# Synergistic effects of diffusion and microbial physiology reproduce the Birch effect in a micro-scale model

Sarah Evans [a, b, c, *], Ulf Dieckmann [a], Oskar Franklin [d, f], Christina Kaiser [a, e]

[a] Evolution and Ecology Program, International Institute for Applied Systems Analysis, Laxenburg, Austria
[b] Department of Ecology and Evolutionary Biology, University of California Irvine, Irvine, CA, USA
[c] Kellogg Biological Station, Department of Integrative Biology, Department of Microbiology and Molecular Genetics, Michigan State University, Hickory Corners, MI, USA
[d] Ecosystem Services and Management Program, International Institute for Applied Systems Analysis, Laxenburg, Austria
[e] Department of Microbiology and Ecosystem Research, University of Vienna, Vienna, Austria
[f] Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Uppsala, Sweden

## ARTICLE INFO

## ABSTRACT

Large rainfall events following drought cause pulses of $CO_2$ flux that are higher than models predict. This phenomenon, named the "Birch effect" after its discoverer, has been observed for decades, and will influence carbon-climate feedbacks as drying—rewetting (DRW) cycles become more common under intensified climates. Yet, the many interacting factors that determine how soil DRW cycles affect C balance have been difficult to separate empirically. Here we use a spatially explicit biogeochemical—microbial model to examine the mechanisms underlying $CO_2$ dynamics under DRW. We independently model physiological activity and diffusion based on how they vary with (constant) moisture levels in nature, and subject the model to DRW to test the importance of different mechanisms in models with one or two microbial functional groups (cheaters and producers). Our model reproduces respiration patterns similar to empirical observations of the Birch effect when we include mechanisms that link water content to microbial growth and to diffusion rate, whereas inclusion of either mechanism alone produces significantly lower pulses upon rewetting. Diffusion limitation under drought increases substrate availability under rewetting, a process mediated by biogeochemical hotspots and continued enzyme activity under drought. At the same time, high microbial growth under rewetting is needed to replenish enzyme pools and to sustain the biomass required to generate respiration pulses under repeated DRW. Inclusion of cheaters in the model dampens the size of the rewetting pulse and the cumulative amount of $CO_2$ release, as cheaters outcompete producers and reduce overall biomass. Our results provide several novel hypotheses regarding the microbial, biogeochemical, and spatial processes that mediate the Birch effect, which will contribute to a better mechanistic understanding of this important deviation from model predictions.

© 2015 Elsevier Ltd. All rights reserved.

## 1. Introduction

Pulses of carbon dioxide ($CO_2$) emitted when dry soils are rewet were first observed by H. F. Birch in 1958 (Birch, 1958). Numerous studies since then have shown that soil respiration is consistently elevated when preceded by an extended dry period, and can release more carbon (C) when exposed to drying—rewetting (DRW) cycles than when held at constant moisture (Austin et al., 2004; Borken and Matzner, 2009). The mechanisms that explain this pattern remain elusive. This continues to limit our ability to predict the magnitude of these pulses, which can make up 90% of the C mineralized from some systems (Jacobson and Jacobson, 1998; Huxman et al., 2004). Most ecosystem models currently underestimate $CO_2$ releases under DRW events, suggesting that the mechanisms that contribute to soil respiration under DRW may differ from those at play under constant moisture (Whitford et al., 1981; Throop and Archer, 2009; Collins et al., 2014). Because DRW cycles will become more common as the earth's hydrologic cycle intensifies, understanding how these rainfall patterns influence C balance is critical (IPCC, 2007).

It has been challenging to precisely describe what gives rise to the Birch effect because the effect is mediated by biological and

---

* Corresponding author. Kellogg Biological Station, Department of Integrative Biology, Department of Microbiology and Molecular Genetics, Michigan State University, Hickory Corners, MI, USA.
*E-mail address:* evanssa6@msu.edu (S. Evans).

physical factors operating on a micro-scale. This makes the involved mechanisms both highly interactive and methodologically challenging to study. Physical and biological mechanisms influence the Birch effect by altering microbial performance, but the former act through substrate limitation, while the latter impose osmotic stress. Physical factors can exert major control on $CO_2$ patterns as moisture varies. When soils are dry, water-soluble substrates have reduced rates of diffusion and mass transport. Microbes rely on these substrates for energy and biomass, so when their diffusion is limited in the absence of water films, microbial activity is inhibited (Skopp et al., 1990; Stark and Firestone, 1995). Some enzyme activity may persist during this time, further increasing dissolved substrates under drought (Lawrence et al., 2009; Manzoni et al., 2014). Thus, one cause of the Birch effect is the accumulation of these diffusion-limited substrates under drought and the sudden availability of resources under rewetting. Physical destabilization of soil aggregates under rewetting could further add to this increased carbon availability of rewetting, and subsequent $CO_2$ pulse (Navarro-García et al., 2012).

Because microorganisms are osmotically regulated, fluctuations in moisture level also impose a direct physiological stress on microbial performance. For instance, when moisture is limited, microbes must allocate more resources toward maintenance and stress tolerance, and less to growth (Schimel et al., 2007). This variation in microbial activity, biomass, and resource allocation can also alter respiration patterns under fluctuating water potentials. At the most extreme, microbial death from osmotic stress under either drought or a sudden rewetting can reduce biotic potential and increase resource (necromass) availability. But susceptibility to these outcomes may vary among taxa, making the traits that characterize a microbial community important for its overall response to water variability. In particular, certain traits or life-history strategies can increase the tolerance of microbial communities to drought or to rewetting stress (Van Gestel et al., 1993; Halverson et al., 2000; Evans and Wallenstein, 2014). Since these traits are involved in tradeoffs, often related to C allocation, changes in the relative abundance of organisms with these traits can alter predictive relationships between C efflux and soil moisture (Evans and Wallenstein, 2012).

While it is generally accepted that both biological and physical mechanisms can contribute to the Birch effect, their relative roles and influences on biogeochemical dynamics have been difficult to identify empirically, due to the scales on which they occur. Using a model, Lawrence et al. (2009) found that bio-available substrate could accumulate through persistent enzyme activity (despite decreased metabolic activity), mediating the Birch effect. This suggests that the greater availability of additional substrate under rewetting is what stimulates a large $CO_2$ pulse. Other studies have found that adding labile C under rewetting amplifies $CO_2$ release (Xiang et al., 2008; Jenerette and Chatterjee, 2012), supporting the idea that microbes are substrate-limited under rewetting, and that additional dry days would cause substrate accumulation and increasingly large rewetting pulses. There is also empirical support for the role of biological processes in mediating the Birch effect. Respiration rates can correlate with microbial biomass and soil C:N ratio (Borken and Matzner, 2009; Jenerette and Chatterjee, 2012), suggesting biotic potential constrains (and possibly controls) pulse size. Carbon dynamics under DRW can also be influenced by microbial community composition (Fierer et al., 2003; Evans and Wallenstein, 2012), presumably because taxa employ different life-history strategies that influence their response to rewetting (Evans and Wallenstein, 2014). Without the ability to measure all processes simultaneously and manipulate them on the (micro-) scale on which they occur, it is difficult to understand their interactions or quantify their individual contributions to respiration.

Individual-based models have been used to link local interactions — like those between microbes and their immediate soil habitat — to emergent properties or functions they mediate. Thus, such models are well suited to address questions in a soil environment, where primary controls on processes are occurring on a vastly different scale than our measurements of the processes (Wang and Or, 2010; Moyano et al., 2013). In this study, we examine the biogeochemical and microbial dynamics that occur under DRW, and study the relative effects of different mechanisms mediating the production of $CO_2$ on fine spatial and temporal scales. We use a spatially explicit individual-based model previously developed by Kaiser et al. (2014), in which microorganisms and the biogeochemical dynamics they mediate are simulated on a 1 mm × 1 mm soil grid containing 10,000 soil microsites in 1-h time steps. By linking diffusion of labile substrates and microbial physiology to moisture level, we address the following three questions:

1) What processes contribute to high rates of $CO_2$ flux after rewetting dry soils?
2) What are the relative roles of biological and physical mechanisms in respiration patterns under DRW?
3) Does microbial functional diversity alter the mechanisms that explain the Birch effect?

## 2. Methods

### 2.1. Model structure

The model used in this study builds upon the individual-based microbial community model described in detail in Kaiser et al. (2014). The model operates on a grid of 100 × 100 microsites that each have a size of 10 μm × 10 μm × 10 μm, resulting in a total grid size of 1 mm × 1 mm. The grid boundaries are cyclic, with each grid edge connecting to its opposite edge, forming a torus. Microorganisms distributed in grid cells produce extracellular enzymes that catalyze organic matter into dissolved organic matter (DOM), which they use for enzyme production and growth. Microbial respiration consists of maintenance respiration (a fixed fraction of biomass) and respiration required for enzyme production and growth (a fraction of C used for biomass/enzyme buildup). Additional microbial "overflow" respiration occurs when the C:N ratio of available DOM exceeds the ratio of the microbes' C:N demand (Schimel and Weintraub, 2003). Microbial cells reproduce and randomly colonize a neighboring microsite when they reach a given maximum cell size. While both microbes and enzymes are immobile in the model (except for microbial dispersal in the course of reproduction), DOM moves between neighboring microsites via diffusion. Microbial community dynamics emerge from competition for resources and space.

We model microorganisms belonging to one of two functional groups that primarily differ in whether they produce extracellular enzymes (producers) or do not produce enzymes (cheaters). Producers also possess a larger cell size (dictating the size they are required to reach before they can replicate) and a higher C:N ratio (9.0), whereas cheaters possess a smaller cell size and a lower C:N ratio (6.2). Differences in C:N ratios are based on averages of empirical measurements for these functional groups (Kirchman, 2012). The traits characterizing both groups are listed in Table A1. When the biomass of an individual microbial cell falls below 1/10 of its maximal possible cell size (i.e. due to starving), the cell enters into a low-metabolic dormant state, in which it still occupies a microsite, but utilizes no resources. Cells revive from this state when resources become available. We use these two groups to examine the effects of functional diversity on DRW respiration.

Both 1-group (producers only) and 2-group (producers and cheaters) models were run to equilibrium and subjected to all experimental DRW scenarios.

## 2.2. Model parameterization and equilibration

We used the model developed by Kaiser et al. (2014) as the core structure in our study, which aimed to examine stoichiometric controls on litter decomposition. The primary changes we made were (1) to adapt the model to a soil environment — where C and N pools and fluxes are in long-term steady state — by creating a continuous input and running the model to equilibrium, and (2) to implement water as a state variable and link it to diffusion and microbial physiology.

Parameters in Kaiser et al. (2014) were calibrated with empirical data using a Bayesian Approach (Markov Chain Monte Carlo simulation [Van Oijen et al., 2005]). This calibration approach was not feasible when we adapted the model to soil, as simulations were run up to equilibrium each time, and therefore much longer than those for litter. Thus, we determined values for new parameters through repeated manual adjustments within predefined ranges obtained from the literature until steady-state values of soil organic matter (SOM)-C, C:N ratio, microbial biomass, and respiration were in the same range as soil properties and respiration at constant moisture levels as observed by Miller et al. (2005). We used Miller et al. (2005) as a reference experiment for our model, because the authors also measured respiration in response to DRW under controlled conditions, which we can qualitatively compare to patterns that emerge in our model under DRW.

We established equilibrium at a constant water content and constant C and N inputs for 1- and 2-group models (Fig. A1). Since the model does not include climatic forcings, environmental factors like temperature did not vary. All pools and fluxes in the model (e.g., total C, total N, microbial biomass C, respiration, etc.) reached a state of dynamic equilibrium after >800 days of spin-up time. This state is characterized by all pools and fluxes oscillating around a mean value that is stable over time.

The dynamic equilibrium is characterized by spatio—temporal interactions between SOM, microbial necromass, and microbial cells. A more complete description of the underlying mechanisms are found in Appendix A and Kaiser et al. (in preparation). In brief, microbes disperse across the model grid in patches, making the initially homogenous primary substrate heterogeneous. Microbial patches advance in the direction of highest concentrations of primary substrate, leaving behind empty areas of depleted primary substrate, which are subsequently refilled by a new supply (as primary substrate is continuously and homogenously added to all microsites and thus accumulates in spots void of degrading microbes). These dynamics result in spatially isolated C- and N-rich hotspots (Fig. A2). Specifically, the hotspots emerge because the areas in front of the microbial patches are primary substrate with a high C:N ratio (35). The rear end of microbial patches primarily consist of microbial necromass and depleted primary substrate, resulting in a overall low substrate C:N ratio (~10), which in turn makes it a hot spot for high N-mineralization. In contrast, areas in the front of microbial patches are N-poor, and N-immobilization predominates (Fig. A2).

Analyses began after a spin-up period of 8000—12,000 days. The dynamic nature of the model's equilibrium state (Fig. A1) made it challenging to minimize the influence of equilibrium state on the results of our short-term DRW study. We addressed this by choosing a study period within which the dynamic equilibria were consistent between 1- and 2-group models (Fig. A3) (i.e. both

starting at either an increase or decrease of the underlying equilibrium oscillation).

## 2.3. Varying soil water in the model and linking it to water-sensitive processes

We implemented water as a new state variable in the model developed by Kaiser et al. (2014). At any one time, soil water content (represented volumetrically in the model) is determined by water input and evaporation, and is equal across all microsites at any one time. Other studies suggest that soil moisture heterogeneity, as influenced by soil physical structure, can affect DRW (Wang and Or, 2010; Blagodatsky and Smith, 2012), but explicitly testing this factor was beyond the scope of our study, so our model treats the physical aspects of soil structure implicitly. Soil water content in the model mimics that induced in a DRW laboratory incubation performed by Miller et al. (2005), whose results have been used by other studies to test models of the Birch effect (Lawrence et al., 2009; Li et al., 2010). During simulated rain, soil water content increases at a constant rate (Table A1), and the water evaporated per hour equals 1.5% of the extant water. The simulated water content cannot exceed 100% of the soil's water holding capacity, at which time we assume it to remain constant, as when water runs off from a saturated soil. Likewise, the simulated water content cannot fall below that of air-dried soils (Table A1, Schimel, unpublished data).

In our model, water content influences two factors: (a) the rate of DOM uptake by soil microorganisms and (b) the distance a DOM molecule travels in one time step. In this way, we made both microorganisms and diffusion sensitive to moisture level, but their effect on $CO_2$ under DRW was an emergent property (i.e. not parameterized with data from DRW responses a priori). We tested the effects of these two mechanisms on respiration under DRW by running model scenarios in which either one of the factors, or both factors, were influenced by water content.

### 2.3.1. Microbial moisture sensitivity

To test the effects of microbial moisture sensitivity on respiration under drying and rewetting, we introduced a function that reduces microbial growth under sub-optimal water levels. We derived this function from observations by Stark and Firestone (1995), who measured the effects of moisture stress on the microbial physiology of nitrifiers independently of the reduction in microbial activity that might be caused by a decreased access to the substrate. Although we acknowledge that nitrifiers may have a moisture sensitivity that differs from other microbial groups, using this empirical relationship gives us the opportunity to model realistic microbial moisture sensitivity independently of diffusion.

Specifically, decreasing water potential, $\psi$, results in a lower physiological stress factor, $\delta$, according to the following relationship: $\delta = e^{0.56\psi}$ (see Table A1 for the relationship between water content and $\psi$). This physiological stress factor (ranging from 0 to 1) proportionally modifies the maximum uptake rate. At optimal water content, $\delta = 1$ and DOM uptake is not constrained by microbial physiology. At lower water contents, a lower physiological stress factor $\delta$ reduces the DOM uptake rate. Microorganisms are likely to have multiple strategies and employ many traits that influence their ability to survive under DRW cycles (Lennon et al., 2012; Evans and Wallenstein, 2014; Manzoni et al., 2014). In our model, we treat variation in the strategies that microbes use to tolerate DRW implicitly, by assuming that all involve a reallocation of resources away from growth (Schimel et al., 2007).

### 2.3.2. Physical access and diffusion

To test the effects of the physical access to substrate on respiration under DRW, we linked water content to the diffusion of low molecular weight substances (i.e. DOM and DIN in the model). Here, we first explain how we model DOM and DIN diffusion, and then describe how we link it to water content in the model.

We model diffusion using an atomistic approach, by simulating the Brownian motion of diffusing particles as a random walk. In a random walk, particles carry out random "jumps" into a random direction in every time step. On a phenomenological level, diffusion coefficients describe how fast a certain substance spreads on average through a given medium (measured, e.g., in units of cm$^2$ per second). We used empirical diffusion coefficients for DOM based on the diffusion coefficients of its components − glucose, amino acids, and humic substances − empirically observed in soils at optimal water content (E. Soroker, unpublished PhD thesis, University of California Berkeley, 1990; Barber, 1995; Chenu and Roberson, 1996) and translated them into a discrete Brownian "jump size" (in model grid cells per model time step) (Kier et al., 1997; Kaiser et al., 2014). Because molecules can diffuse (or "jump") in every direction on the grid, the diffusion rate is described as the radius (in microsites) of the area over which DOM from one microsite can be spread within one time step. This approach of simulating diffusion as Brownian motion of individual particles has been widely used in cellular automata models of reaction−diffusion systems (Weimar and Boon, 1993; Kier et al., 1997; Weimar, 1997). A small fraction of all diffusing elements is lost by leaching during the transition (Kaiser et al., 2014, in press). For further details and a full derivation of this model component, see Appendix A.

When soil water content is sub-optimal, diffusion slows because molecule path length around soil substructures and water films (tortuosity) increases and mass transport rates are reduced (Tinker and Nye, 2000). The diffusion coefficient for DOM measured at optimal water content, $D_0$, serves as the maximum diffusion coefficient in our model. To determine an effective diffusion coefficient, $D_E$, applicable at lower water contents, we reduce $D_0$ using a fractional impedance factor, $\gamma$, which modifies $D_E$ in the following way: $D_E = \gamma D_0$. This impedance factor, which ranges from 0 to 1, thus decides the proportion effective diffusion is reduced from $D_0$, and varies with gravimetric water content ($\phi$) as described by Tinker and Nye (2000): $\gamma = 0.132\phi - 0.02$. In this approach, diffusion rate does not vary across space at any one time, but the effect of soil structure on diffusion under different water levels is included implicitly through the impedance factor.

From these calculations, we obtain an effective diffusion coefficient, which we use to determine the number of grid cells DOM moves within a time step (as described above), and that decreases as water content decreases, in the same way it does as soils dry. Using the principles described above, this translates into a jump-size radius that varies with water content, reaching 0 (no diffusion) at the minimum water content (see Appendix A for more details). We also examined the relationship between water and respiration when water potential was held constant to verify this relationship was similar to that observed in previous measurements (Manzoni et al., 2012). To do this we ran six simulations for which water potential remained at −0.033, −0.05, −0.1, −0.2, −0.5, −1, −2, and −4 MPa.

### 2.4. Experimental model scenarios

After linking diffusion and microbial moisture sensitivity to water content in both 1- and 2-group models, we subjected equilibrated soils to DRW cycles under different scenarios, with the goal of isolating the effects of different factors. The DRW pattern we imposed consisted of an initial wet-up, followed by a 28-day drying period before rewetting. Such drying−rewetting was repeated four times, in a pattern similar to DRW cycles imposed in the four-week DRW scenario used by Miller et al. (2005).

To identify the mechanisms responsible for respiration patterns under DRW in our model (research question 1 in the Introduction), we simply observed how microbial and biogeochemical pools varied across space and time, and the patterns that emerged from their interactions. We documented these dynamics under repeated DRW cycles, as well as more closely during a single DRW event.

We quantified the roles of microbial moisture sensitivity and diffusion on DRW respiration (research question 2 in the Introduction) by running scenarios that include/exclude these two mechanisms. As these two mechanisms were the only ones that linked water to model dynamics, we did not include a model scenario that excludes both mechanisms (which did not produce a $CO_2$ pulse after rewetting; results not shown).

All scenarios were run for two different models: one including only producer functional groups (1-group model) and one including producers and cheaters (2-group model). We focused on cheater and producer functional groups because they have been well-characterized empirically and theoretically (Allison, 2005; West et al., 2007; Allison et al., 2014; Christina Kaiser et al., in press), and may be differentially affected by DRW due to diffusion sensitivity (Allison, 2005). We used these groups to investigate whether the interactions that emerge from the inclusion of two functional groups influence DRW-C dynamics (research question 3 in the Introduction).

### 2.5. Data analyses

We observed microbial and biogeochemical dynamics in the model, both as they varied across the grid and when summed across the whole grid. We ran six replicate runs of every scenario to account for any differences due to the stochasticity inherent in the model, which emerges because many individual events in the model, such as microbial dispersal or mortality are driven by probability functions. To compare DRW respiration dynamics among model runs, we focused on two properties of the respiration curve: (1) the increase in respiration upon rewetting, which we quantified by subtracting the respiration rate one time step before the first rewetting (after initial wet-up) from the maximum respiration rate within three days of the first rewetting, and (2) average respiration rate, which we calculated by taking the mean over the entire 116-day period. Compared to rewetting respiration, the average respiration rate provides an indicator of cumulative $CO_2$ release, in the same units (per day) as rewetting respiration. We statistically analyzed differences in respiration curve properties among scenarios using ANOVA and multiple comparisons using least square means.

## 3. Results

### 3.1. Respiration pulses under DRW

Our model performs well under constant moisture conditions. Relationships between constant moisture level and respiration were similar to those summarized in a recent meta-analysis by Manzoni et al. (2012) (see Figs. B1 and B2). Respiration patterns that emerged under DRW were characteristic of the Birch effect (Fig. 1A) when both diffusion and microbial moisture sensitivity were included (see Section 3.3 for further discussion of mechanisms). On average, the post-rewetting respiration rate in the 1- and 2-group models equals 4.5 times and 2.6 times the (pre-pulse) baseline, respectively, and reaches its maximum 13−19 h after initiation of
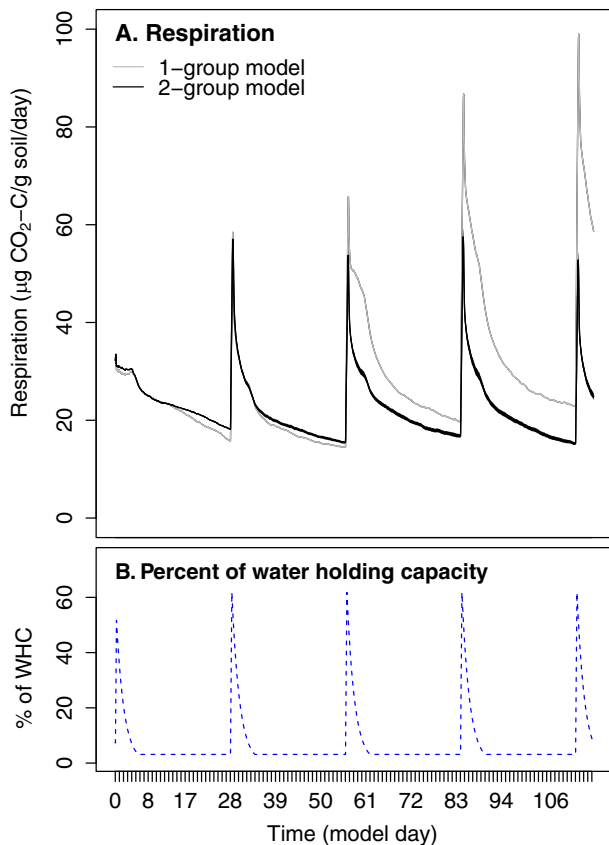
Fig. 1. Mean soil respiration (A) in response to changes in percent of water holding capacity (WHC) induced by soil drying and rewetting (B) simulated by our individual-based model over 116 days. In (A), the 2-group model (gray) includes cheaters, while the 1-group model includes only producers (black), and line thickness represents 95% confidence interval around a mean respiration rate (N = 6 model runs).

the wet-up. Percent of water holding capacity (WHC) in a single pulse increases from 3% to 60% over 9 h. Water level remains above 10% for 89 h (3.7 days) as it evaporates (Fig. 1B) to about 3.1% of WHC, the minimal water level that can be reached in the model (Table A1). Interestingly, when the preceding dry period is slightly wetter (specifically, remaining above 6.4% of WHC or 1.46% gravimetric moisture), respiration after the pulse only increases by 7%. This threshold corresponded to the water level at which diffusion "jump size" reaches 0, at which point there is no transport of DOM among microsites (Fig. B3).

Both the implementation of diffusion and microbial moisture sensitivity were important for simulating patterns resembling the Birch effect. Models that include only one of these mechanisms produced much smaller respiration pulses after rewetting (see Section 3.3). Both models result in respiration rates similar, but not identical, to those observed by Miller et al. (2005), whose experimental conditions we aimed to mimic (Fig. B4). Miller et al. (2005) observed a mean maximum rate after rewetting of 82.8 μg $CO_2$–C/g, which was similar to our values of 77.8 and 59.2 μg $CO_2$–C/g soil increase for the 1- and 2-group models, respectively. However, the relative increase of respiration from baseline to maximum respiration after rewetting was lower in our simulations, since respiration under drought was higher than that observed by Miller et al. (2005) (which was essentially zero). Although not the focus of this study, maximum respiration rates after 2-week rewetting events were only slightly lower than those in a 4-week simulation, resembling 2-week DRW patterns in Miller et al. (2005) (data not shown).

In the 1-group model (no cheaters), respiration shows an overall increasing trend over multiple DRW cycles (Fig. 1; Fig. B6, Movie S1, Respiration pane). Respiration does not display a positive or negative trend in the 2-group model, but shows a decrease in microbial biomass and an increase in cheater biomass (Movie S2).

Supplementary video related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2015.10.020

### 3.2. Biogeochemical dynamics of a single drying–rewetting (DRW) event

We examined a single DRW pulse in detail, so as to understand the simultaneous trends of multiple factors contributing to the Birch effect (Fig. 2). During the 28-day dry period, microbial biomass and enzyme activity decrease. At the same time, dissolved organic carbon (DOC) and dissolved inorganic N (DIN) accumulate (Fig. 2A). As soils dry (Fig. 2B), DOC and DIN pools accumulate in spatially separated hotspots (Fig. 2C). The spatial separation of C and N hotspots emerges due to patterns that develop under equilibrium through interactions among primary substrate, microbial activity, and microbial death (see text in Methods, Kaiser et al., in preparation, and Appendix A for a full description of this pattern and its implications). We observe distinct areas where the substrate was primarily available as microbial remains (necromass), and areas where the primary substrate (new input) made up a larger proportion of the substrate pool (Movies S1 and S2). Under drought, diffusion limitation caused both DOC and DON to accumulate, but in different areas. In areas characterized by high concentrations of microbial necromass with lower C:N ratios, microbes are C-limited and DIN accumulates. In neighboring areas of high primary substrate, microbes are N limited, causing DOC accumulation (Fig. 2C). Under rewetting, transport among microsites resumes, alleviating limitations and stimulating microbial biomass and enzyme C pools (Fig. 2B).

We observe shifts in the relative abundance and spatial configuration of cheaters and producers over DRW cycles, due to differences in functional traits and competitive ability. When included, cheaters colonize the outside areas of colonies of producers (Fig. 2C). Producers, on average, make up a larger proportion of microbial biomass C than cheaters (77% across the 116-day period) (Fig. B5), but because cheaters have smaller cell sizes, producers do not necessarily always occupy more grid cells than cheaters (Fig. 2C). The proportion of total biomass that consisted of cheaters averages 4% under drought and reaches a maximum of 32.6% post-rewetting (Fig. B5). See Movie S1 (1-group model) and Movie S2 (2-group model) for excellent illustrations of how these dynamics coincide temporally and spatially.

### 3.3. Effect of diffusion and physiological stress mechanisms on DRW respiration

We tested the relative influence of microbial moisture sensitivity and diffusion by running scenarios (for both 1-group and 2-group models) that included/excluded these mechanisms (Fig. 3). On this basis, we investigated the biogeochemical dynamics that explained differences in these three model scenarios (Fig. 4). The model scenario that combines both mechanisms is the only one resembling respiration patterns observed under DRW in this soil (Miller et al., 2005). On average, the respiration pulses resulting from physiological stress or diffusion alone are 22% and 14% of the respiration pulse in the full model, respectively. Including diffusion and microbial sensitivity alone produce similar pulse sizes, but including only diffusion results in a slightly larger pulse when tested in the 2-group model (Fig. 3B).
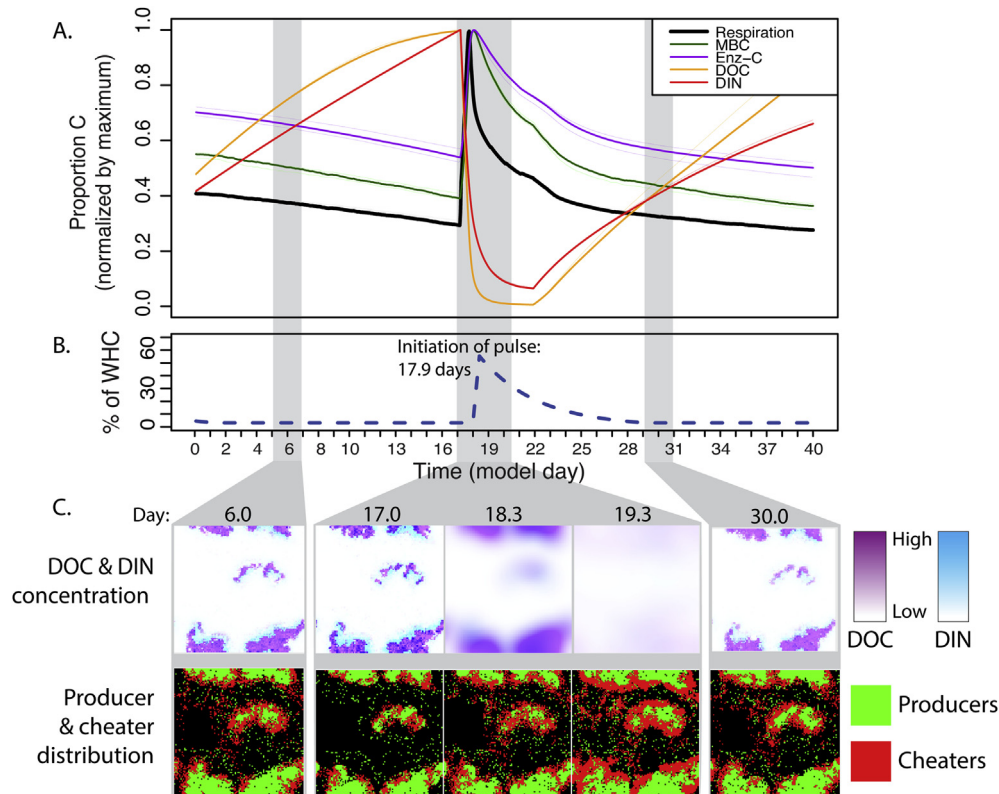
**Fig. 2.** Microbial and biogeochemical pools shown as a proportion of each pool's maximum (A) in response to changes in percent water holding capacity (WHC) under a single drought and rewetting (B) in our individual-based model. Line thickness in A represents 95% confidence intervals of means ($N = 6$ model runs). (C) Grid images of DOC and DIN pools and distribution of microbial functional groups at 5 time points throughout the drying and rewetting cycle (with three time points shown within the pulse). Images show one replicate simulation of a 1 mm × 1 mm area of soil comprised of 100 × 100 grid cells. See Movies S1 and S2 for real-time simulations of these dynamics.

The response of average respiration rate (over four DRW pulses) to diffusion and physiological stress differs from that of a single rewetting pulse (Fig. 3A,B). The inclusion of a physiological stress mechanism results in higher overall microbial biomass in both 1- and 2-group models, while diffusion alone results in lower average respiration in the 1-group model. These trends also reflect differences in the slope of the average respiration at any one point in time; inclusion of physiological stress results in a greater average respiration rate over time, while diffusion alone has a negative effect, in both 1- and 2-group models. This is largely mediated by differences in microbial biomass under diffusion and physiological stress (Fig. 4), which continue to decrease through subsequent pulses in models that include diffusion alone.

## 4. Discussion

### 4.1. Biological and physical mechanisms are both needed to reproduce the Birch effect

Numerous studies have documented the large respiration pulse emitted when dry soil is rewet (Borken and Matzner, 2009), but the underlying biogeochemical and microbial dynamics have been difficult to identify. Here we have used a spatially explicit biogeochemical–microbial model to examine the patterns that emerge under soil drying–rewetting (DRW), and to test the relative influence of different mechanisms on $CO_2$ release. We constructed and parameterized the model based on dynamics observed at constant moisture levels, linking water content to diffusion rate and microbial growth based at the micro-scale. DRW cycles prompted synergies among these mechanisms that resulted in respiration patterns characteristic of the Birch effect,

and that Miller et al. (2005) observed in a laboratory incubation. These patterns emerged only when both diffusion of DOM and microbial growth were linked to water content throughout DRW cycles. In contrast, the inclusion of either of these two mechanisms alone results in substantially lower respiration pulses after rewetting (Fig. 3), which allowed us to study the contribution of each to the biogeochemical patterns we observe in the full model.

In our model, diffusion limitation and continued enzyme activity under drought result in large increases in DOM and DIN in spatially separated hotspots. When rates of diffusion increase under rewetting, these DOM hotspots are distributed over the model grid, providing a source of labile DOM for microbes to rapidly mineralize into $CO_2$. DOM accumulation as a mechanism for the large $CO_2$ pulses after rewetting has been supported by both empirical observations (Miller et al., 2005; Long and Or, 2007; Xiang et al., 2008) and models (Lawrence et al., 2009). Some studies even suggest this to be the predominant control on microbial responses to moisture variation (Manzoni et al., 2012; Manzoni and Katul, 2014), which has important implications for predicting the Birch effect using models. If the linear accumulation of DOM in soils over time sufficed to explain the extent of $CO_2$ release upon rewetting, pre-rewetting dry days would be a good predictor of pulse size. Although this correlation has been observed (Fay et al., 2000; Fierer and Schimel, 2002; Miller et al., 2005; Manzoni et al., 2014), and used to improve predictions of short-term pulses (Del Grosso et al., 2001), our study does not support such a relationship.

Instead, our model reveals specific dynamics that change the nature of DOM accumulation and redistribution, which can inform how we understand this mechanism. During the 20-day dry period
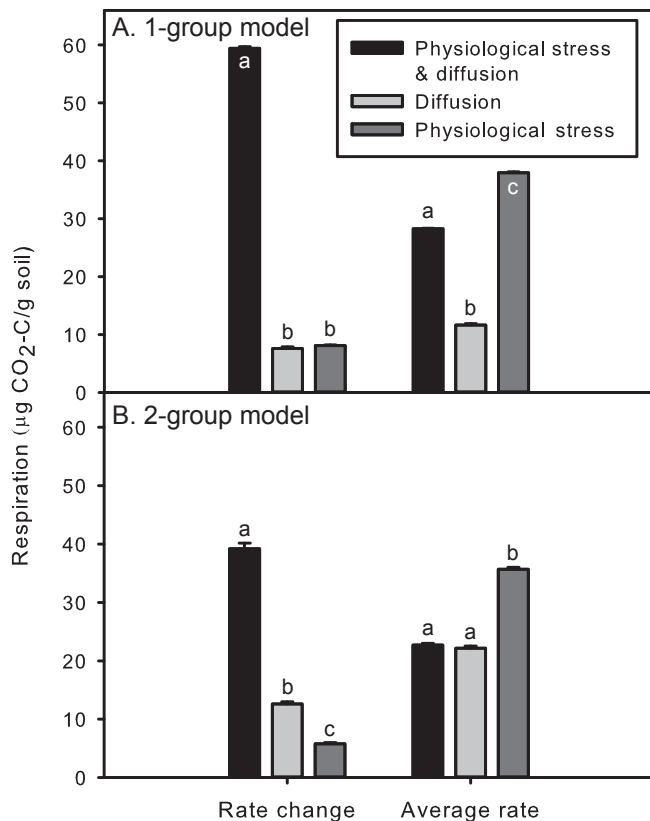
**Fig. 3.** Relative influence of different mechanisms on the change in respiration rate after rewetting (calculated by subtracting maximum respiration after rewetting from baseline respiration pre-pulse), and the average respiration rate over four dry-ing–rewetting pulses in models with one (A) and two (B) microbial functional groups. The relative influence of each mechanism was determined by running models that include both physiological stress and diffusion mechanisms, and models that include only one or the other. Bars represent means ($N = 6$ model runs), and error bars show the standard errors of those means. Different lower case letters indicate significant differences ($p < 0.01$) as analyzed by multiple comparison tests within a model (1 or 2-group) and respiration response variable (rate change or average rate).

simulated in our model, diffusion ceased about four days after a rewetting event. This cessation of diffusion is critical: when drying does not reach this threshold, DOM does not accumulate enough to produce the Birch effect (Fig. B3). Manzoni and Katul (2014) found a similar threshold effect that corresponded to the moisture level at which micropores were no longer connected, and substrate limitation (and subsequent accumulation) increased.

In addition to altered DOM availability, our model also suggests that the Birch effect could be further influenced by the spatial dynamics of C and N. Under drought, DOC and DON not only accumulate in hotspots, but in *different* hotspots (Fig. 2C, Movies S1 and S2). As a result, microorganisms in C-rich and N-rich hotspots are N- and C-limited, respectively, but limitations are alleviated when diffusion links microorganisms and microsites with different C:N ratios. This possible contributor to the Birch effect is dependent on the emergence of C and N-rich regions, which develop under equilibrium in our model (Kaiser et al., in preparation, Fig. A1), but similar patterns of C and N hotspots are also found in soils (Parkin, 1987; McClain et al., 2003). Recently Vogel et al. (2014) observed spatial variation in soils on scales similar to those we model. Our model suggests that hotspots emerge through interactions between microbial biomass, necromass, and substrate input, and that this C and N separation contributes to limitation of microbial activity under drought and resumption under rewetting. The chain of events described here presents a possible (and testable) hypothesis

for the dynamics that give rise to the Birch effect, building on previous conceptual models that include microsites (Schimel and Bennett, 2004).

An important finding of our study is that variation in microbial growth with water content is equally important for recovering the Birch effect as is diffusion limitation. A key aspect of microbial growth that contributes to this pattern is its stimulation under higher water content. In contrast, reduced microbial growth and activity under drought is not a major contributor to respiration after rewetting, because it has a similar effect as diffusion on biomass, and does not cause DOM accumulation (Fig. 4). A higher growth rate under rewetting allows microbes to build biomass (and produce enzymes) during this brief period, providing sufficient biotic potential to make use of the available DOM and bolstering enzymatic activity that persists (though at a decreasing rate) under drought.

Other studies have hinted at our finding that physical and biological mechanisms co-contribute to the Birch effect. In particular, Jenerette and Chatterjee (2012) found that adding substrate during a rewetting event increased $CO_2$ flux (suggesting substrate limitation), but only in more biologically active soils (suggesting biotic limitation). In addition, Xiang et al. (2008) showed that respiration after rewetting increased in surface soils, but not subsurface soils, where limited C may not have resulted in the accumulation of DOM. Our model does not include mechanisms that can provide additional C to fuel high respiration rates under rewetting, such as the release of labile C from protection by aggregates under rewetting, or C released from microbial death or osmolyte production and release (Kieft et al., 1987; Halverson et al., 2000; Denef et al., 2001; Navarro-García et al., 2012). It is possible that including some or all of these mechanisms would elevate rewetting respiration in our model closer to that observed by Miller et al. (2005); a more comprehensive evaluation of the effect of different Birch effect mechanisms is clearly needed. Our model also excludes other environmental factors that influence microbial drought stress, like temperature. Understanding these interactions will be necessary to accurately estimate and generalize responses to DRW.

We find that the period of microbial growth under rewetting is also critical for the long-term viability of the biomass pool. This growth sustains respiration pulses over a longer period, causing biomass to increase or remain constant over repeated DRW, in agreement with empirical observations (Xiang et al., 2008) (Figs. 3 and B4). Consequently, average respiration rates across DRW cycles were sensitive to the inclusion of the biological mechanism. This finding is important because it suggests that microbial sensitivity to DRW may control changes in C balance under DRW in the long term, while diffusion may simply redistribute C from stored to respired pools. It also calls for additional estimates of the sensitivity of microbial growth to DRW. In our model, different microbial responses to DRW (e.g., dormancy, osmoregulation, predation avoidance; Manzoni et al., 2012) are subsumed into one function, but this relationship could vary depending on which strategies predominate.

### 4.2. Cheaters alter $CO_2$ dynamics under DRW by constraining total biomass

The ability to produce enzymes is a microbial trait that has been shown to influence species interactions and emergent community functions (Allison, 2012), but the contribution of this functional trait has not been examined in relation to DRW. In our model, cheaters are sensitive to drought, but out-compete producers under rewetting (Fig. 4). This is not surprising: the smaller cell size of cheaters and their dependence on a 'public good' (enzymes) makes high-diffusion, high-resource environments like those after a
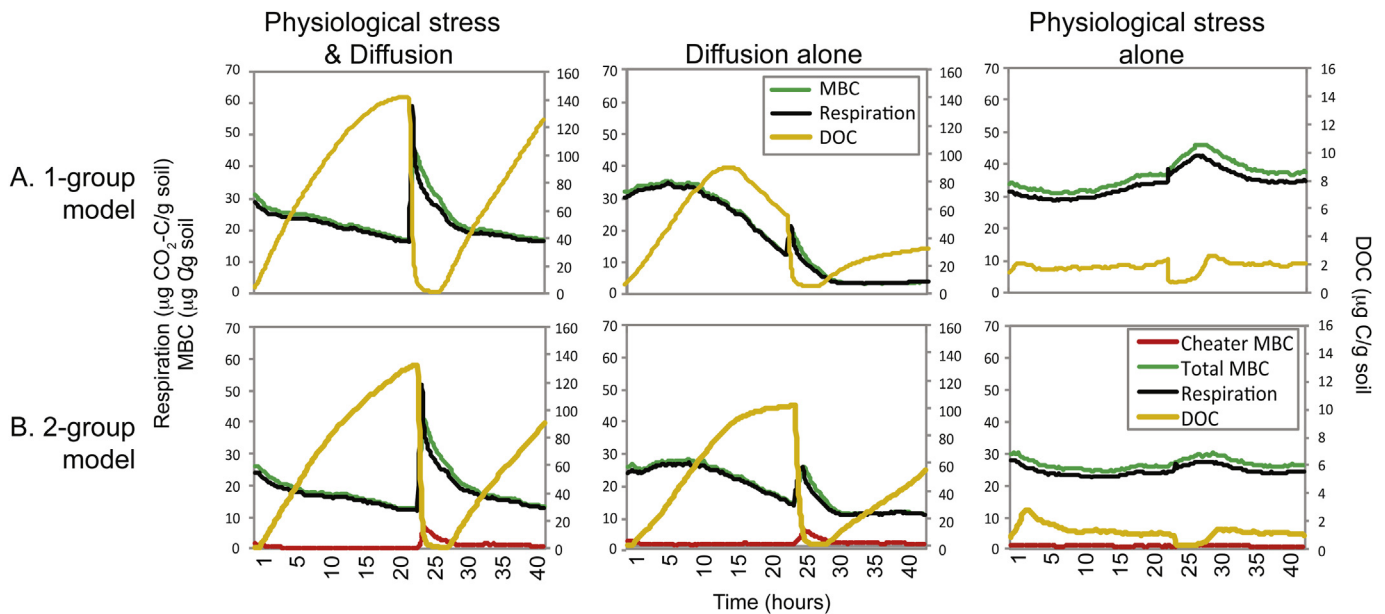
**Fig. 4.** Changes in respiration rate (left vertical axes), microbial biomass carbon (MBC, left vertical axes), and dissolved organic carbon (DOC, right vertical axis) over the course of one drying—rewetting pulse in the 1-group model (A) and 2-group model (B). The three columns compare models that include both physiological stress and diffusion mechanisms, and models that include only one or the other. Note the reduced range of the DOC axis in the third column.

rewetting event advantageous to them (Allison, 2012, 2005). Cheaters' sensitivity to changes in diffusion could also explain why diffusion is a more important mechanism for respiration in our 2-group model than in our 1-group model (Fig. 3). Over time, high growth rates of cheaters during brief periods of rewetting is sufficient to generate an overall increase in cheater biomass in the four-pulse simulation (Fig. B4). That is, despite the negative effect of diffusion limitation on cheater survival, their fast response time under rewetting is sufficient for them to outcompete producers in our model. The competitive ability of cheaters may have been enhanced by spatial patterns: cheaters colonize areas surrounding producers, and reproduce (a mechanism for movement) at a lower cell-size threshold. In our model, both of these factors may prevent the colonization of new grid cells by producer cells under rewetting.

Although cheaters benefit from single and multiple rewetting pulses, including them as part of the modeled microbial community results in a smaller respiration pulse after rewetting, and a lower average respiration rate over all pulses, compared to the 1-group model. The inability of cheaters to produce enzymes reduces the capacity of the entire microbial community to build biomass. Thus, survival under drought is compromised by reduced enzyme production under rewetting. Building biomass is an important contributor to the Birch effect in our model, so in this way cheaters constrain biogeochemical function by outcompeting producers, as Allison (2005) also observed. Although the 2-group model results in lower average and single-pulse respiration (Figs. 1 and 3), it is important to note that neither scenario is better than the other at reproducing the observations reported by Miller et al. (2005): the average change in respiration for both scenarios deviates from observed rates by 10 μg C/g soil. Furthermore, both increasing and decreasing sizes of respiration pulses have been observed over DRW cycles in empirical studies (Borken and Matzner, 2009).

There are many microbial strategies (Evans and Wallenstein, 2014) and traits (Lennon et al., 2012) for tolerating DRW stress. We focus on only one functional group axis (producers and cheaters), so cannot make broad conclusions about linkages between microbial community composition and the Birch effect. However, our model does suggest that these traits are relevant to Birch effect mechanisms. We found that cheaters could alter C dynamics under DRW by decreasing microbial biomass and constraining enzyme production under rewetting. Our results do support the hypothesis that investment in enzyme production could be a strategy for tolerating DRW by promoting DOC production under drought (Manzoni et al., 2014). However, in our model any advantage gained by enzyme production are eliminated in the presence of cheaters, which outcompete producers under DRW. Our findings direct future empirical studies to further examine how variation in enzyme production rates among microbial communities alters biogeochemical responses to DRW.

## 5. Conclusions

Rainfall regimes are expected to become more intense in the future, creating more instances of drying and rewetting (IPCC, 2007). The effect of DRW on C balance has been difficult to study because the responsible mechanisms interact on fine spatial and temporal scales. Here we have presented several testable hypotheses to advance our understanding of the Birch effect. (1) Accumulation of DOM is important for the size of respiration pulses, but relates nonlinearly to preceding dry days; low diffusion under drought may limit microbial activity through C- and N-limitation in N- and C-rich hotspots, respectively, as well as through resource availability. (2) Microbial sensitivity to DRW exerts a major control over long-term C release, compared to diffusion-mediated changes in substrate availability, which may simply redistribute C release temporally. (3) Increases in cheater biomass can constrain total biomass pools under DRW, which could constrain the mobilization of existing soil C under recurrent DRW over time. Future studies should consider not only the contribution of different mechanisms to the size of the respiration pulse after rewetting, but also what their relative contribution means for long-term C dynamics. In future studies, it will be important to consider not only the mechanism mediating the size of the respiration pulse, but also

how these mechanism differ in their effect on long-term C dynamics under DRW.

## Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2015.10.020.

## References

Allison, S.D., 2012. A trait-based approach for modelling microbial litter decomposition. Ecology Letters. http://dx.doi.org/10.1111/j.1461-0248.2012.01807.x.

Allison, S.D., 2005. Cheaters, diffusion and nutrients constrain decomposition by microbial enzymes in spatially structured environments. Ecology Letters 8, 626–635. http://dx.doi.org/10.1111/j.1461-0248.2005.00756.x.

Allison, S.D., Lu, L., Kent, A.G., Martiny, A.C., 2014. Extracellular enzyme production and cheating in Pseudomonas fluorescens depend on diffusion rates. Frontiers in Microbiology 5. http://dx.doi.org/10.3389/fmicb.2014.00169.

Austin, A.T., Yahdjian, L., Stark, J.M., Belnap, J., Porporato, A., Norton, U., Ravetta, D.A., Schaeffer, S.M., 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. Oecologia 141, 221–235. http://dx.doi.org/10.1007/s00442-004-1519-1.

Barber, S.A., 1995. Soil Nutrient Bioavailability: a Mechanistic Approach, second ed. John Wiley & Sons, New York.

Birch, H.F., 1958. The effect of soil drying on humus decomposition and nitrogen availability. Plant and Soil 10, 9–31. http://dx.doi.org/10.1007/BF01343734.

Blagodatsky, S., Smith, P., 2012. Soil physics meets soil biology: towards better mechanistic prediction of greenhouse gas emissions from soil. Soil Biology and Biochemistry. http://dx.doi.org/10.1016/j.soilbio.2011.12.015.

Borken, W., Matzner, E., 2009. Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. Global Change Biology 15, 808–824. http://dx.doi.org/10.1111/j.1365-2486.2008.01681.x.

Chenu, C., Roberson, E.B., 1996. Diffusion of glucose in microbial extracellular polysaccharide as affected by water potential. Soil Biology and Biochemistry 28, 877–884. http://dx.doi.org/10.1016/0038-0717(96)00070-3.

Collins, S.L., Belnap, J., Grimm, N.B., Rudgers, J.A., Dahm, C.N., D'Odorico, P., Litvak, M., Natvig, D.O., Peters, D.C., Pockman, W.T., Sinsabaugh, R.L., Wolf, B.O., 2014. A multiscale, hierarchical model of pulse dynamics in arid-land ecosystems. Annual Review of Ecology, Evolution, and Systematics 45, 397–419. http://dx.doi.org/10.1146/annurev-ecolsys-120213-091650.

Del Grosso, S., Parton, W.J., Mosier, A.R., Hartman, M.D., Brenner, J., Ojima, D.S., Schimel, D.S., 2001. Simulated interaction of carbon dynamics and nitrogen trace gas fluxes using the DAYCENT model. In: Shaffer, M.J., Ma, Liwang, Hansen, Soren (Eds.), Modeling Carbon and Nitrogen Dynamics for Soil Management. CRC Press, Boca Raton, FL.

Denef, K., Six, J., Bossuyt, H., Frey, S.D., Elliott, E.T., Merckx, R., Paustian, K., 2001. Influence of dry-wet cycles on the interrelationship between aggregate, particulate organic matter, and microbial community dynamics. Soil Biology & Biochemistry 33, 1599–1611.

Evans, S.E., Wallenstein, M.D., 2014. Climate change alters ecological strategies of soil bacteria. Ecology Letters 17, 155–164. http://dx.doi.org/10.1111/ele.12206.

Evans, S.E., Wallenstein, M.D., 2012. Soil microbial community response to drying and rewetting stress: does historical precipitation regime matter? Biogeochemistry 109, 101–116. http://dx.doi.org/10.1007/s10533-011-9638-3.

Fay, P.A., Carlisle, J.D., Knapp, A.K., Blair, J.M., Collins, S.L., 2000. Altering rainfall timing and quantity in a mesic grassland ecosystem: design and performance of rainfall manipulation shelters. Ecosystems 3, 308–319.

Fierer, N., Schimel, J.P., 2002. Effects of drying-rewetting frequency on soil carbon and nitrogen transformations. Soil Biology & Biochemistry 34, 777–787.

Fierer, N., Schimel, J.P., Holden, P.A., 2003. Influence of drying-rewetting frequency on soil bacterial community structure. Microbial Ecology 45, 63–71. http://dx.doi.org/10.1007/s00248-002-1007-2.

Halverson, L.J., Jones, T.M., Firestone, M.K., 2000. Release of intracellular solutes by four soil bacteria exposed to dilution stress. Soil Science Society of America Journal. http://dx.doi.org/10.2136/sssaj2000.6451630x.

Huxman, T.E., Snyder, K.A., Tissue, D., Leffler, A.J., Ogle, K., Pockman, W.T., Sandquist, D.R., Potts, D.L., Schwinning, S., 2004. Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. Oecologia 141, 254–268. http://dx.doi.org/10.1007/s00442-004-1682-4.

IPCC, 2007. Climate Change 2007: Synthesis Report.

Jacobson, K.M., Jacobson, P.J., 1998. Rainfall regulates decomposition of buried cellulose in the Namib Desert. Journal of Arid Environments 38, 571–583. http://dx.doi.org/10.1006/jare.1997.0358.

Jenerette, D.G., Chatterjee, A., 2012. Soil metabolic pulses: water, substrate, and biological regulation. Ecology 93, 959–966. http://dx.doi.org/10.1890/11-1527.1.

Kaiser, C., Evans, S., Dieckmann, U., Widder, S. The influence of microbial physiology and microscale spatial pattern formation on the amount of C and N stored in soils at steady state: a modeling analysis (in preparation).

Kaiser, C., Franklin, O., Dieckmann, U., Richter, A., 2014. Microbial community dynamics alleviate stoichiometric constraints during litter decay. Ecology Letters. http://dx.doi.org/10.1111/ele.12269.

Kaiser, C., Franklin, O., Richter, A., Dieckmann, U., 2015. Social dynamics within decomposer communities lead to N retention and organic matter build-up in soils. Nature Communications. http://dx.doi.org/10.1038/ncomms9960 (in press).

Kieft, T.L., Soroker, E., Firestone, M.K., 1987. Microbial biomass response to a rapid increase in water potential when dry soil is wetted. Soil Biology & Biochemistry 19, 119–126.

Kier, L.B., Cheng, C.K., Testa, B., Carrupt, P.A., 1997. A cellular automata model of diffusion in aqueous systems. Journal of Pharmaceutical Sciences 86, 774–778. http://dx.doi.org/10.1021/js9700513.

Kirchman, D.L., 2012. Processes in Microbial Ecology. Oxford University Press, New York.

Lawrence, C.R., Neff, J.C., Schimel, J.P., 2009. Does adding microbial mechanisms of decomposition improve soil organic matter models? A comparison of four models using data from a pulsed rewetting experiment. Soil Biology and Biochemistry 41, 1923–1934. http://dx.doi.org/10.1016/j.soilbio.2009.06.016.

Lennon, J.T., Aanderud, Z.T., Lehmkuhl, B.K., Schoolmaster, D.R., 2012. Mapping the niche space of soil microorganisms using taxonomy and traits. Ecology. http://dx.doi.org/10.1890/11-1745.1.

Li, X., Miller, A.E., Meixner, T., Schimel, J.P., Melack, J.M., Sickman, J.O., 2010. Adding an empirical factor to better represent the rewetting pulse mechanism in a soil biogeochemical model. Geoderma 159, 440–451. http://dx.doi.org/10.1016/j.geoderma.2010.09.012.

Long, T., Or, D., 2007. Microbial growth on partially saturated rough surfaces: simulations in idealized roughness networks. Water Resources Research 43. http://dx.doi.org/10.1029/2005WR004781.

Manzoni, S., Katul, G., 2014. Invariant soil water potential at zero microbial respiration explained by hydrological discontinuity in dry soils. Geophysical Research Letters 41, 7151–7158. http://dx.doi.org/10.1002/2014GL061467.

Manzoni, S., Schaeffer, S.M., Katul, G., Porporato, A., Schimel, J.P., 2014. A theoretical analysis of microbial eco-physiological and diffusion limitations to carbon cycling in drying soils. Soil Biology and Biochemistry 73, 69–83. http://dx.doi.org/10.1016/j.soilbio.2014.02.008.

Manzoni, S., Schimel, J.P., Porporato, A., 2012. Responses of soil microbial communities to water stress: results from a meta-analysis. Ecology 93, 930–938.

McClain, M.E., Boyer, E.W., Dent, C.L., Gergel, S.E., Grimm, N.B., Groffman, P.M., Hart, S.C., Harvey, J.W., Johnston, C.A., Mayorga, E., McDowell, W.H., Pinay, G., 2003. Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. Ecosystems. http://dx.doi.org/10.1007/s10021-003-0161-9.

Miller, A., Schimel, J., Meixner, T., Sickman, J., Melack, J., 2005. Episodic rewetting enhances carbon and nitrogen release from chaparral soils. Soil Biology and Biochemistry 37, 2195–2204. http://dx.doi.org/10.1016/j.soilbio.2005.03.021.

Moyano, F.E., Manzoni, S., Chenu, C., 2013. Responses of soil heterotrophic respiration to moisture availability: an exploration of processes and models. Soil Biology and Biochemistry 59, 72–85. http://dx.doi.org/10.1016/j.soilbio.2013.01.002.

Navarro-García, F., Casermeiro, M.Á., Schimel, J.P., 2012. When structure means conservation: effect of aggregate structure in controlling microbial responses to rewetting events. Soil Biology and Biochemistry 44, 1–8. http://dx.doi.org/10.1016/j.soilbio.2011.09.019.

Parkin, T.B., 1987. Soil microsites as a source of denitrification variability. Soil Science Society of America Journal 51 (5), 1194.

Schimel, J., Balser, T.C., Wallenstein, M., 2007. Microbial stress-response physiology and its implications for ecosystem function. Ecology. http://dx.doi.org/10.1890/06-0219.

Schimel, J.P., Bennett, J., 2004. Nitrogen mineralization: challenges of a changing paradigm. Ecology. http://dx.doi.org/10.1890/03-8002.

Schimel, J.P., Weintraub, M.N., 2003. The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: a theoretical model. Soil Biology and Biochemistry 35, 549–563. http://dx.doi.org/10.1016/S0038-0717(03)00015-4.

Skopp, J., Jawson, M.D., Doran, J.W., 1990. Steady-state aerobic microbial activity as a function of soil water content. Soil Science Society of America Journal 54 (6), 1619.

Stark, J.M., Firestone, M.K., 1995. Mechanisms for soil moisture effects on activity of nitrifying bacteria. Applied and Environmental Microbiology 61, 218–221.

Throop, H., Archer, S., 2009. Resolving the dryland decomposition conundrum: some new perspectives on potential drivers. Progress in Botany 171–194.

Tinker, P.B., Nye, P.H., 2000. Solute Movement in the Rhizosphere. Oxford University Press, USA.

Van Gestel, M., Merckx, R., Vlassak, K., 1993. Microbial biomass responses to soil drying and rewetting: the fate of fast- and slow-growing microorganisms in soils from different climates. Soil Biology and Biochemistry. http://dx.doi.org/10.1016/0038-0717(93)90249-B.

Van Oijen, M., Rougier, J., Smith, R., 2005. Bayesian calibration of process-based forest models: bridging the gap between models and data. Tree Physiology 25, 915—927. http://dx.doi.org/10.1093/treephys/25.7.915.

Vogel, C., Mueller, C.W., Höschen, C., Buegger, F., Heister, K., Schulz, S., Schloter, M., Kögel-Knabner, I., 2014. Submicron structures provide preferential spots for carbon and nitrogen sequestration in soils. Nature Communications 5, 2947. http://dx.doi.org/10.1038/ncomms3947.

Wang, G., Or, D., 2010. Aqueous films limit bacterial cell motility and colony expansion on partially saturated rough surfaces. Environmental Microbiology 12, 1363—1373. http://dx.doi.org/10.1111/j.1462-2920.2010.02180.x.

Weimar, J., 1997. Cellular automata for reaction-diffusion systems. Parallel Computing 23, 1699—1715. http://dx.doi.org/10.1016/S0167-8191(97)00081-1.

Weimar, J.R., Boon, J.-P., 1993. A new class of cellular automata for reaction-diffusion systems. Physical Review E 49, 4.

West, S.A., Diggle, S.P., Buckling, A., Gardner, A., Griffin, A.S., 2007. The social lives of microbes. Annual Review of Ecology, Evolution, and Systematics. http://dx.doi.org/10.1146/annurev.ecolsys.38.091206.095740.

Whitford, W., Meentemeyer, V., Seastedt, T., 1981. Exceptions to the AET model: deserts and clear-cut forest. Ecology 62, 275—277.

Xiang, S.-R., Doyle, A., Holden, P.A., Schimel, J.P., 2008. Drying and rewetting effects on C and N mineralization and microbial activity in surface and subsurface California grassland soils. Soil Biology and Biochemistry 40, 2281—2289. http://dx.doi.org/10.1016/j.soilbio.2008.05.004.