Microbial dormancy promotes microbial biomass and respiration across pulses of drying-wetting stress

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Abstract

Recent work suggests that metabolic activation and deactivation of microbes in soil strongly influences soil carbon (C) dynamics and climate feedbacks. However, few soil C models consider these transitions. We hypothesized that microbes' capacity to enter and exit dormancy in response to unfavorable and favorable environmental conditions decreases the sensitivity of microbial biomass and cumulative respiration to environmental stress. To test this hypothesis, we collected data from a rewetting experiment and used it to design and parameterize dormancy in an existing microbe-based soil C model. Then we compared predictions of microbial biomass and soil heterotrophic respiration (R_H) under simulated cycles of stressful (dryness) and favorable (wet pulses) conditions. Because the influence of moisture on microbial processes in soil generally depends on temperature, we collected data and tested predictions at

different temperatures. When dormancy was not taken into account, simulated microbial biomass and cumulative microbial respiration over five years were lower and decreased faster under lengthening drying-wetting cycles. Differences due to dormancy increased with temperature and with the length of the dry periods between wetting events. We conclude that ignoring both the capacity of microbes to enter and exit dormancy in response to the environment and the consequences of these metabolic responses for soil C cycling results in predictions of unrealistically low R_H under warming and drying-wetting cycles.

Keywords: microbial dormancy, microbial biomass, soil heterotrophic respiration, drying-wetting cycle, soil carbon model.

1. Introduction

Changes in global climate such as warming and altered precipitation patterns (Stocker et al. 2014) will trigger carbon (C) cycle feedbacks with the capacity to either accelerate or slow climate change. Global soil respiration (R_S), the second largest terrestrial carbon flux to the atmosphere (~70 Pg C y^{-1}; Raich and Schlesinger, 1992), has been increasing with temperature (~3.3 Pg C y^{-1} $°C^{-1}$) over the observational record of approximately 5 decades (Bond-Lamberty and Thomson, 2010; Hashimoto et al. 2015). R_S responses to warming are influenced by soil moisture. Although warming generally increases R_S (Bond-Lamberty and Thomson, 2010; Hashimoto et al. 2015), prolonged droughts can offset the effects of warming on R_S (Schindlbacher et al., 2012, Suseela et al., 2012). In many areas of the world, rainfall events are becoming less frequent and more extreme (Stocker, 2014). In order to predict future changes in R_S and their potential to accelerate climate change, we need to understand the mechanisms that control the responses of R_S to climate. Generally 50-70% of R_S is produced by microbial

decomposers (i.e. heterotrophic respiration, R_H), with the rest coming from plant roots and root-associated microbes (i.e. autotrophic respiration, R_A) (Bond-Lamberty et al., 2004). Therefore, understanding the ways in which microbes respond to changes in temperature and moisture is a critical step towards developing the modeling tools needed to predict soil C-climate feedbacks.

Earth system models (ESMs), which couple terrestrial C cycling (including soils) to other components of the global carbon cycle-climate system, are powerful tools for predicting global and regional changes in biogeochemistry and climate. However, much uncertainty remains as to the magnitude and even direction of carbon cycle feedbacks to climate. Predictions from the Coupled Model Intercomparison Project Phase 5 (CMIP5) suggest that by 2100, terrestrial ecosystems could act as either a global C sink or a source (Friedlingstein et al., 2014). None of these ESMs explicitly represented microbial processes in soil. Microbes play a major role in regulating the global C cycle (Schimel et al. 2007; Allison et al. 2010, Wieder et al. 2013), and the use of soil C models that explicitly represent microbial processes (i.e. 'microbial-explicit' models) is being increasingly explored as an approach that could reduce uncertainty in predictions of terrestrial C cycle-climate feedbacks (Todd-Brown et al., 2012; Treseder et al., 2012; Wieder et al., 2015). Microbial-explicit models generally include a single pool representing total microbial biomass, which is used to predict extracellular enzyme production or decomposition of soil organic matter. However, a large proportion of microbes in soil is generally metabolically inactive or dormant (Lennon and Jones, 2011). Under this state, microbes almost entirely reduce production of extracellular enzymes and all metabolic activities related to decomposition (Blagodatskaya and Kuzyakov, 2013). Generally, less than 10-20% of microbes in soil are metabolically active and capable of driving soil biogeochemical processes (Lennon and Jones, 2011).

Metabolic activation and deactivation of microbes in soil can affect R_H (Placella et al., 2012; Aanderud et al., 2015; Barnard et al., 2015). Activation of dormant cells has been used to explain pulses of R_H after wetting dry soils (a phenomenon known as the Birch effect; Birch, 1958) in a variety of ecosystems, including grasslands (Bottner, 1985; Alvarez et al., 1998; Placella et al., 2012; Aanderud et al., 2015; Barnard et al., 2015), forests (Aanderud et al., 2015; Salazar-Villegas et al., 2016), and agricultural fields (Aanderud et al., 2015). The pulses of R_H that follow wetting of dry soils can contribute a significant fraction of the annual net C emissions from ecosystems such as deciduous forests (Borken et al. 2003), Mediterranean ecosystems (Xu et al., 2004; Placella et al., 2012) and arid/semi-arid ecosystems (Huxman et al. 2004). These types of observations have motivated the incorporation of microbial dormancy into some soil C models (e.g., Blagodatsky & Richter, 1998; Wang et al., 2014; He et al., 2015). These models have modeled dormancy either by estimating the active fraction of the microbial biomass pool (e.g., Blagodatsky & Richter, 1998) or by explicitly simulating transfers between active and dormant biomass pools (e.g., Wang et al., 2014; He et al., 2015). In these models active microbial biomass fraction was assumed to depend on specific external factors such as bioavailable substrate concentration, and typically changed over a time scale of several hours to days. Although predictions of soil C pools and fluxes from these models are strongly dependent on the amounts of active and dormant microbial biomass, the sizes and dynamics of these pools in models have rarely been directly tested against observations of active and dormant microbial biomass. This is likely because the measurements needed to directly test model predictions of active and dormant fractions are scarce. Predictions from models that explicitly represent dormancy are generally tested against observations of total microbial biomass (e.g., Stolpovsky et al., 2011; Wang et al., 2014), R_H (He et al., 2015; Wang et al., 2015), or litter decomposition (Hunt, 1977). Because of the strong link between R_H and the amount of active microbial biomass in soil (Placella et al., 2012; Aanderud et al., 2015; Barnard et al., 2015), it seems reasonable to expect that models that are designed and calibrated to capture fluctuations of

102 active and dormant microbial biomass in soil would be able to predict R_H with higher fidelity than
103 models that do not.
104
105 In this study we used a model-data comparison to quantify the implications, in terms of R_H, of
106 including dormancy in a microbial-explicit soil C model. To do this, we measured R_H and active
107 and dormant microbial biomass before, during, and after several rewetting events. We used
108 these data to parameterize an explicit representation of microbial dormancy in an existing
109 microbial-explicit soil C model that has previously been applied at both ecosystem and global
110 scales (Sulman et al., 2014). To our knowledge, this is the first time that a microbial model that
111 explicitly represents dormancy has been calibrated with empirical data of active and dormant
112 microbial biomass in soil. In designing the dormancy model, we attempted to build on previous
113 model implementations in two ways. First, we represented dormancy and activation in a way
114 that integrated the features of the microbial growth environment, including chemical factors such
115 as substrate availability and quality along with physical factors such as soil moisture and
116 temperature. In order to reduce the number of assumptions specific to environmental factors we
117 designed the model to calculate activation and dormancy using potential microbial growth rate
118 rather than functions tied to individual environmental factors such as substrate concentration.
119 Second, to match the rapid changes in active microbial biomass fraction observed in
120 experiments, we designed the model to simulate these changes over time scales of less than
121 one hour, assuming that active and dormant fractions of microbial biomass adjusted quickly to
122 an equilibrium determined by environmental conditions. To test the generalizability of the
123 relationship between R_H and microbial biomass and activity across soil types, we compared
124 soils from different regions and ecosystems. Because temperature is important for microbial
125 activity in soil (Allison et al. 2010, Salazar-Villegas et al. 2016), we compared soils acclimated to
126 different temperatures. We compared predictions from the dormancy model with predictions
127 from a model using the previous structure in which decomposition is controlled by a single

active biomass pool. Because microbial dormancy is virtually ubiquitous in the microbial world (Sussman and Douthit, 1973), transitions between active and dormant state are inherently faster than microbial growth (Blagodatskaya and Kuzyakov, 2013), and active biomass has been shown to be a better predictor of R_H than total microbial biomass (TMB) (Alvarez et al., 1998; Placella et al., 2012; Barnard et al., 2015; Salazar-Villegas et al., 2016), we hypothesized that pulses of R_H immediately following rewetting of dry soils would be better explained by rapid activation of dormant microbes than by net growth (i.e. by fraction of active microbial biomass, FAMB, rather than by TMB), irrespective of soil type and acclimation temperature. Also, because dormancy is a strategy that allows microbes to rapidly respond to adverse environmental conditions (e.g. drought) and survive (i.e. no loss of microbial C biomass), we hypothesized that incorporation of dormancy into the soil C model would lead to reductions in the sensitivity of TMB and (microbially-regulated) R_H to environmental stress.

2. Methods

2.1. Sampling sites and soil collection

We tested our hypotheses using soils from both shrubland and forest, from each of two regions with different mean annual temperature (MAT) and precipitation (MAP): 1) the Coweeta Long Term Ecological Research (LTER) Network site, NC, 35°03'36.0"N 83°25'49.9"W, with MAT 13 °C and MAP 2000 mm; and 2) the Purdue Wildlife Area (shrubland soil), IN, 40°26'45.2"N 87°03'01.8"W, and the Ross Biological Reserve (forest soil), IN, 40°24'45.0"N 87°03'46.7"W, both with MAT 11.4 °C and MAP 953 mm. Soil classifications and properties are summarized in Table 1.

We sampled 3 soil cores (0-15 cm) from each site using a soil core sampler and slide hammer (AMS, Inc.). Soil cores were taken every 10 m along a linear transect. Samples were stored in double plastic bags, labeled, transported in coolers with ice packs, and stored in the laboratory at 4 °C for 1-4 weeks. Soil structure was partially disrupted during soil sampling and transportation. Soils were not sieved, but rocks and roots were manually removed before each analysis.

2.2. Experimental design

We measured R_H and pools of total and active microbial biomass in soils at different times (0, 2, 3, and 5 h) after a rewetting event (soils were brought from 10 to 60% water holding capacity, WHC).

With the aim of having primarily dormant microbial communities at the beginning of the experiment, we acclimated the soils to moisture-limited conditions (10 % WHC) in sealed glass jars for 2-3 days. To account for the influence of temperature on respiration and microbial activity, we compared soils acclimated to two temperatures: 19.5 ± 0.1 °C (hereafter unheated soils) and 28.4 ± 0.6 °C (hereafter heated soils). These acclimation temperatures are within the range of temperatures commonly experienced by soils in the sampling sites during the growing season (NOAA, 2017). We regulated the temperature of jars in the heated and unheated treatments by partially immersing them in a temperature-controlled water bath. We continuously monitored temperatures inside the microcosms with temperature probes (HOBO, Onset Computer Corporation). Half of the soil samples from each region were unheated and the other half were heated during this acclimation period.

178 After acclimation, we increased soil moisture to 60% of WHC (optimum for microbial processes)
179 by homogeneously adding sterile, deionized water to the soils with a sterile syringe through a
180 septum. We estimated WHC and gravimetric moisture content of all soils (each core
181 individually) before acclimation, and monitored changes in soil moisture after rewetting by
182 weight. We estimated WHC as the water retained in soils after being saturated and then free-
183 drained for 24 h (similar to Clemente et al., 2008).
184
185 After rewetting the soils, we monitored R_H, total microbial biomass, and its active and dormant
186 fractions. Because the method that we used to measure microbial biomass is destructive (see
187 section 2.4), we used different sample units for R_H and for microbial biomass (total, active, and
188 dormant). For example, we acclimated unheated grassland soil from Indiana as described
189 above. After rewetting, we used three sample units to measure R_H (section 2.3) and 12 sample
190 units (3 per each time point) to measure total and active microbial biomass (section 2.4).
191
192 *2.3. Soil respiration measurements*
193
194 To measure R_H in microcosms at different times after water and substrate additions, we used an
195 Infrared Gas analyzer (EGM-4, PP systems) connected to a set of valves, each valve being
196 connected to a sample unit (Fig. S1). Each sample unit was a 0.8 L glass jar with 25 g of soil
197 (dry weight), connected to a vessel with 12 g of soda lime. The soda lime allowed the
198 replacement of the gas sampled from the jars (0.1 L min^{-1}, 2 min every 1 h) with CO_2-free air.
199 Valves were opened and closed by an AC/DC controller (SDM16AC, Campbell Sci.) that was
200 connected to a datalogger (CR1000, Campbell Sci.). The datalogger was also connected to the
201 IRGA and stored CO_2 concentration measurements every second. We collected the data from
202 the datalogger at the end of each run, one run being the time from a few hours before the
203 rewetting event to the end of the substrate-induced respiration period (see next section). We

monitored 16 units, i.e. 15 samples and one empty jar (control), in each run. Each valve was programmed (software package LoggerNet 3.4.1) to be open for 2 min. The valve connected to an empty jar was opened between samples, so that in one hour each of the 15 units was sampled once (2 min each), and the empty jar was sampled 15 times (2 min each).

We calculated R_H based on the hourly (t=1 h) differences in CO_2 concentration in each jar (C_i-C_{i-1}), the volume of the microcosm headspace (V=0.8 L), and the dry mass of the soil (W=25 g).

$$\frac{\qquad\qquad}{\qquad\qquad} \quad (1)$$

We measured C_i in ppm and transformed it to g C L^{-1} using the ideal gas equation (as in Gul et al., 2012). We calculated R_H in g C m^{-2} h^{-1} by taking into account the bulk density of the soils from each site (Table 1) and specifying a depth of 15 cm.

2.4. Estimation of microbial parameters

We estimated TMB and its active and dormant fractions using the kinetic approach proposed by Panikov and Sizova (1996). Briefly, we stimulated substrate-induced respiration rates by homogeneously spreading a solution (1 mL per jar) containing 10 mg glucose, 1.90 mg $(NH_4)SO_4$, 2.25 mg K_2HPO_4, and 3.62 mg $MgSO_4$ per gram of soil (as in Salazar et al., 2016). We represented substrate-induced respiration rates as a function of initial respiration rates coupled (R_C) and uncoupled (R_U) with microbial growth, microbial specific growth rate (μ_m), and time (t).

(2)

We estimated R_U, R_C, and μ_m by fitting (gnls function in R 3.2.3) this model to our observations of R_H (t) (as in Wutzler et al., 2012). To meet assumptions of the method, we did not consider data points outside the exponential phase of R_H. We used R^2 as an indicator of goodness-of-fit (to the linearized log(R_H); Table S1). In the few cases (see Table S1) where the observed R_H did not follow an exponential growth pattern, the samples were excluded from subsequent calculations. After calculating R_U, R_C, and μ_m, we estimated TMB as:

(3)

Where λ represents the ratio between productive (i.e. coupled with ATP synthesis and growth) and total respiration, and was assumed to be a stoichiometric constant equal to 0.9, due its narrow range of variation across microbial species (Akimenko et al., 1983). Y_{CO2} is biomass yield per unit of CO_2 and was assumed to be constant and equal to 1.5 (Payne, 1970). FAMB is the fraction of active microbial biomass and is estimated based on the ratio between R_C and total respiration (as in Wutzler et al., 2012):

(4)

We estimated AMB as:

(5)

247 Estimations of R_U, R_C, and μ_m, and calculations of TMB, AMB, and FAMB are summarized in
248 Table S1. We emphasize that, even though the statistical model is fitted to observations of R_H
249 after substrate addition, the microbial parameters (TMB and FAMB) estimated with this
250 approach reflect the time point immediately before the substrate input. More details about this
251 and other methods to estimate total and active microbial biomass can be found in the work from
252 Blagodatskaya and Kuzyakov (2013).
253
254 *2.5. Statistical analysis: rewetting experiment*
255
256 To estimate the influence of acclimation temperature, region, and ecosystem, as well as TMB
257 and FAMB on R_H, we conducted a linear model analysis and selected the best explanatory
258 statistical model based on the Bayesian Information Criterion (BIC), which accounts for
259 differences in the number of explanatory factors during model comparison. For model selection,
260 we used the *glmulti* package (Calcagno and de Mazancourt, 2010) in the statistical package R
261 3.2.3. We had three replicates per treatment.
262
263 *2.6. Process-based model structure and design*
264
265 We conducted process-based model simulations using a modified version of the Carbon
266 Organisms, Rhizosphere, and Protection in the Soil Environment (CORPSE) model (Sulman et
267 al., 2014). The original version of the model used a single microbial biomass pool to predict
268 decomposition rates:
269

(6)

270

271 Where B_M is microbial biomass, C_i is substrate C, which is divided into three chemically-defined
272 types (labile, chemically resistant, and microbial necromass) denoted with the *i* subscript, T is
273 temperature, $Vmax_i$ is temperature-dependent maximum decomposition rate for each substrate
274 type, and is soil moisture expressed as fraction of saturation.
275
276 We modified the model by splitting total microbial biomass into active and dormant fractions.
277 Only the active fraction was used to predict organic matter decomposition:
278

(7)

279
280 Active and dormant fractions had different biomass turnover and maintenance respiration rates
281 (see Table S2 for a full list of parameters). FAMB was calculated every hour based on the
282 assumption that microbes become more active under conditions that supported greater biomass
283 accumulation relative to biomass loss. Potential biomass accumulation rate was calculated
284 using the same functional form as the CORPSE decomposition function, which is sensitive to
285 temperature, moisture, and available substrate C as described above, but assuming microbial
286 biomass was equal to total substrate carbon in order to calculate an upper limit:
287

(8)

288
289 where G_B is potential microbial biomass growth rate and CUE_i is the microbial C use efficiency
290 for each C type. G_B was compared to a factor representing the potential loss rate of microbial
291 biomass but using total substrate carbon as a potential upper limit to microbial biomass, as in
292 Equation 8:

293

(9)

294

295 Where L_B is the AMB loss rate factor and T_{mic} is the turnover time of AMB. Note that L_B is
296 proportional to total substrate C rather than AMB or TMB. While actual microbial biomass loss is
297 proportional to AMB, the potential biomass growth and loss calculations use total substrate C so
298 that the result is driven by the properties of the microbial environment rather than changing
299 rapidly with fluctuations in microbial biomass. TMB as a function of total soil organic C is
300 generally well constrained (Xu et al., 2012), so we can reasonably assume that potential TMB is
301 proportional to soil organic C while eliminating unrealistic feedbacks caused by using actual
302 TMB to calculate these factors. While actual microbial biomass is much smaller than total
303 substrate C, limiting this equation to a smaller fraction of total substrate C did not change the
304 model results, since the factor was accounted for in other parameters. FAMB was calculated
305 using a saturating function of the ratio between G_B and L_B:

306

(10)

307

308 Where $FAMB_{max}$ is maximum active fraction and k_{act} is the half-saturation parameter for
309 activation. In contrast to previous approaches using dynamic fluxes between active and dormant
310 microbial biomass pools, this approach allows the model to respond very rapidly to changes in
311 environmental conditions, which is consistent with observations showing that microbial biomass
312 can change from dormant to active over time scales of an hour or less (Blagodatskaya
313 Kuzyakov, 2013). Biologically, this equation represents the equilibrium state of a microbial

community balancing the benefit of biomass growth against the cost of biomass loss. Because a diverse community contains some taxa that activate rapidly and others that activate more conservatively, the rate of FAMB increase declines as conditions become more optimal for growth, reflecting the shift of the still-dormant portion of the community toward more conservative taxa. $FAMB_{max}$ reflects observed values of FAMB, which are less than 100% even under optimal soil conditions. Because it is calculated using the same decomposition and biomass turnover equations that control microbial biomass, model FAMB integrates chemical, biological, and physical factors affecting decomposition and microbial growth rates (such as temperature and moisture effects on decomposition as well as substrate availability and microbial carbon use efficiency) as well as changes affecting microbial physiology (such as temperature effects on active biomass turnover) without requiring additional assumptions about direct connections between factors like substrate concentration and microbial activation.

In addition to the representation of dormancy and activation, the model was also modified to introduce a Q_{10} temperature dependence in T_{mic} and a linear temperature dependence in $FAMB_{max}$ and k_{act}.

2.7. Model initialization

We ran the model in the active/dormant configuration described above (hereafter referred to as the dormancy model), and in a one-pool configuration with k_{act} set to zero and $FAMB_{max}$ set to 1.0 so that FAMB was fixed at 100% (hereafter the no-dormancy model). In this case, all microbial biomass was considered active and the model was equivalent to the previous one-pool version. Both model versions were spun up to equilibrium under conditions designed to approximate field conditions. In spinup simulations, temperature was a sinusoid function with a

period of one year, a maximum of 25ºC, and a minimum of -10ºC, based on the normal annual pattern observed at the Indiana field site. Soil moisture was kept constant at 50% of saturation. Inputs were added at a constant rate of 60 mg C m^{-2} h^{-1}. Parameters were adjusted so that both model versions simulated steady state annual average substrate C and microbial biomass, and so that annual average total soil C and TMB were approximately the same for both the dormancy and no-dormancy models (Fig. S2). This allowed us to attribute differences between models in respiration rates over time to dormancy processes rather than differences in microbial biomass at steady state.

2.8. Model calibration

We calibrated the dormancy and no-dormancy models so predictions of R_H and TMB in both models matched observations. Because only the dormancy model explicitly represented transitions of C between active and dormant biomass pools, only this model could be calibrated based on observations of active biomass (section 3.2). We selected parameter values (Table S2) based on our observations. For example, because microbial biomass and respiration changed with temperature (see Results), some parameters (e.g. the Michaelis-Menten parameter for microbial active fraction, k_{act}) have different values for heated and unheated soils (Table S2). For the parameters that did not change after incorporation of dormancy, we used values from the original version of the CORPSE model (Sulman et al., 2014).

In the dormancy model, dormant and active pools differed in their microbial turnover rate (T_{mic}), Michaelis-Menten parameter (k_C, which controls the relationship between microbial biomass and decomposition rate), and the fraction of biomass turnover not converted to CO_2 via maintenance respiration (e_t) (see Table S2 for a listing of all parameter values). For example, instead of using

364 one single T_{mic} for all microbes in soil, as in the no-dormancy model, cells in the dormant state
365 had a lifetime approximately 25 times longer than those in the active state, which is consistent
366 with observations and theory (Lennon and Jones, 2011).
367
368 *2.9. Model sensitivity to drying and wetting cycles*
369
370 Here we define *sensitivity* as the percent change (e.g., in cumulative R_H) after 5 years of
371 simulated drying-wetting events. In each wetting event, soils were wetted (i.e. moisture
372 increased immediately from suboptimal, 10% WHC, to optimal, 60% WHC, for microbial
373 processes) and then they dried out exponentially (back to 10% WHC). To simulate different
374 levels of drying-wetting stress we changed the length of the dry periods (LDP) between wetting
375 events from 0 (i.e. no stress) to 100 (i.e. high stress) days. Because temperature influenced
376 microbial biomass and respiration (see Results), we ran simulations at heated and unheated
377 conditions.
378

379 **3. Results**

380
381 *3.1. Observed pulses in R_H after rewetting*
382
383 R_H rapidly increased in all soils after rewetting (Fig. S3). R_H was greater in heated than in
384 unheated soils and increased with the fraction of active biomass (Fig. 1 and Table 2). R_H was
385 not different among soils from different regions or ecosystems (Table 2). Although the combined
386 effect of region, ecosystem, acclimation temperature, TMB, and FAMB accounted for much of
387 the treatment effects ($P<0.05$, BIC=-98), differences in R_H were better explained ($P<0.05$, BIC=-
388 106; best statistical model) by acclimation temperature and FAMB alone.

389

390 *3.2. Model simulations: repeated rewetting events*

391

392 The calibrated model matched observations of TMB, FAMB, and R_H for both heated and
393 unheated treatments (Fig. 2).

394

395 Incorporation of dormancy in the soil C model changed predictions of TMB and R_H in response
396 to drying-wetting cycles (Fig. 3). Differences in predictions between the dormancy and no-
397 dormancy models were larger for heated (Fig. 3) than unheated (Fig. S4) soils. Both dormancy
398 and non-dormancy models predicted pulses of microbial growth when dry soils were wetted,
399 and decreases of biomass during the dry periods (Fig. 3b), but the magnitude of net changes in
400 TMB after repeated drying-wetting events were markedly different. After 1 year of simulated
401 drying-wetting cycles, with 100 dry days between wetting events, the dormancy model predicted
402 a 17% decrease in TMB of heated soils whereas the no-dormancy model predicted a drastic
403 88% decrease (Fig. 3b). This resulted in different predictions of R_H (Fig. 3a). The size of the
404 wetting-induced pulse in R_H predicted by the dormancy model during the fourth wetting event
405 was approximately double that of the no-dormancy model. Overall, microbial biomass and R_H
406 were more severely affected by drying stress when dormancy was not taken into account.

407

408 *3.4. Model simulations: R_H under different levels of drying stress*

409

410 Predictions of cumulative R_H from the dormancy model were larger than those from the no-
411 dormancy model in all the drying-wetting scenarios (Fig. 4). Both the dormancy and the no-
412 dormancy models predicted decreases in cumulative R_H as LDP increased, but decreases in R_H

were greater when dormancy was not taken into account (Fig. 4). Differences in predictions between models increased with the level of stress, and were magnified by warming (Fig. 4). The largest difference in predicted R_H was in heated soils with dry periods of 100 days between wetting events. Under these conditions, incorporation of dormancy resulted in predictions of cumulative R_H 43% larger than with the no-dormancy model.

4. Discussion

Our results add to the increasing body of evidence showing that a large proportion of microbes in soil are in a dormant state (Lennon and Jones, 2011), that they can quickly enter and exit dormancy in response to changes in their environment (Stenström et al., 2001; Blagodatskaya and Kuzyakov, 2013), and that these metabolic transitions have implications for soil C dynamics (Bottner, 1985; Alvarez et al., 1998, Placella et al., 2012; Aanderud et al., 2015; Barnard et al., 2015; Salazar-Villegas et al., 2016).

Results from our rewetting experiment support previous observations that dormant microbes in dry soils rapidly (few hours) become metabolically active in response to water inputs (Placella et al., 2012; Aanderud et al., 2015; Barnard et al., 2015), that warming can magnify this effect (Salazar-Villegas et al., 2016), and that this activation helps to explain pulses of R_H (Placella et al., 2012; Aanderud et al., 2015; Barnard et al., 2015; Salazar-Villegas et al., 2016). The metabolic responses of microbial communities to rewetting and warming were consistent across the soils analyzed in this study. This could be in part because, despite differences in climate between the Indiana and North Carolina sites (section 2.1), all soils in this study had similar physicochemical properties (Table 1) and were from mesic temperate ecosystems, so microbial communities may have been adapted to similar levels of drying-wetting stress and to similar

temperature ranges. Although this relationship remains untested in many ecosystems, the consistent response across soils from different regions and ecosystems in our experiment suggests that it may be possible to generalize relationships between R_H and FAMB in models across soil types.

Although both the dormancy and the no-dormancy models were calibrated to match observations of R_H and microbial biomass, the differences in the parameters used for calibration suggest two different mechanistic explanations for the influence of soil microbes on R_H (Table S2). All microbes in the no-dormancy model had the same lifespan and respired the same amount of CO_2 per unit of assimilated C. In the dormancy model, active microbes could increase (by two orders of magnitude) their lifespan by entering dormancy when external factors such as moisture became unfavorable. Also, the Michaelis-Menten parameter (K_C), which controls the relationship between microbial biomass and decomposition rate, was different by a factor of 100 between the models, reflecting the large difference between active and total microbial biomass. Finally, in the dormancy model active cells had a lower fraction of turnover not converted to CO_2 (e_t) than dormant cells. This reflects the fact that active cells can grow and build up new biomass, and therefore do not convert all substrate into CO_2. In contrast, when cells are dormant they do not accumulate C in biomass, and a larger fraction of their C ends up being respired (although at a much lower rate than when they are active; Anderson and Domsch, 1985). Taken together, these large parameter differences imply that calibrating microbial-explicit soil C models using observations of TMB could lead to unrealistic parameter values and results if in reality only a small fraction of TMB is actively involved in soil C decomposition and R_H.

When we changed the structure of the CORPSE model and calibrated it (based on experimental data from our rewetting experiment) to simulate microbes entering and exiting dormancy, TMB

463 was significantly more resistant and resilient to simulated drying stress. A similar result was
464 reported by Wang et al. (2015) when comparing predictions from the microbial enzyme-
465 mediated decomposition model with (MEND) and without (MEND_wod) dormancy. In that study,
466 the authors did not compare predictions under a drying-wetting scenario, but at different times
467 after pulses of labile C. Similar to our results, TMB was less responsive to changes in external
468 conditions when dormancy was taken into account. MEND_wod predicted increases in TMB a
469 few (4) days after the substrate input, followed by sharp decreases in TMB after 150-270 days.
470 This no-dormancy model (MEND_wod) overestimated increases in TMB immediately after
471 substrate inputs and overestimated decreases in TMB a few days after that. In contrast, their
472 dormancy model (MEND) did a better job at reproducing observations of TMB. In our study, the
473 no-dormancy model also suggests sharper decreases in TMB than the dormancy model under
474 unfavorable external conditions. Taken together, these findings suggest that models that do not
475 take dormancy into account do not realistically simulate TMB responses to environmental stress
476 and substrate availability.
477
478 The amount of soil C respired to the atmosphere under stressful conditions depends on the
479 sensitivity of microbes to the environment. In a previous modeling experiment (Tang and Riley,
480 2015), making the metabolism of soil microbes more 'plastic' to the environment (conceptually
481 homologous to considering their capacity to switch between active and dormant state), made
482 soil respiration less responsive to warming. This resulted in predictions of weaker soil C-climate
483 feedbacks (Tang and Riley, 2015). In our study, incorporation of dormancy also decreased the
484 sensitivity of soil respiration to changes in the environment. In particular, dormancy made R_H
485 less sensitive to drying-wetting stress. Together, the findings from these studies suggest that
486 the magnitude of soil C-climate feedbacks depends on the metabolic responses of soil microbes
487 to the environment. Under warming and long drying-wetting cycles, our dormancy model

predicts nearly double the soil C emissions predicted by the model that does not take dormancy into account.

Although our results suggest that dormancy is key to understanding soil C responses to warming and drying-wetting cycles, the question of timing remains open: when is dormancy important for soil C cycling and when is not? Given that dormancy is a strategy to cope with stress, it seems reasonable to expect dormancy to be important for soil C cycling under stressful conditions other that drying-wetting cycles (e.g. low C availability; Wang et al. 2015). Also, given the responsiveness of microbial metabolism to the environment, it seems reasonable to expect dormancy to be more important for soil C cycling under fluctuating environmental conditions than in fairly stable environments. Finally, given the speed at which changes between active and dormant state happen (i.e. hours-to-days; Blagodatskaya and Kuzyakov, 2013), it seems reasonable to expect dormancy to be especially important for soil C cycling when environmental and nutritional conditions change quickly (e.g. the birch effect; Evans et al. 2016). The time scale of transitions between active and dormant states varies among existing models, with some previous models having time scales on the order of ten hours (e.g. Wang et al., 2014) in contrast to our model, which assumed that the microbial community adjusted to an optimum FAMB within a single hourly time step. Testing these hypotheses, especially under field conditions and at long (months-to-years) temporal scales (since most work on microbial activity in soil has been done in laboratory conditions and at short temporal scales; e.g. Alvarez et al., 1998; Barnard et al., 2015, and Salazar-Villegas, et al., 2016) will further build confidence in our ability to realistically represent dormancy in models.

Overall, our results suggest that as Earth's surface keeps getting warmer, and in many places the mean LDP between wetting events keeps getting longer (Stocker, 2014), microbial dormancy will become increasingly relevant for soil C-climate feedbacks. Specifically, our

514 results suggest that under warming and long LDP between wetting events, microbes in soil will
515 respire more than would be predicted by models that do not take dormancy into account.
516

517 **5. Conclusions**

518

519 The capacity of microbes to enter and exit dormancy under alternating stressful and favorable
520 environmental conditions has important implications for soil C cycling. Microbial biomass and
521 respiration are less sensitive to drying-wetting stress when dormancy is taken into account.
522 Differences in predictions with and without dormancy increase with warming and with LDP.
523 Overall, our results suggest that models that do not consider microbial dormancy could
524 underestimate (by as much as ca. 40%) R_H responses to warming and drying-wetting cycles.
525

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527

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538

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712 **Figure legends**

713

714 **Figure 1.** Relationship between R_H and FAMB in heated (red) and unheated (blue) soils.
715 Symbols represent the region (circles and triangles are North Carolina and Indiana,
716 respectively) and ecosystems (open and closed symbols are forest and shrubland, respectively)
717 where soils were sampled. Each point represents mean values for R_H (n = 12) and FAMB (n =
718 3) from a given soil sample based on measurements of subsamples. Equation of regression
719 line: $R_H = 0.39 + 0.05(\text{logitFAMB})$.

720

721 **Figure 2.** Observed and predicted a) R_H, b) TMB, c) AMB, and d) FAMB. Predictions are from
722 the dormancy and no-dormancy models. Notice that predictions of AMB and FAMB are only
723 from the dormancy model.

724

725 **Figure 3.** Simulated changes in a) R_H, b) total microbial biomass, and c) the fraction of active
726 microbial biomass, after repeated rewetting events. Initial conditions in these simulations were
727 parameterized based on observations of *heated* soils. We ran simulations for 5 years but show
728 results for 1 year here to make the differences between predictions (e.g. dashed line in panel a)
729 easier to see. Predictions based on observations of *unheated* soils are in Fig. S4.

730

731 **Figure 4.** Model predictions of cumulative R_H after five years, with and without considering
732 microbial dormancy.

733

734

735

736

737

738 **Table captions**

739

740 **Table 1.** Soil classification and physicochemical properties (USDA, 2017).

741

742 **Table 2.** Significance of temperature, region, ecosystem, TMB and logitFAMB for explaining R_H.
743 Overall, this model explains approximately 50% (R^2=0.50, P<0.05) of the variation in R_H. FAMB
744 was transformed to meet homogeneity of variances assumption.

745

Table 1. Soil classification and physicochemical properties (USDA, 2017).

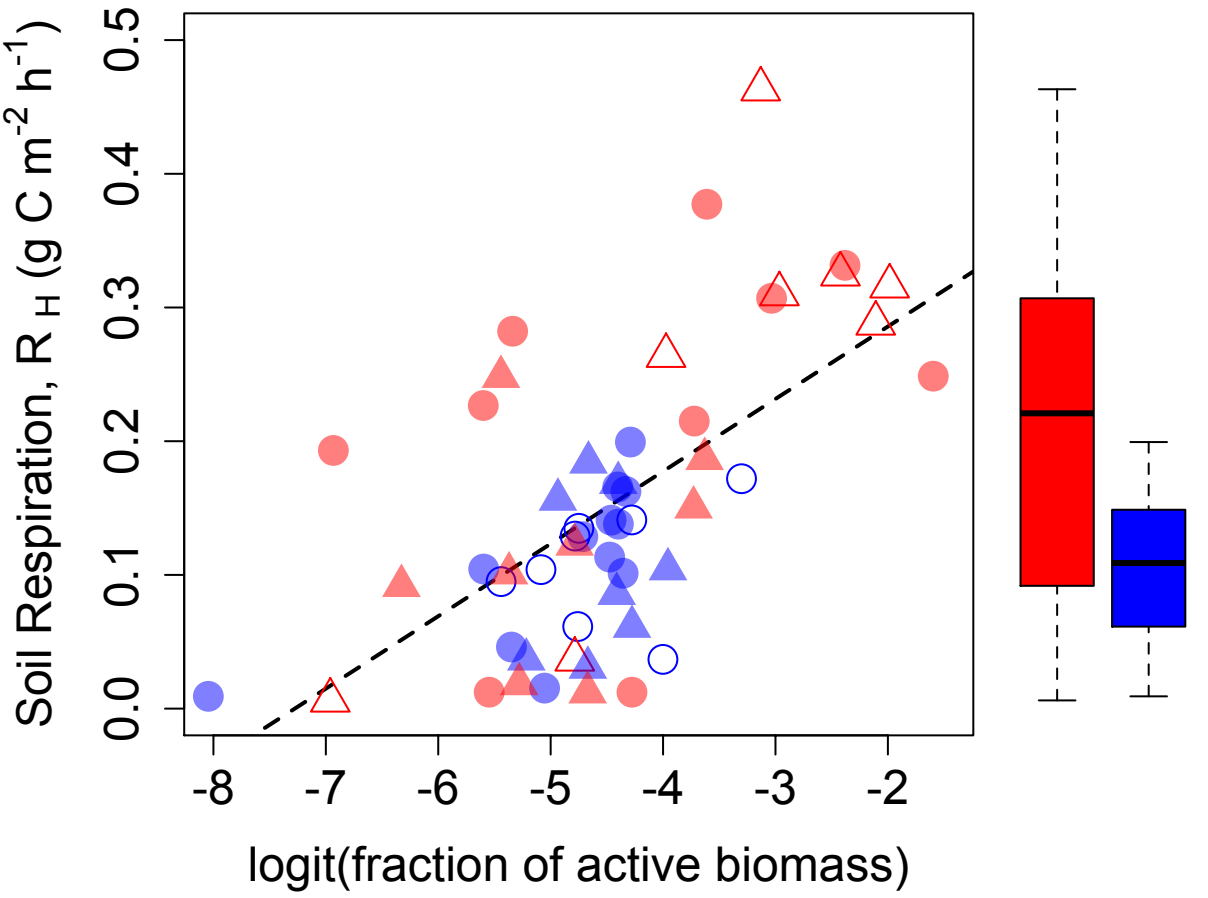
Region	Ecosystem	Soil classification	Abbreviation	Slope (%)	pH (0-15 cm)	Bulk density (g cm^{-3})	SOM (%)[a]
NC	Shrubland	Reddies fine sandy loam	ReA	0 to 3	6.4	1.40	6
	Forest	Fannin fine sandy loam	FaD	15 to 30	5.5	1.40	3
IN	Shrubland	Rainsville silt loam	RaB2	2 to 6	6.5	1.45	2
	Forest	Richardville silt loam	RdB2	2 to 6	6.2	1.45	1.5

[a]Soil organic matter (SOM) is expressed as the percentage, by weight, of the soil material with diameter < 2 mm.

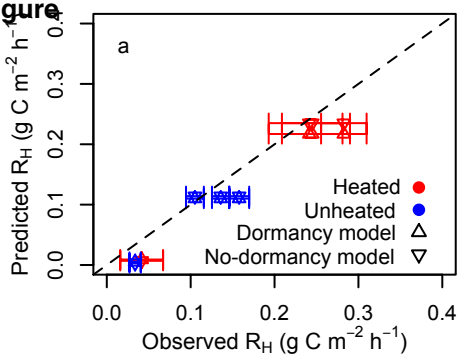
Table 2. Significance of temperature, region, ecosystem, TMB and logitFAMB for explaining R_H. Overall, this model explains approximately 50% (R^2=0.50, P<0.05) of the variation in R_H. FAMB was transformed to meet homogeneity of variances assumption.

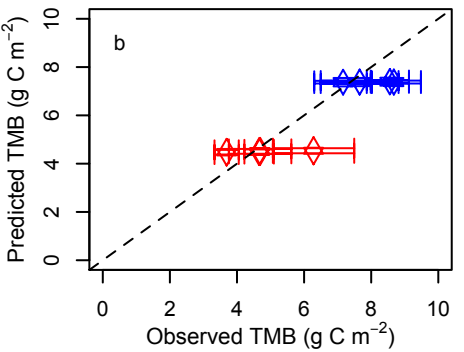
Factor	Estimate	Std. error	t value	P value
Intercept	0.348	0.055	6.353	< 0.05
Temperature	-0.090	0.026	-3.473	< 0.05
Region	0.030	0.232	1.253	0.216
Ecosystem	0.004	0.027	0.153	0.879
logit(FAMB)	0.0467	0.010	4.915	< 0.05
TMB	0.006	0.004	1.452	0.153

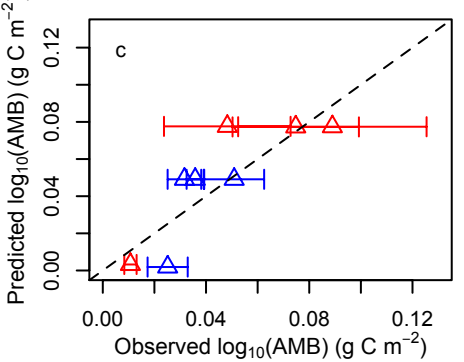
Figure

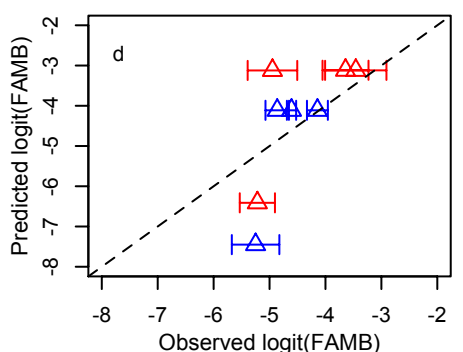

Soil Respiration, R_H (g C m^{-2} h^{-1})
0.0
0.1
0.2
0.3
0.4
0.5
-8
-7
-6
-5
-4
-3
-2
logit(fraction of active biomass)

Figure

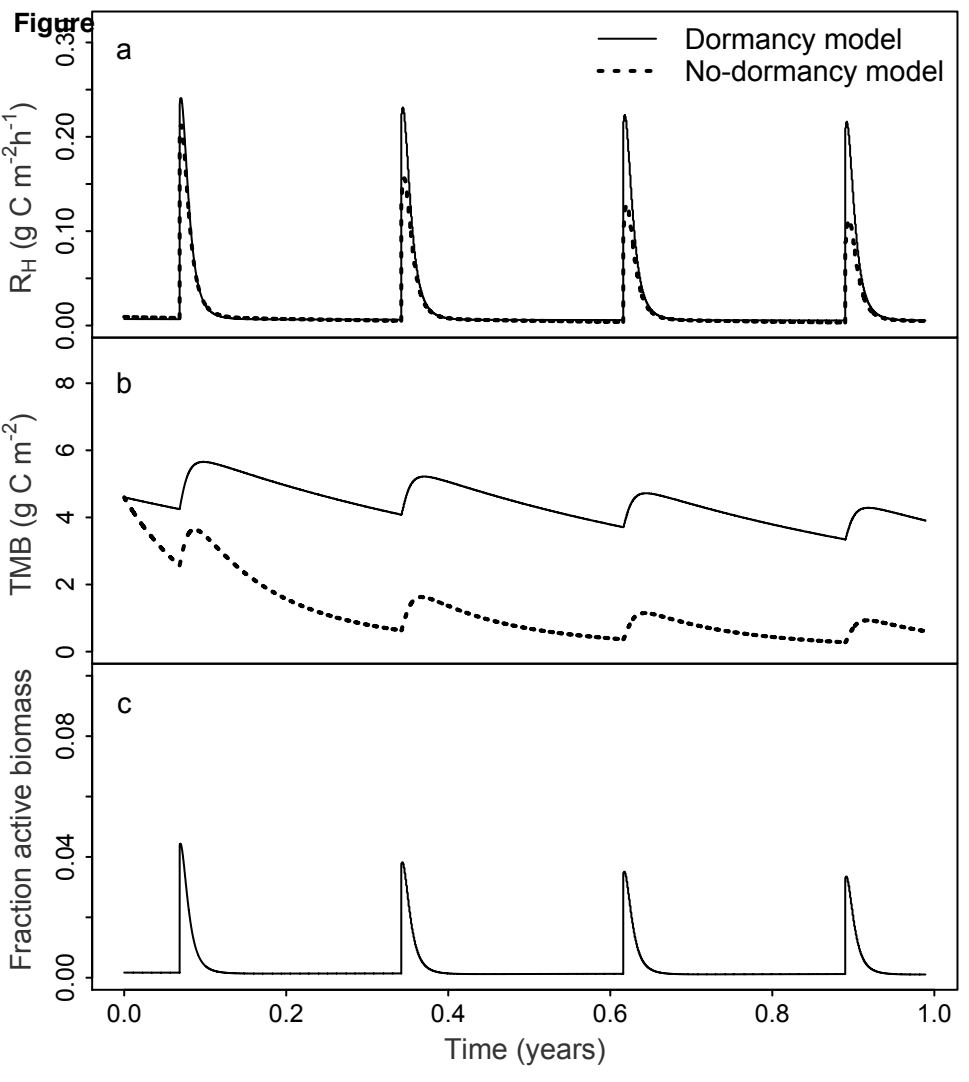

a
Predicted R_H (g C m^{-2} h^{-1})
Observed R_H (g C m^{-2} h^{-1})
Heated
Unheated
Dormancy model
No-dormancy model
0.0
0.1
0.2
0.3
0.4


b
Predicted TMB (g C m^{-2})
Observed TMB (g C m^{-2})
0
2
4
6
8
10

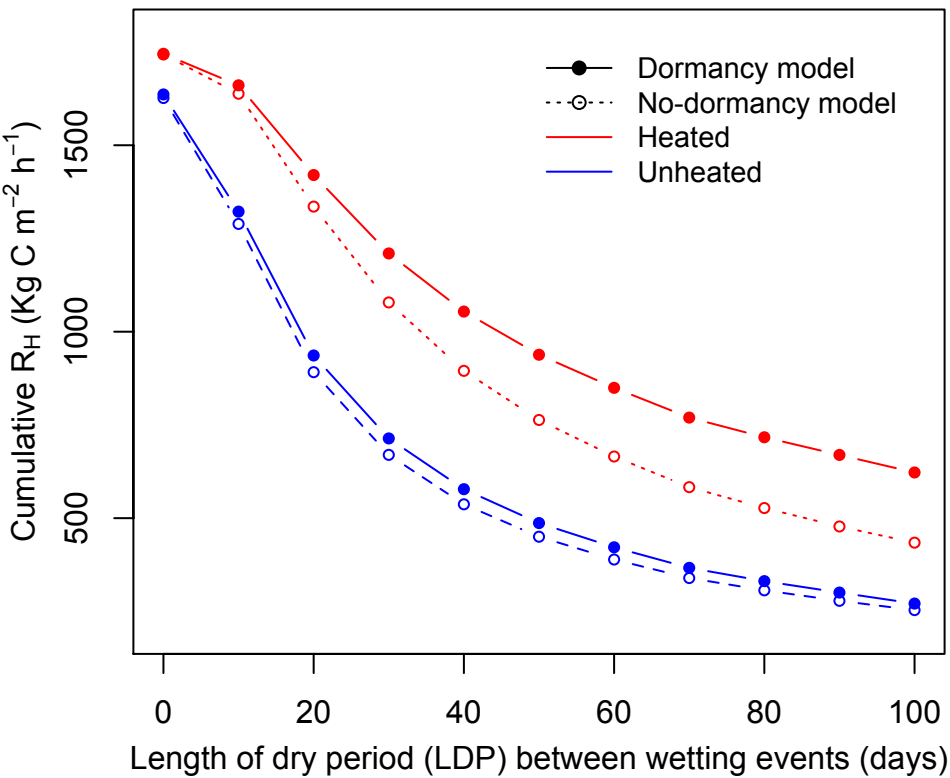

c
Predicted $\log_{10}$(AMB) (g C m^{-2})
Observed $\log_{10}$(AMB) (g C m^{-2})
0.00
0.04
0.08
0.12

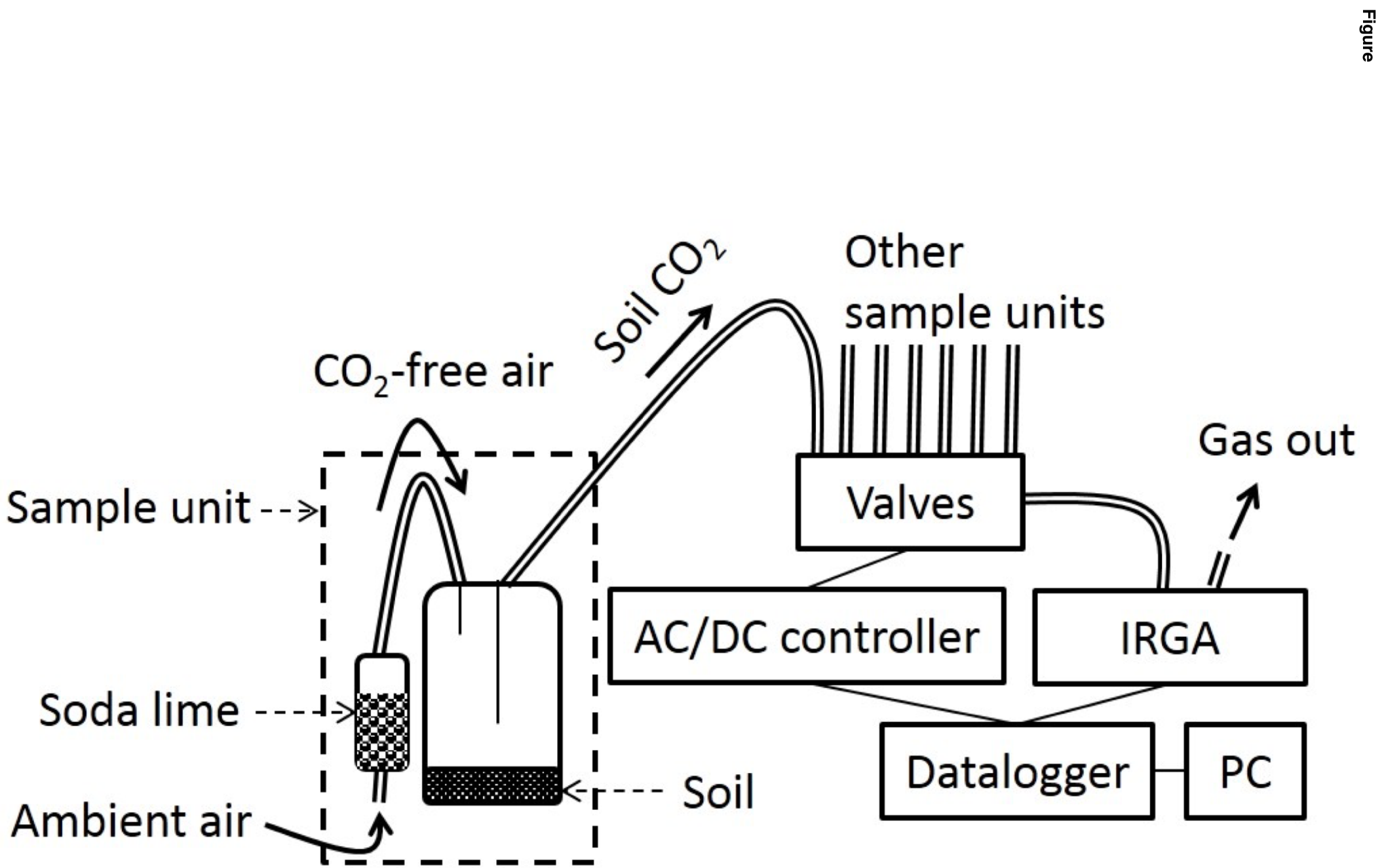

d
Predicted logit(FAMB)
Observed logit(FAMB)
-2
-3
-4
-5
-6
-7
-8

Figure


a
b
c
Dormancy model
No-dormancy model
R_H (g C $m^{-2}h^{-1}$)
TMB (g C m^{-2})
Fraction active biomass
0.00
0.10
0.20
0.30
0
2
4
6
8
0.00
0.04
0.08
0.0
0.2
0.4
0.6
0.8
1.0
Time (years)

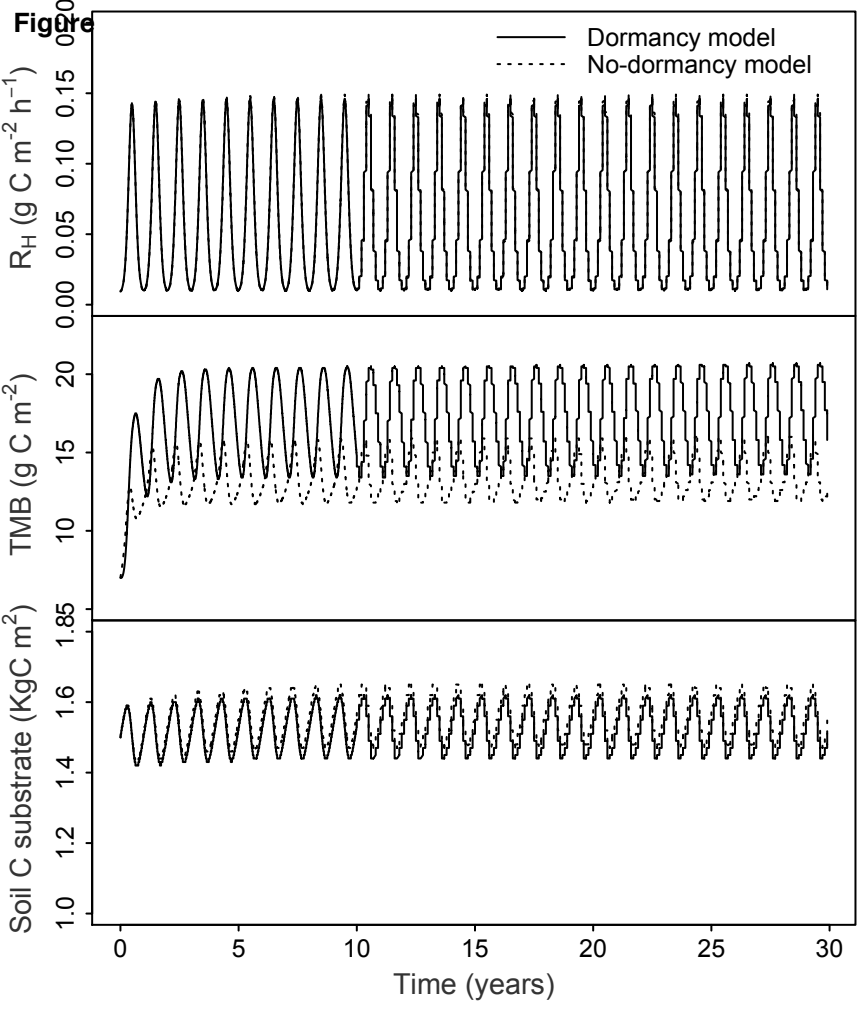
Figure


Dormancy model
No-dormancy model
Heated
Unheated
Cumulative R_H (Kg C m^{-2} h^{-1})
500
1000
1500
0
20
40
60
80
100
Length of dry period (LDP) between wetting events (days)

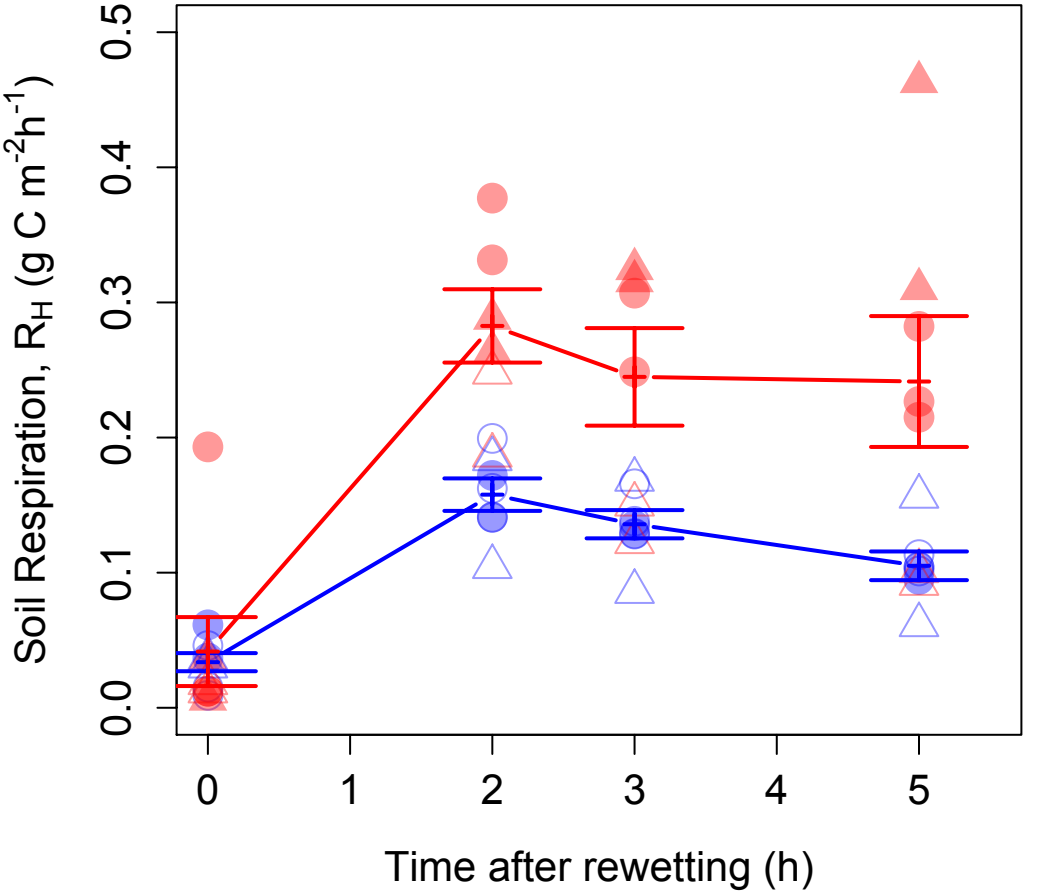

Soil CO_2
Other
sample units
CO_2-free air
Gas out
Sample unit
Valves
AC/DC controller
IRGA
Soda lime
Datalogger
PC
Soil
Ambient air

Figure

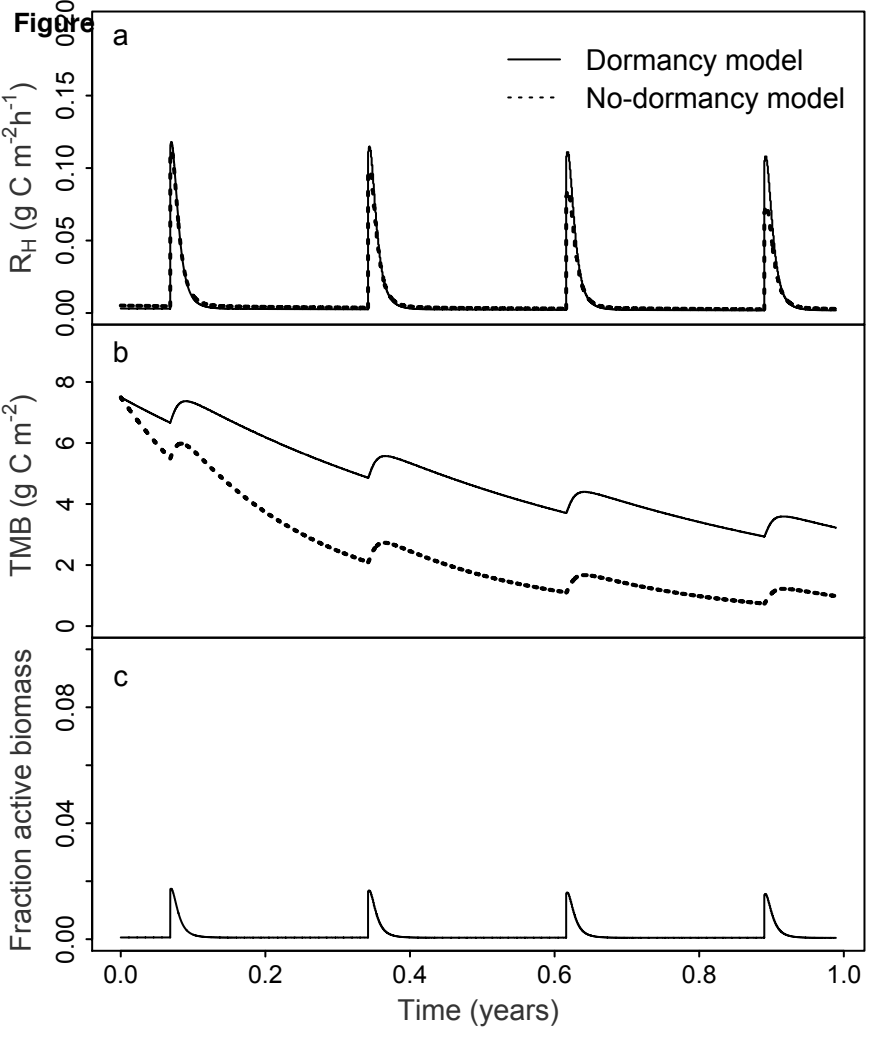
Figure


Dormancy model
No-dormancy model
R_H (g C m^{-2} h^{-1})
0.00
0.05
0.10
0.15
0.20
TMB (g C m^{-2})
10
15
20
Soil C substrate (KgC m^2)
1.0
1.2
1.4
1.6
1.85
0
5
10
15
20
25
30
Time (years)

Figure


Soil Respiration, R_H (g C $m^{-2}h^{-1}$)
0.0
0.1
0.2
0.3
0.4
0.5
0
1
2
3
4
5
Time after rewetting (h)

Figure


a
b
c
Dormancy model
No-dormancy model
R_H (g C $m^{-2}h^{-1}$)
TMB (g C m^{-2})
Fraction active biomass
Time (years)
0.00
0.05
0.10
0.15
0.20
0
2
4
6
8
0.04
0.08
0.0
0.2
0.4
0.6
0.8
1.0

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