heterogeneities. In this study, we also 499 tested the sensitivity of F_s and componential fluxes to the changes in a number of site-specific

500 parameters (Table 4). These parameters included pH, nitrogen content, water-thermal conditions, root

501 biomass, production rates and decomposition rates of litters, which are often key factors regulating the

soil C processes but likely to vary within and among ecosystems (see e.g. Ma et al., 2011; Gong et al.,

503 2016; Wang et al., 2016). Furthermore, we tested the model sensitivities to several newly defined

parameters (i.e. n_R , n_p and f_m), to understand their effects on model uncertainties. F_s and componential

fluxes at interspace were simulated by varying single parameter value by 10% or 20%. The sensitivity

506 of each tested flux was described by the difference (dF) in the annual flux rate simulated using 507 manipulated parameter, as compared to the rate simulated under no-change conditions.

508

509 2.5.4 Comparing model sensitivities between plant cover and interspace

In order to study the effects of plant-interspace heterogeneity on soil CO2 efflux, Test 5 simulated 510 annual F_s and componential fluxes at plant cover and compared the values to interspace. The 511 simulation set-ups were almost same as those employed in Test 1-3; only exception was that same 512 513 initial values of SOC storages (650 gC m-2) and root biomass (200 g m-2) were used for under-514 canopy and interspace areas for comparison purpose. Based on Test 4, we further compared the plantinterspace differences in the C-flux sensitivities to most important site-specific parameters, i.e. soil 515 temperature (Ts), water content (θ) and root biomass (M^{R}) (see Section 3.2). The differences in 516 parameter sensitivities were calculated by comparing the absolute values of sensitivities (|dF|, see 517 518 section 2.5.3 and Table 4) from the area with plant cover to without (interspace).

519

520 **3. Results**

521 **3.1 Model validity**

Comparing to the EC site in previous work (Gong et al., 2016), the soil in this study was much 522 coarser and the measured θ at 10 cm depth was constantly lower (Fig. 4), indicating the necessity of 523 524 re-parameterization and validation of the water-energy algorithms. Figure 4a shows the modelled 525 hourly Ts and θ at 10 cm depth with the mean values measured from the Fs site during year 2013. 526 Based on the site-specific vegetation and soil texture parameters, our model explained 97% of the 527 variations in the measured hourly Ts. The model underestimated the temperature mainly in summer 528 time (i.e. day 150-250, Fig. 4a). The underestimation was more pronounced around the noontime in 529 the diurnal cycle. As the water-content sensors may not accurately capture the moisture dynamics 530 during freezing period, only the simulation during ice-free period were compared to measured data 531 (Fig. 4b). During the ice-free period, the model explained 83% of the variations in the measured mean 532 water contents at 10 cm depth. The biases in the modelled temperature and moisture content were less

than the spatial variations observed in this area (e.g. Wang et al., 2015). Therefore, our model couldbe able to reproduce the time series for the measured water-energy fluxes at the site.

535 Our model explained 87 and 83% of the variations in the hourly F_s measured on the non-crusted surface in year 2013 and 2014 (Fig. 5a). The root-mean-square errors (RMSE) were 0.43 µmol m⁻² s⁻¹ 536 and 0.29 μ mol m⁻² s⁻¹ respectively. The model mainly underestimated the daytime F_s during the 537 freezing periods. During the ice-free periods, the model mainly overestimated the efflux in early 538 springs. The biases in modelling largely showed a diurnal pattern (Fig. 5b), that F_S was mainly 539 540 underestimated in noon hours (i.e. from 10 a.m. to 3 p.m.) but slightly overestimated in the afternoon 541 and evening. At the daily level, our model explained 94% of the variations in measured daily efflux 542 during the two-year period (Fig. 5c).

Compared to the non-crusted soil (C1), the simulated F_s for crusted surfaces (C2 and C3) showed 543 greater deviations from measured data. At the hourly scale, our model explained 75 % (year 2013) 544 and 68 % (year 2014) of variations in measured Fs from C2 (Fig. 6a), and 68 % (year 2013) and 61 % 545 (year 2014) of variations in the F_s measured from C3 (Fig. 6b). For the two-year period, RMSE of the 546 modelled hourly F_s were 0.25 µmol m⁻² s⁻¹ and 0.35 µmol m⁻² s⁻¹ for C2 and C3, respectively. The 547 magnitudes of biases $(|\zeta|)$ were generally greater during the rainfall period (i.e. from the start of 548 raining to 24 hours after end of rainfall) than the inter-rainfall period (Fig. 7). The simulated F_S for C2 549 showed similar diurnal pattern of biases as compared to C1, suggesting ineligible contributions from 550 551 the biases in simulated subsoil emissions. Introducing photosynthesis and photodegradation of 552 biocrust to the system (C3) led to greater overestimations in F_s , and these were more obvious in the afternoon hours (i.e. from 12 a.m. to 6 p.m.) and during wetting period. Nevertheless, at the daily 553 scale, the model explained 91% (C2, Fig. 5c) and 86% (C3, Fig. 5d) of the variations in the measured 554 F_S during the two-year period. There were no significant systematic deviations between the measured 555 556 and the modelled daily values, as indicated by the regression slopes close to 1 and the intercepts close 557 to 0 (Figs. 4 and 5).

The results above showed that, the model was able to describe the seasonal variations of F_s for both non-crusted and lichen-crusted soils. Moreover, the model captured the strong variability of hourly/daily F_s in wetting-drying cycles. Comparing to earlier statistic modelling by Wang et al. (2014a, 2014b), this model showed equal or improved accuracy. In this sense, we assume that our model has included the main mechanisms controlling the F_s dynamics in the soil system, and could be used for further analysis on componential C processes and their parameter sensitivities.

564

565 **3.2 Modelled C flux components of F**_s

Test 4 showed that, Rs was the main contributor to the root-zone CO₂ production, which accounted for a major source of effluxes (F_s). Our measurements showed large diurnal and seasonal variations in F_s regardless the existence of crust covers (Fig. 5 and Fig. 6). Particularly, the F_s dynamics depended

- strongly on rain events. Even at non-crusted soil (i.e. C1), F_s dropped significantly from the pre-
- 570 rainfall level even to near-zero, but rebound rapidly and peaked after rain stopped (Fig. 5a). This
- 571 could relate to the mismatched trends of CO_2 production (Rs + Ra) and emission (F_T) from the rooting
- zone with respect to the wetting-drying cycles (Fig. 8a). Compared to CO₂ production, the responses
- 573 of F_T to rainfall were generally lagged and smoothed (see examples in Fig. 8b 8d), irrespective of
- 574 the size of rain events. In the simulation, soil rewetting increased CO_2 production rapidly but
- 575 depressed F_T , which increased after rain ceased. In all the examples (Fig. 8b 8d), F_T exceeded R_P 576 within 48 hours after the ending of rain events. At the annual level, the total R_P was larger during 577 wetting period (i.e. raining days plus 1 day after rainfall) than the rest days of the year (i.e. drying
- 578 period), whereas the total F_T was greater during the drying period (Fig. 8e).

579 On the annual basis, CO₂ production (Rs+Ra) and emission (F_T) from root-zone soil were mismatched (Table 3), and the former was more than 15 % greater than latter. Such a gap was mainly 580 due to the root uptake and transport of dissolved CO_2 (i.e. 36 gC m⁻² year⁻¹), whereas the loss of 581 dissolved CO₂ via seepages or pore-mediated horizontal flows were limited (i.e. 7.4 gC m⁻² year⁻¹). 582 The photosynthesis rate of topcrust was 31.1 gC m⁻² year⁻¹ at interspace. After rainfall, the C uptake 583 by topcrust increased significantly, even turned the soil from net C source to sink during a few hours 584 to one day (Fig. 6, Fig. 8). However, at annual scale, the C losses via respiration and photodegradation 585 accounted for 90 % of the photosynthetic products, leading to a near-zero contribution of topcrust to 586 $F_{\rm S}$ during the two year period (i.e. < 5 gC m⁻² year⁻¹). 587

588 Analysis of parameter sensitivity showed that, the modelled F_s and the component fluxes were more sensitive to ± 2 °C in Ts or ± 10 % in θ , as compared to the effects of ± 10 % or ± 20 % in the 589 590 other parameters (Table 4). Varying θ by 10 % produced greater impacts on the simulated R_P and crust-related fluxes (i.e. P_{Ct} , R_{Ct} and F_P), as compared to changing Ts by ± 2 °C. Increasing θ by 10 % 591 592 enhanced the simulated P_{Ct} and F_{Ct} by 41 % and 28 %, and doubled the net C sequestration $(F_{Ct} - F_P)$ by topcrust. However, the contribution of such changes to annual F_s was minor, and amounted for 593 594 only 2.0 % of the total efflux. Beside Ts and θ , the simulated efflux was also sensitive to changes in root biomass (M^R). Manipulating root biomass by ±10 % changed the annual F_T and F_S by about 7%, 595 and such effects were 100% greater than ± 10 % changes in M_{tot} in soil. Adjustment of other 596 597 parameters, e.g. n_p (eq. (31)) and f_m (eq. (38)), produced little influences on the modelled F_s and the componential fluxes (Table 4). In addition, the model was robust to the adjustment of several crust-598 related parameters, i.e. k_{mc} , M_{Ct} and M_{CA} : M_{CH} . Hence, algorithms correspondent to those parameters 599 600 could be simplified in future developments.

601

602 **3.3 Modelled plant-interspace differences in C flux components**

At either plant-covered or interspace area, Rs was a major contributor to root-zone CO₂ produced and F_T dominated the total effluxes (Table 3). The C loss at interspace was 14% faster than under-

- 605 canopy on an annual basis, if root biomass and SOC were homogeneous at plant cover and interspace.
- 606 The lower F_s rate at plant cover mainly attribute to the lower CO_2 production (R_s+R_a) from subsoil.
- 607 The C loss via seepage and root transport, which is the gap between subsoil CO_2 production and
- 608 emission (F_T), was slightly higher under canopy (17%) than at interspace (15%). Comparing to
- 609 interspace, the photosynthesis of biocrust (P_{Cl}) was 34% lower under canopy. This reduced the under-
- 610 canopy F_{Ct} by 42% in comparison with interspace. However, such a different was largely offset by the
- 611 reduced photodegradation rate under canopy, leading to limited plant-interspace differences in net
- 612 sequestration by topcrust (i.e. by $1.4 \text{ gC m}^{-2} \text{ year}^{-1}$).

613 We further compared the flux sensitivities at plant cover and interspace to the changes in three most effective parameters (i.e. T_s , θ and M^R , see Table 5). For subsoil-mediated fluxes (i.e. F_s , F_T , R_a , R_s), 614 the sensitivity values differed by less than 2 % from plant cover to interspace. On the other hand, the 615 sensitivities of crust-related fluxes (i.e. P_{Ct} , F_{P}) showed greater differences between plant cover 616 and interspace. Comparing to interspace, F_s and F_T at plant-covered area were more sensitive to Ts 617 618 changes, but less sensitive to manipulations in θ . On the other hand, the plant cover reduced the 619 sensitivity of CO₂ effluxes to changes in root biomass. P_{Ct} , F_{Ct} and F_P were generally more sensitive to warming and θ manipulations at plant cover than interspace, except that plant cover decreased the 620 sensitivity of F_P to -10 % changes in θ . Nevertheless, their contribution to the sensitivity of F_S was 621 marginal, due to the low flux rates of crusts. 622

623

624 **4.** Discussions

625 4.1 The roles of componential C processes in regulating soil CO₂ efflux

626 Our process-based model provided a tool to separate the multiple soil C processes and investigate their roles in regulating F_s dynamics in dryland ecosystems. So far, efforts to quantify the soil C loss 627 in terrestrial ecosystems have considered soil C efflux as a synonym of respired CO₂. However, based 628 on this work, cautions must be taken when extrapolating the Fs responses from the chamber to 629 630 ecosystem scale and from short-term to long-term periods. Processes other than autotrophic and 631 heterotrophic respiration could significantly modify the F_s responses to climatic variability. Our simulation highlighted decoupled CO₂ production and emission during the wetting-drying cycle, as 632 633 regulated by the CO₂ transport in soil profile. The simulated CO₂ production in soil profile were much 634 greater than effluxes during rain pulses (e.g. Fig. 7). This indicated that, the low F_s during rewetting 635 was mainly due to the increase in CO₂ dissolution, instead of the reduced respiration rates by low O₂ supply (e.g. Fang and Moncrieff, 1999). This finding is further supported by the measurement of 636 637 Maier et al. (2011), which showed that 40% of the respired CO₂ could be stored temporally in soil pore-space after rainfalls. The dissolved CO₂ then released gradually with the evaporation of pore 638 639 water, leading to lagged responses of efflux as compared to respirations. Regarding that a major 640 fraction of CO₂ was produced during the wetting periods (Fig. 5e), such a lagging effect should be

- carefully examined when analysing the climatic sensitivity of F_s . Our simulations showed that a considerable fraction of CO₂ produced could be removed by root uptake and leave the volume measured by the respiration chamber. Bloemen et al. (2016) showed that the CO₂ concentration in root xylems could be higher than in soil solutions. This implies that such a "missing source" might be even greater than the model estimation, although knowledge is still limited about the efficiency of the removal and the diffusion/release of CO₂ during the transport (Bloemen et al., 2016).
- The contributions of biocrusts as C sink or source have remained largely unknown (Castillo-647 Monroy et al., 2011). This is mainly due to the difficulty to separate the CO_2 exchanges of crust 648 organisms from the background respirations (Castillo-Monroy et al., 2011; Sancho et al., 2016). As 649 650 demonstrated in our work (Fig. 5b - 5d), the photosynthesis of topcrust could be masked by background emission quickly (e.g. within 1 day) after rain events. The simulated F_{Ct} was 31 g C m⁻² 651 year⁻¹ at interspace. Considering a 30% coverage of lichens over the sampling area (Feng et al., 2014), 652 the interspace-level NPP was 9.3 g C m⁻² year⁻¹. This value was largely greater than the lab-based 653 estimation for the site (Feng et al., 2014). However, it was in range of the values reported from 654 several other dryland ecosystems (i.e. 5.3 - 29 g C m⁻² year⁻¹, Sancho et al., 2016). Our simulations 655 also suggested that photodegradation might offset about 48 % of the CO₂ photosynthesized by 656 657 biocrust. It could explain the much higher F_s measured from the transparent chamber (C3) than the opaque chamber (C2) during dry daytime periods (e.g. Fig. 9). It should be also noticed that the litter 658 659 from shrub canopy was not included in the measurement nor modelling. Also the interactions between 660 photodegradation and biotic decaying were not considered either. Hence, the contribution of photodegradation to soil C balance could be greater than our estimation at the ecosystem level (see e.g. 661 Gliksman et al., 2016). Although the contribution of surface exchanges were only marginal as 662 compared to the annual CO₂ efflux, removing the biocrust processes would substantially reduce the 663 model validity. For example, the goodness of fitting (i.e. R²) in Test 3 dropped from 0.65 to 0.45 for 664 the two-year period, if F_{Ct} and F_P were neglected. Therefore, delineating the gas exchange of biocrust 665 666 could be helpful, in order to upscale the modelling of C balance from chamber to ecosystem level, where the distribution of crust cover may vary from one site to another. 667
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669 4.2 Plant-interspace differences in soil C fluxes

670 Clumped distributions of foliage and biomass are critical features for the adaptation and functioning 671 of vegetation in arid and semiarid environments. Previous studies have mainly emphasized the shrub 672 effects on ecohydrology (e.g. Rongo et al., 2006; Gong et al., 2016) and enrichment of sediments and 673 nutrients, known as "resource island" effect (Reynolds et al., 1999; Rietkerk et al., 2004). Our 674 simulations showed that the presence of shrub canopy also influenced soil C exchanges. The presence 675 of shrub cover affected the C functioning of biocrust mainly through shading, which reduced 676 photosynthesis more than respiration and photodegradation. Comparing to interspace, the simulated

- annual F_s was 13% lower under canopy (Test 5). As we ruled out the differences in SOC and root biomass and limited the C-flux differences contributed by biocrusts between plant-covered and interspace areas, such a decrease in plant-cover F_s was probably due to the cooling effect of canopy
- 680 (Gong et al., 2016). This effect was close to the modelled responses of F_s to ± 2 °C in soil temperature
- 681 or \pm 10% in soil water content. As the root density and litter production rate are commonly larger
- under canopy than interspace (e.g. Zhang et al., 2008), the lower respiration rate under canopy tends
- to facilitate the accumulation of biomass and organic matters and feedback to functioning of "resource
- 684 islands" during prolonged periods.
- 685 Our simulation further indicated considerable differences in the C-flux sensitivities between areas with plant cover and without. As the C processes and initial conditions were set to be homogeneous, 686 those differences could mainly result from the different water-thermal conditions at plant cover and 687 interspace. For example, the higher temperature sensitivities of F_T , F_S and F_{Ct} may relate to the 688 cooling effect of canopy (see Gong et al., 2016), which may lead to a greater Q10 value for respiration 689 690 estimations (i.e. eq. (27)). Moreover, the slower decomposition in under-canopy soil could also lead to 691 the lower sensitivities of F_T and F_S to changes in root biomass and SOM contents. On the other hand, water advection from interspace to plant cover, which may support over 30% of water loss from 692 693 under-canopy soils (Gong et al., 2016), could help to lower the F_s sensitivity to water content changes at plant cover. The increased water-thermal sensitivities of C exchanges of biocrust could be 694 695 explained by the less-stressful environment for curst organisms, e.g. higher moisture content but lower radiation and temperature, although the photosynthesis of lichens (P_{Ct}) could be reduced by 696 shading (Table 3). Such heterogeneity of C-flux sensitivities thus should be considered in future 697 698 studies on the ecosystem-level responses to climate change and extreme climatic events.
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700 4.3 Modelling uncertainties and future research needs

Our model showed its ability to describe the dynamics of soil temperature, moisture content and C effluxes measured for the studied semiarid ecosystem. Major uncertainty of the modelling, however, may refer to the concept of equifinality (Beven, 1993, 2006). The question of equifinality arises from the fact that the structures and mechanisms being modelled are based on insufficient information. Consequently, alternative models using different functions and parameter sets may fit equally well to observations, thus the mechanisms quantified in modelling are difficult to be justified or falsified. Regarding this work, the modelling equifinality and uncertainty could relate to several aspects.

Firstly, the representative land unit (RLU) was a statistical simplification to the target ecosystem at footprint scale (Gong et al., 2016), and may not fully capture the spatially explicitly of soil environment and biogeochemistry at ecosystem scale. For example, the model assumed Poisson probability of mutual shading (Bégué et al., 1994), and the probability of shading increased continuously with solar zenith (Gong et al., 2016). However, for explicit space-time, shading is binary.

- This possibly leads to the biases in the estimations of net radiation (Gong et al., 2016) and collar
- temperature around midday, which sequentially affected the simulated diurnal pattern of F_s (see Fig.
- 715 3b). Moreover, field observations showed considerable spatial variations of soil temperature, water
- content and biogeochemistry (e.g. pH, litter quality and root biomass) within a distance of 3-5 meters.
- 517 Such variations could well exceed a magnitude of 10 %, and even over 100 % (e.g. Zhang et al., 2008;
- Find the spatiality of soil Figure 4., 2013; Wang et al., 2015). Therefore, the variation of F_s driven by the spatiality of soil
- factors could be greater than the responses to ± 2 °C in soil temperature or ± 10 % in soil water content.
- 720 Therefore, future modelling may need to consider spatially explicit settings, in order to further
- 721 minimize the gaps between model settings and the reality.
- 722 Secondly, the high sensitivity of simulated F_s to soil pH indicated that unconsidered processes of 723 inorganic C could strongly affect the accuracy of modelling. Our modelling for CO₂ transport considered gaseous and liquid phases. However, the solid phase was not included, despite the high 724 725 lime content (2300-5400 kg ha⁻¹) in the soil (Feng et al., 2013; Wang et al., 2015). Based on soil samples of similar lime content (2700 kg ha⁻¹), Buysee et al. (2013) showed that neglecting the 726 727 inorganic C exchanges by solids may lead to underestimation of F_s during the heating phase of a day, but overestimation of F_s during the cooling phase. This is very similar to the diurnal pattern of biases 728 in simulated F_s (Fig. 3d). Therefore, further improvement on the modelling may need to consider the 729 730 solid phase as well.
- 731 Thirdly, the current model still lacked descriptions on growths of plant and soil microbes. 732 Comparing to many other ecosystems, drylands often feature high root-shoot ratio (Jackson et al., 733 1996) but low SOC storages. Changes in plant physiology and growth can readily influence root 734 metabolisms and labile SOC pools, hence modify F_s dynamics (Wang et al., 2015). On the other hand, large fluctuation of diurnal and seasonal temperature may drive the microbial communities to shift 735 736 between warm-adapted to cold-adapted (Van Gestel et al., 2013), which could largely change soil respiration and its sensitivity to freeze-thaw cycles (Van Gestel et al., 2013; Liu et al., 2016). Both the 737 biotic controls are mixed with the legacy effects of climatic variability over annual and inter-annual 738 courses (Sala et al., 2012; Jia et al., 2016; Shen et al., 2016), and could affect the C-water simulations 739 cumulatively through the feedbacks between biomass accumulation and soil biogeochemistry 740 741 (Bradford et al., 2016). This may explain the decreasing trend of model validity from year 2013 to 742 2014 (Fig. 3, Fig. 4). Therefore, the dynamics of plants and microbial communities are required in 743 future modelling, in order to improve the F_s simulations regarding inter-annual and long-term periods.
- *In addition*, proper field data are still needed to support the future modelling work. The dataset used in our model validation mainly separated the influences of biocrusts from subsoil respirations. However, some processes like photodegradation and lateral CO_2 transport by root or water flows still require more support from observation. Also, respiration data from shrub-covered soil remains unavailable, as the settlement of soil collars and respiration chambers under canopy could easily interrupt the biophysiology of shrubs. The C functioning of crust organisms is especially sensitive to

750 water content (Table 4). However, track the water content in the very thin layer of topcrust can be 751 very challenging using hour-based meteorological data. Nocturnal water inputs (e.g. dewfalls) are 752 important to the metabolisms of crust organisms (e.g. Liu et al., 2006), but they are hard to be 753 quantified precisely by EC measurement, or models derived from EC data. Moreover, we presumed 754 structural homogeneity for the crust layer and employed constant regime for crust processes. In reality, 755 there may not be clear boundaries between topcrust and subcrust, and even topcrust itself may contain 756 significant variations in microstructure and communities even within one centimetre (Williams et al., 757 2012; Raanan et al., 2016). The C sequestration of biocrust can be strongly modified by microbial 758 communities directly (Belnap, 2003; Pointing and Belnap, 2012; Feng et al., 2014; Maestre et al., 759 2015) and through other factors e.g. surface albedo (Chamizo et al., 2012), dew falls (Liu et al., 2006), soil pore forming (Williams et al., 2012; Felde et al., 2014). So far, many questions remain 760 761 unanswered about the mechanisms that control the colonization, adaption and succession of microbial 762 communities and the structure-function of biocrust (Pointing and Belnap, 2012). Further knowledge 763 on these mechanisms will be helpful to validate or falsify the modelled C functioning in response to 764 climate change and extreme climatic events.

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767 5. Conclusions

This work represents a first attempt to integrate the CO₂ production, transport and surface 768 exchanges (e.g. biocrust photosynthesis, respiration and photodegradation) in F_s modelling for 769 770 dryland ecosystems with high plant-interspace heterogeneities. Our model reproduced the F_s 771 dynamics measured from non-crusted and lichen-crusted soil collars during year 2013-2014, although 772 introducing the gas exchanges of lichen crust decreased the model performance at the hourly scale. However, further model development may still be required on several aspects, e.g. by including: i) the 773 774 spatial-explicit schemes for surface conditions and soil biogeochemistry; ii) influences of lime and 775 solids on CO₂ transport; iii) growth dynamics of plants; iv) high-resolution dynamics of surface 776 water-thermal conditions and v) the dynamics of microstructure and microbial communities of 777 biocrusts.

778 Our model simulations highlighted that, the transport processes of inorganic C and the metabolisms 779 of biocrusts could strongly modify the CO₂ efflux, and these influences are closely linked to soil hydrology. Soil rewetting could enhance CO_2 dissolution and delay the emission of CO_2 produced 780 781 from root-zone. In addition, an ineligible fraction of respired CO₂ could be removed via lateral flows 782 and root uptake, and become "missing" from volumes under respiration chambers. The lichen-crusted 783 soil could temporally shift from net CO₂ source to sink during rewetting, as driven by the 784 photosynthesis of lichens and the restrained CO₂ emissions from subsoil. Whereas after rain events, the CO₂ exchanges of lichens could be easily masked by background emissions from subsoil. Based 785

on our modelling, the annual NPP was 9.3 gC m^{-2} by topcrust at interspace. However, the net C sequestration by topcrust could be marginal, if the photodegradation was accounted. Our modelling further showed different componential C fluxes and sensitivities between plant-covered and interspace areas. The presence of plant cover tended to decrease the root-zone CO₂ production and biocrust C sequestration, but increase the temperature sensitivities of these fluxes. On the other hand, the sensitivities of root-zone emissions to water content were lower under canopy. This may be due to the advection water flows from the interspace to plant cover. To conclude, the complexity and plant-interspace heterogeneities of soil C processes should be carefully considered when extrapolating findings from chamber to ecosystem scales, in order to predict the ecosystem responses to climate change and extreme climatic events. Our model can serve as a useful tool to simulate the soil CO₂ efflux dynamics in dryland ecosystems.

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1099 Tables

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1101 Table 1. Configuration of soil collars used in this study

Collars	C1	C2	C3
Surface type	Non-crusted	Lichen-crusted	Lichen-crusted
Chamber type	Opaque	Opaque	Transparent
Root biomass (g m^{-3})	420	106	92
Gap of data (%)	12.9	10.5	9.85
Annual C efflux (gC m ⁻²) ^a	259	194	192

^a The values were calculated from the measured hourly FS data excluding data gaps.

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1104 Table 2. Parameters for soil water retention and C turnover

Parameter	Equation	Unit	Value		
α_h	_ a	-	0.0355 ^b		
n	_ ^a	-	1.5215 ^b		
k_{I}	(11)	$g g^{-1} da y^{-1}$	0.01 ^c		
k_2	(11)	$g g^{-1} da y^{-1}$	0.08^{d}		
k_3	(11)	$g g^{-1} da y^{-1}$	0.001 ^d		
k_g	(15)	$g g^{-1}$	0.15 ^e		
k_{cr}	(19)	$g g^{-1} s^{-1}$	0.0014^{-f}		
k_p	(24)	g g ⁻¹ year ⁻¹	0.23 ^g		
k_{RO}	(25)	$g g^{-1} da y^{-1}$	0.002 ^e		
а	(26)	-	0.1 ^h		
b	(26)	-	24 ^h		
С	(26)	-	0.89 ^h		
Q_{Ct}	(32)	-	1.585 ^f		
a_{RC}	(32)	-	-0.0525 f		
b_{RC}	(32)	-	$2.602^{\text{ f}}$		
C_{RC}	(32)	-	-1.653 ^f		
a_{Pt}	(33)	-	$0.9837^{\rm f}$		
b_{Pt}	(33)	-	-0.1385 ^f		
C_{Pt}	(33)	-	$0.0095^{\rm f}$		
d_{Pt}	(33)	-	-1.6318E-4 ^f		
a_{Pw}	(33)	-	-0.3501 ^f		
b_{Pw}	(33)	-	5.5884 ^f		
C_{Pw}	(33)	-	-7.1783 ^f		
d_{Pw}	(33)	-	2.6837 ^f		

^a See Eq. (26) in Gong et al. (2016). Sources of parameter values: ^b This study, see section 2.3.2; ^c Lai et al.

1106 (2016); ^d Gong et al. (2014); ^e Chen et al. (1999); ^f This study, see section 2.4.4 and Fig. 3; ^g Wang et al., 2014a.

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1110 Table 3. Simulated component CO_2 fluxes (gC m⁻² year⁻¹) for areas with plant cover and without (interspace).

Surface type	F_S	F_T	$Rs+Ra^{a}$	Ra	P_{Ct}	F_{Ct}	F_P	$F_{Ct} - F_P^{b}$
Interspace	244	249	295	113	54.6	31.1	26.1	5.0
Plant covered	214	218	263	108	36.3	18.2	14.6	3.6

1111 ^{*a*} Rs + Ra represents the total CO₂ production from soil respirations. Ra is the total autotrophic respiration ($Ra = \sum_{i} Ra_{i}$, see Eq. (10)) and Rs is the total heterotrophic respiration ($Rs = \sum_{i} Rs_{i}$, see Eq. (12)); ^{*b*} $F_{Ct} - F_{P}$ represents 1113 the net CO₂ exchanges of topcrust, see Eq. (17) and Eq. (24) for correspondent algorithms of the variables. For 1114 definitions of other fluxes, see Eq. (1) for F_{S} , Eq. (3) for F_{T} , Eq. (17) for F_{Ct} , Eq. (18) for P_{Ct} and Eq. (24) for F_{P} .

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1116 Table 4. Sensitivity of simulated F_s and its componential fluxes to manipulations of parameter values.

Change of parameter	$F_S{}^a$	F_T	$Ra+R_S$	Ra	P_{Ct}	F_{Ct}	F_P	F_{Ct} - F_P
n _R +20 %	$+3.3^{b}$	+3.2	+2.7	+7.9	/ ^c	/	/	/
<i>n</i> _{<i>R</i>} -20 %	-2.9	-2.8	-3.4	-8.8	/	/	/	/
n_P +20 %	+1.6	+1.6	+1.0	/	/	/	/	/
<i>n</i> _P -20 %	/	/	-1.4	/	/	/	/	/
f_m +20 %	/	/	/	/	+2.9	+3.8	+3.4	+6.0
f_m -20 %	/	/	/	/	+1.2	/	-5.7	+30
$Ts + 2 \ ^{\circ}C$	+9.5	+9.6	+7.1	+11	+4.9	+3.9	+1.5	+16
<i>Ts</i> -2 °C	-9.0	-9.2	-8.1	-11	-1.3	-2.9	/	-20
heta +10 %	+3.6	+5.6	+7.5	+14	+41	+28	+14	+102
heta -10 %	-5.0	-5.6	-8.1	-14	-16	-13	-8.4	-34
M_{tot} +10 %	+2.9	+2.8	+2.0	/	/	/	/	/
M_{tot} -10 %	-2.5	-2.4	-3.1	/	/	/	/	/
M^{R} +10 %	+7.0	+6.8	+6.8	+8.8	/	/	/	/
M^{R} -10 %	-7.0	-6.8	-7.1	-8.9	/	/	/	/
N_{tot} +10 %	/	/	/	/	/	/	/	/
N _{tot} -10 %	/	/	/	/	/	/	/	/
<i>k</i> ₁ +10 %	+2.9	+2.8	+2.4	/	/	/	/	/
<i>k</i> ₁ -10 %	-2.5	-2.4	-3.1	/	/	/	/	/
k_{mo} +10 %	+4.1	+4.0	+3.4	/	/	/	/	/
<i>k_{mo}</i> -10 %	-3.3	-3.2	-3.7	/	/	/	/	/
k_{mc} +10 %	/	/	/	/	/	/	+1.5	-8.0
<i>k_{mc}</i> -10 %	/	/	/	/	/	/	-2.3	+8.0
M_{Ct} +10 %	/	/	/	/	/	/	/	/
M_{Ct} -10 %	/	/	/	/	/	/	/	/
$M_{CA}:M_{CH}$ +10 %	/	/	/	/	/	/	/	/
$M_{CA}:M_{CH}$ -10 %	/	/	/	/	/	/	/	/
pH +5 %	-8.6	-8.4	/	/	/	/	/	/
pH -5 %	+7.0	+6.8	/	/	/	/	/	/

1117 ^{*a*} Definitions of fluxes see Table 3 and Section 2.5.3; ^{*b*} Value represents the percentage (%) of change (dF) in

1118 correspondent C flux with manipulated parameter value, as compared to the no-change condition. A positive

- 1119 value represents the percentage of increase in the simulated flux whereas a negative value represents the
- 1120 percentage of decrease; ^{*c*} the change in simulated C flux was smaller than 1 %.
- 1121
- 1122 Table 5. Plant-interspace differences in the sensitivities of C fluxes to changes in soil temperature (*Ts*), water
- 1123 content (θ) and root biomass (M^R).

Change of parameter	F_{S}^{a}	F_T	$Ra+R_S$	Ra	P_{Ct}	F_{Ct}	F_P
<i>Ts</i> +2 °C	$+0.38^{b}$	+0.45	+0.87	+0.49	+1.7	+2.7	+1.2
	(+4.0)	(+4.7)	(+12)	(+4.6)	(+34)	(+70)	(+78)
<i>Ts</i> -2 °C	-1.6	-1.3	-0.61	/ C	-2.8	-0.40	-3.1
	(+18)	(+14)	(+7.4)	/	(+222)	(+14)	(+615)
heta +10 %	-1.8	-1.5	/	-0.27	+8.7	+13	+2.9
	(-49)	(-27)	/	(-1.9)	(+21)	(+46)	(+20)
0 10 0/	+0.84	+0.58	/	+1.5	-3.5	-4.5	+0.9
<i>θ</i> -10 %	(-17)	(-10)	/	(-10)	(+22)	(+36)	(-11)
<i>M</i> ^{<i>R</i>} +10 %	-0.44	-0.41	-0.31	-0.52	1	1	
	(-6.3)	(-6.0)	(-4.7)	(-5.8)	/	/	
<i>M</i> ^{<i>R</i>} -10 %	+0.44	+0.41	+0.65	+5.2	1	/	
	(-6.3)	(-6.0)	(-9.2)	(-5.8)	/	/	

^{*a*} Definitions of fluxes see Table 3 and Section 2.5.3; ^{*b*} Values shows the plant-interspace difference in parameter sensitivities by value (outside bracket, $dF_p - dF_i$) and by percentage (inside bracket, $100 \times (|dF_p| |dF_i|) / |dF_i|$), where dF_p and dF_i are parameter sensitivities (dF, definitions see Table 4 and Section 2.5.3.) for plant-covered and interspace areas, respectively. A positive percentage (inside bracket) indicates a greater sensitivity (|dF|) of the flux at plant cover than interspace, whereas a negative value indicates a lower sensitivity. Definitions of fluxes and sensitivities see Table 3 and Section 2.5.3. ^{*c*} the difference in sensitivity are smaller than 0.1% by value.

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Figure 1. Site position (a), overlook of measured ecosystem (b), appearance of soil surface at collar
C1 (c), C2 (d) and C3 (e), and layout of representative land unit (RLU, adopted from Gong et al.,

1146 2016)

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Figure 2. Conceptual framework of process-based modelling. Solid arrows represent flows of massesand dash arrows represent flows of information.





1153 Figure 3. Measured and fitted bulk respiration (a) and photosynthesis (b) of the lichen topcrust as

1154 functions of temperature and water content.

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Figure 4. Measured and modelled soil temperature (a) and soil moisture content (b) at 10 cm depth for
F_s site, and as compared to the EC site in year 2013 by Gong et al. (2016).



1161 Figure 5. Measured and modelled hourly F_s for non-crusted soil (a), the temporal pattern of the bias of

simulated hourly F_s (b) and the comparison of measured and modelled daily F_s (c) during 2013-2014.





Figure 6. Measured and modelled F_s of lichen-crusted soils for opaque (a, c) and transparent chambers (b, d) at hourly (a, b) and daily (c, d) scales during 2013-2014.





- 1169 Figure 7. Diurnal patterns of biases (ζ) in the simulated hourly F_S for lichen-crusted soils using
- 1170 opaque (a) and transparent chambers (b), and the cumulative probability of the biases during wetting
- and drying periods (c) during 2013-2014. The wetting period included the raining days and a 1-day
- 1172 period after each rainfall. The drying period included the rest time of the years other than the wetting
- 1173 period.
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Figure 8. Simulated component CO_2 exchanges by biocrust and root-zone soil (a), the simulated CO_2 fluxes before and after example rain events of 2.3 mm (b), 7.6 mm (c) and 12.8 mm (d) sizes, and the comparison of F_T and R_R during wetting and drying periods during 2013-2014. The wetting period included the raining days and a 1-day period after each rainfall. The drying period included the rest time of the years other than the wetting period.



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1183 Figure 9. Comparison of the measured F_s from lichen-crusted surfaces using opaque and transparent

1184 chambers during a dry period (day 83-103) in spring 2013.