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Romain Barnard, Steven Blazewicz, Mary Firestone

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## Rewetting of soil: revisiting the origin of soil CO<sub>2</sub> emissions

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Romain L. Barnard<sup>1\*</sup>, Steven J. Blazewicz<sup>2</sup>, Mary K. Firestone<sup>3</sup>

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<sup>1</sup> Agroécologie, AgroSup Dijon, INRAE, Univ. Bourgogne, Univ. Bourgogne Franche-Comté,

9

F-21000 Dijon, France

10

11

<sup>2</sup> Lawrence Livermore National Laboratory, 7000 East Avenue, Livermore, CA 94550, USA

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<sup>3</sup> Department of Environmental Science, Policy and Management, University of California,

14

Berkeley, 140 Mulford Hall, Berkeley CA 94720, USA

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\*Corresponding author:

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Romain Barnard, [romain.barnard@inrae.fr](mailto:romain.barnard@inrae.fr), phone +33 380 69 37 45

20 **Abstract**

21

22 Rewetting dry soils is associated with a burst of microbial activity and mineralization,  
23 which manifests itself as a pulse in soil CO<sub>2</sub> emissions, long-known as the Birch effect. In  
24 arid and semi-arid systems, soil CO<sub>2</sub> losses upon rewetting at the end of extended dry  
25 periods can contribute a significant fraction to the overall carbon (C) budget. Microbial  
26 biomass is one of the sources of mineralized C, as was demonstrated over 30 years ago  
27 (Kieft et al., 1987). The present paper offers a perspective on how the field has  
28 progressed since the 1987 paper was published in *Soil Biology & Biochemistry*, what it  
29 means in terms of current concerns about global climate change, and the needs and  
30 potential emphases of future research. Many studies since 1987 have addressed the  
31 origin of this CO<sub>2</sub> pulse, finding multiple possible C sources involving both biotic and  
32 abiotic processes. We propose that the magnitude of the rewetting event ( $\Delta\psi$ )  
33 determines the relative contribution from the array of substrates that contribute to the  
34 soil CO<sub>2</sub> pulse upon rewetting. The magnitude of the CO<sub>2</sub> pulse is likely related to soil  
35 physical characteristics and to the size of the available C pool, which is partly controlled  
36 by plants. Further, the relative contributions of the mechanisms generating soil CO<sub>2</sub>  
37 pulses upon rewetting are likely to be modified by climate change. To understand and  
38 predict the magnitude of soil CO<sub>2</sub> pulses upon rewetting, we advocate continued cross-  
39 disciplinary research involving soil microbial ecology, soil physics, soil chemistry, as  
40 well as increased integration and recognition of the importance of plant-soil interactions  
41 in controlling the soil C pools contributing to soil CO<sub>2</sub> pulses.

## 42 **Introduction**

43

44           The ecology of soil rewetting is especially relevant to drylands, which include arid,  
45 semi-arid and dry sub-humid subtypes. Drylands represent 45% of terrestrial surface (i.e.  
46  $66.7 \times 10^6 \text{ km}^2$ ) and carry 39% of the world population (Prävălie, 2016; Huang et al., 2017;  
47 Plaza et al., 2018). Soil wet-up is particularly important for terrestrial ecosystems in  
48 Mediterranean and savanna climates that experience sustained periods of very low or no  
49 rainfall, followed by significant rainfall. Mediterranean climates (dry summers and wet  
50 winters) occur between  $30^\circ$  and  $45^\circ$  latitude and are found in Africa, Europe, western  
51 South America, Southwest and West Australia, and western North America, for a total area  
52 of  $\sim 3 \times 10^6 \text{ km}^2$ . Savanna climates occur between  $25^\circ$  and  $30^\circ$  latitude, and include  
53 almost half the surface of Africa, large areas of Central & South America, eastern India,  
54 southeast Asia, eastern and northern Australia, totaling  $\sim 33 \times 10^6 \text{ km}^2$ .

55           Rewetting of dry soil can have global consequences. At the ecosystem scale it  
56 results in a large soil  $\text{CO}_2$  efflux pulse, also known as the Birch effect, named after H.F.  
57 Birch who reported mineralization peaks upon rewetting soils in East Africa (Birch,  
58 1958). However, the phenomenon had already been documented 35 years earlier by soil  
59 microbiologists (Waksman and Starkey, 1923; Winogradsky, 1924). Its putative  
60 mechanisms at the soil microbial scale started gaining attention in the 1980s (Bottner,  
61 1985). The sudden increase in microbial activity upon rewetting triggers a burst in carbon  
62 (C) and nitrogen (N) mineralization (Miller et al., 2005; Xiang et al., 2008; Boriken and  
63 Matzner, 2009; Dijkstra et al., 2012). The amount of C emitted due to rain pulses is  
64 comparable in magnitude to the net annual  $\text{CO}_2$  exchange of many terrestrial ecosystems  
65 (Xu et al., 2004). In ecosystems that are characterized by distinct dry-wet seasons, the  $\text{CO}_2$   
66 pulses associated with rewetting can represent a large part of the annual C budget (Jarvis

67 et al., 2007; Ma et al., 2012; Rey et al., 2017). For example, following intense rainfall, up  
68 to 20 % of the annual CO<sub>2</sub> flux from soil to atmosphere occurred in an African savanna  
69 ecosystem (Fan et al., 2015). While a rapid change in soil water potential results in an  
70 overall microbial reactivation, it exposes soil microorganisms to a radical change in  
71 environmental conditions. The soil dry-down and subsequent rewetting provide such an  
72 extreme change in microbial environment, that bacterial and fungal death commonly  
73 results (Blazewicz et al., 2014; Blazewicz et al., 2020).

74         The 1987 study by Kieft et al. was designed to investigate the fate of soil microbial  
75 biomass C after the rapid rewetting of a dry soil. Using two Californian soils from a  
76 Mediterranean-type climate, Kieft and his colleagues found a net loss of microbial biomass  
77 C upon rewetting, that could be due to the death of microbial cells or the rapid  
78 decomposition of the microbial solutes; the authors favoured the latter explanation.  
79 Mechanisms of C loss, the nature of the lost C, and changes in microbial community  
80 composition or relation to biogeochemical functioning were not investigated. However,  
81 by opening the microbial 'black box' in the general context of dry-wet cycles, this study  
82 brought attention to the large influence that rapid increases in soil water content can  
83 exert on microbial and terrestrial ecosystem functioning. Exploration of the processes  
84 comprising the Birch effect has been a particularly active field of research lately, as global  
85 change impacts precipitation cycles worldwide. In many regions, especially under  
86 Mediterranean climates, more extreme climate conditions increase the contrast between  
87 dry and wet conditions to which ecosystems are exposed. It has been more than three  
88 decades since the Kieft et al. study was published; here we provide a perspective on the  
89 current status of the field, its importance in the context of global change, and areas in need  
90 of more research.

91

92 **What is wet-up and where does it occur?**

93           We use the term wet-up to describe a real or simulated precipitation input of liquid  
94 water to dry soil causing a large and rapid change in soil water potential ( $\Delta\psi$ ). The  
95 magnitude of the change in water potential is a determinant of the size of the resulting  
96 soil CO<sub>2</sub> efflux pulse (Lado-Montserrat et al., 2014). Here we suggest that the addition of  
97 liquid water to a very dry soil causes CO<sub>2</sub> pulses that differ not only in rate/magnitude but  
98 also in available carbon sources and impact on microbial physiology and survival  
99 depending on the magnitude of the water potential increase. Since soil wet-up includes a  
100 prominent biological component, we focus on the biologically active zone of the soil, i.e.  
101 between 0 and ~50 cm depth; this zone can experience rapid rewetting from very dry  
102 conditions, depending on presence of macropores, surface cracking, and soil texture.  
103 While we will not concentrate on other inputs of moisture in this article, it is important to  
104 note that in arid and semi-arid ecosystems, several other processes can introduce  
105 moisture to dry surface soil. For example, surface litter decomposition occurs in response  
106 to fog and dew events and even as a result of high relative humidity, particularly in  
107 combination with UV-mediated degradation of exposed surface litter (Dirks et al., 2010;  
108 Jacobson et al., 2015). Adsorption of water from atmospheric humidity has been  
109 demonstrated to extend into soil (perhaps to a depth of 5 cm) over a range of atmospheric  
110 relative humidity (20-60%) and to stimulate CO<sub>2</sub> production (McHugh et al., 2015). Thus,  
111 transient episodes of decomposition at or near the soil surface occur in arid and semi-arid  
112 ecosystems in response to non-precipitation events (fog, dew, sorption from atmospheric  
113 humidity) and can drive CO<sub>2</sub> fluxes that are significant in ecosystem C budgets (Dirks et  
114 al., 2010). Recognition and understanding of the importance of these alternative means of  
115 increasing soil moisture (non-rainfall) has developed over the past 30 years and are  
116 important advances in the subject.

117 We present a perspective that primarily addresses rewetting dynamics of soil near  
118 the soil surface and in the rooting zone of shallow-rooted plants. Under laboratory  
119 conditions, drying-rewetting cycles resulted in the release of “old” C from soil layers  
120 below 20 cm (Schimel et al., 2011). While macropore flow of incident rain water might  
121 result in the wet-up of soil deeper than 20 cm, rapid rewetting of soil by rainfall will be  
122 most important near the surface of soil and generally play a less important role in the  
123 mobilization of deep old soil carbon.

124

### 125 **C released upon rewetting: origin and mechanisms**

126 The CO<sub>2</sub> pulse upon rewetting typically exhibits a pattern of very high rates during  
127 the first minutes and hours after rewetting and this response declines over time (Kim et  
128 al., 2012). The origin of the CO<sub>2</sub> pulse upon rewetting soil can be both abiotic and biotic.  
129 Abiotic processes include solubilization of carbonates (depending on carbonate  
130 concentration in soils), CO<sub>2</sub> displacement from the soil pores to the atmosphere by water,  
131 as well as the quantitatively low degassing of CO<sub>2</sub> dissolved in rain and soil degassing due  
132 to the decrease in barometric pressure over time (Lee et al., 2004; Barnard et al., 2015).  
133 However, in non-carbonate-rich soils, abiotic processes generate less CO<sub>2</sub> than do the  
134 biotic processes, which are the main contributors of the soil CO<sub>2</sub> pulse upon rewetting.  
135 The nature and sources of the C compounds that are mineralized upon rewetting a dry  
136 soil has been extensively explored and somewhat fervently argued. Here we highlight the  
137 most prevalent sources and mechanisms that fuel the C mineralization pulse: compatible  
138 solutes; microbial necromass; changes in water film connectivity; sustained extracellular  
139 enzyme activity during dry-down; C desorption from mineral surfaces; and disruption of  
140 aggregates. Each of these is discussed below.

141 Compatible solutes, accumulated by microbial cells in response to drying, were  
142 suggested by Kieft et al. (1987) as candidate compounds fueling the soil CO<sub>2</sub> efflux pulse;  
143 this substrate pool was also addressed by later studies (Halverson et al., 2000; Fierer and  
144 Schimel, 2003; Schimel et al., 2007). Soil microorganism accumulation of compatible  
145 solutes within their membrane-bound cells reduces cell dehydration, but cells are  
146 required to rapidly dispose of them upon rewetting, or face membrane rupture  
147 (plasmolysis). These processes will release solutes, such as proline, glutamine, glycine  
148 betaine, and trehalose into the soil (Kempf and Bremer, 1998; Halverson et al., 2000;  
149 Welsh, 2000; Warren, 2019) and these can be assimilated and mineralized rapidly by  
150 other microorganisms. Some of the earlier studies focusing on the intracellular  
151 accumulation of compatible solutes as soil gets drier, found no evidence for osmolytes as  
152 a significant C-source (Boot et al., 2013; Kakumanu et al., 2013). More recent evidence  
153 (Warren, 2014; Warren, 2016) for this mechanism however provides some support.  
154 While some studies detected no increased amount of compatible solutes in the soil upon  
155 rewetting (Williams and Xia, 2009; Warren, 2014), recent studies have reported an  
156 accumulation of osmolytes in microbial communities during dry periods (Chowdhury et  
157 al., 2019; Malik et al., 2019; Slessarev et al., 2020). The elusive nature of osmolytes may  
158 be related to: (i) their low residence time in the soil, as they are produced and consumed  
159 at measurable rates even in moist soils (Warren, 2019), albeit at lower rates than in dry  
160 soils (Warren et al, unpubl. data); and (ii) their probable specificity to a microbial  
161 community. Some microbes may not accumulate compatible solutes and instead undergo  
162 passive water loss, especially under conditions of rapid drying (Potts, 1994). Possible  
163 fates of these plasmolyzed cells are death from water loss, death upon rewetting, or  
164 survival of both desiccation and re-wetting.

165



166           Microbial death due to the rapid water potential increase (from very negative  
167 values to zero or nearly zero) upon rewetting was also invoked by Kieft et al. (1987) as a  
168 possible source of C substrates. Dead microbial cells can provide mineralizable substrates  
169 upon rewetting a dry soil, arising from cells that died during the previous dry-down  
170 period or as a direct result of the rewetting. Evidence for this mechanism has been  
171 presented by measuring gross rates of bacterial death and growth upon rewetting  
172 (Blazewicz et al., 2014; Blazewicz et al., 2020). High bacterial mortality was documented  
173 to have occurred within the first three hours after a rewetting event. The authors noted  
174 that some of the mortality is likely to have occurred during the dry-down process but the  
175 microbial necromass remained largely intact until the wet-up event.

176           Bacteriophage predation may also contribute to cell death after rewetting. Phages  
177 infect a large proportion of soil bacteria (Williamson et al., 2007) and can become lytic  
178 when soil conditions become favorable for the growth of their hosts (Williamson et al.,  
179 2017). Indeed, viral abundance in the soil has been shown to be correlated with soil water  
180 content (Williamson et al., 2005), possibly due to the effects of soil water content on  
181 bacterial numbers as well as on the adsorption of viruses in the soil (Zhao et al., 2008).  
182 Viral diffusion/advection is also enhanced by soil wetting, increasing the chances of virus-  
183 host encounter and attachment. At this time, however, there is no direct evidence for wet-  
184 up-associated predation as a significant mechanism of cell death and labile C input.  
185 Similarly, eukaryotic predation may contribute to microbial mortality upon soil wetting,  
186 but, to our knowledge, this has not been demonstrated.

187           Upon rewetting a dry soil, microorganisms have to access and then metabolize  
188 organic substrates. Connectivity of soil water films is gradually lost as soils dry and this  
189 restricts diffusional access to substrate (Manzoni et al., 2012) but enhances bacterial  
190 coexistence and diversity (Carson et al., 2010) by limiting competitive exclusion (Wang

191 and Or, 2013; Štoviček et al., 2017b). Conversely, rewetting a soil restores water film  
192 connectivity (Smith et al., 2017), providing conditions for highly competitive and mobile  
193 microorganisms to access substrates and to thrive, thereby generating a soil CO<sub>2</sub> efflux  
194 pulse (see modelling study by Evans et al., 2016).

195 Another possible source of substrates during rewetting requires sustained  
196 extracellular enzyme activity during dry-down (Miller et al., 2005; Schimel et al., 2017).  
197 The reduction in microbial activity as soils dry can lead to a net increase in substrate that  
198 may become available to soil microorganisms upon rewetting (Lawrence et al., 2009;  
199 Zhang et al., 2014; Fraser et al., 2016). However, a recent study found no evidence for  
200 sustained exoenzyme activity in drying soils (Homyak et al., 2018).

201 Soluble organic compounds in the soil can associate with minerals, particularly  
202 during dry periods (Qualls, 2000). Upon rewetting, the desorption of organic compounds  
203 from mineral surfaces can become a source of C (Blankinship and Schimel, 2018) as  
204 changes in pH and ionic strength can directly affect organic matter-mineral binding  
205 (Clarke et al., 2011; Newcomb et al., 2017).

206 In dryland ecosystems, photodegradation of surface litter increases the  
207 breakdown of carbon compounds to substrates that can be metabolized by  
208 microorganisms upon rewetting (Austin and Vivanco, 2006; Baker and Allison, 2015; Day  
209 et al., 2018). Although photodegradation alone cannot explain differences in  
210 decomposition rates across an aridity gradient (Brandt et al., 2010), it enhances soil CO<sub>2</sub>  
211 emissions upon soil rewetting (Ma et al., 2012).

212 Disruption of organic matter occlusion in soil aggregates is another physical  
213 consequence of rewetting that can enhance substrate availability. Rewetting a dry soil can  
214 break up aggregates, exposing organic substrates that were previously occluded (Denef

215 et al., 2001a; Cosentino et al., 2006; Borken and Matzner, 2009; Navarro-García et al.,  
216 2012).

217 Modeling has provided solid insight into the mechanisms that drive the soil CO<sub>2</sub>  
218 pulse associated with rewetting. Most modeling studies have focused on the sources of  
219 soil organic matter at a large scale (Lawrence et al., 2009) and were not designed to take  
220 into account the biophysical mechanisms at the pore-scale. The gap between pore physics,  
221 soil organic matter cycling and microbiology has been bridged, using empirical models  
222 and simplified model systems (Moyano et al., 2013; Manzoni et al., 2016; Tecon and Or,  
223 2017), yet challenges remain (Baveye et al., 2018). Recent modeling efforts support the  
224 coexistence of physical as well as microbiological processes as drivers of the rewetting  
225 soil CO<sub>2</sub> pulse (Zhang et al., 2014; Evans et al., 2016; Šťovíček et al., 2017b; Yan et al.,  
226 2018).

227 The question of which C sources fuels the Birch effect has been under discussion  
228 for many decades. It is an important topic in the context of global change, as rainfall  
229 patterns and amounts change in areas around the globe, potentially impacting the C  
230 budget of ecosystems (Kim et al., 2012; Vargas et al., 2012).

231

### 232 **Soil microbial response**

233 Ascribing the CO<sub>2</sub> released upon rewetting to a particular source of C can be akin  
234 to the Indian parable of six blind men examining an elephant, each of them failing to  
235 consider the multiple facets of the objective truth while experiencing it from their own  
236 limited perspective. Many C sources contribute to the soil CO<sub>2</sub> pulse upon rewetting  
237 (Unger et al., 2010; Evans et al., 2016). Apart from carbonate solubilization, CO<sub>2</sub> emissions  
238 from the soil upon rewetting are driven by coupled biophysical or biochemical

239 mechanisms, in which soil microorganisms act as catalysts, conditional upon whether or  
240 not they have access to substrate.

241         In arid and semi-arid systems, adaptation to cyclic dry-down and rewetting  
242 enables soil functions to be carried out under alternating contrasting environmental  
243 conditions. Soil microorganisms seem to have evolved life strategies related to prolonged  
244 dry periods followed by rapid rewetting (Placella et al., 2012; Barnard et al., 2013; Evans  
245 and Wallenstein, 2014). At the seasonal scale, microbial strategies during dry-down differ  
246 from strategies during rewetting (Evans et al., 2014). Soil microorganisms that are able  
247 to sustain activity longer as soils dry down may access easily degradable organic matter  
248 under less intense competitive conditions, while the other microorganisms that are not  
249 able to maintain activity under dry conditions have already entered a state of reduced  
250 activity, or even dormancy (including formation of spores). This mechanism could  
251 support the existence of taxa (e.g. bacteria belonging to the Sphingomonadaceae,  
252 Comamonadaceae and Oxalobacteraceae; Aanderud et al., 2015) that are present in low  
253 relative abundance in the soil (Lennon and Jones, 2011; Meisner et al., 2018). The  
254 duration of the dry period can affect the response to subsequent rewetting (Barnard et  
255 al., 2015), especially in microbial communities that have not evolved in contrasting dry-  
256 wet conditions (Meisner et al., 2015; Meisner et al., 2017). For example, in soils where  
257 microbes are not adapted to drought or cyclic dry periods, a lag period before exponential  
258 microbial growth has been detected, the duration of which depended on the intensity of  
259 drying (Meisner et al., 2017). Indeed, altered precipitation patterns before rewetting  
260 impacted not only the community structure of the microorganisms that were active upon  
261 rewetting, but also of those that were not, as they were recruited into the active bacterial  
262 pool (Engelhardt et al., 2019).

263           The importance of microbial death as a source of C for the CO<sub>2</sub> pulse has been  
264 measured using quantitative <sup>18</sup>O stable isotope probing. Upon rewetting a soil from a  
265 Mediterranean climate, initial bacterial growth was detected in select taxa dominated by  
266 Proteobacteria (*Azotobacter*, *Pseudomonas*, *Vibrio*) and Firmicutes (*Streptococcus*,  
267 *Clostridium*, *Mycoplasma*) while mortality was taxonomically widespread (Blazewicz et  
268 al., 2020). In addition, the density-dependence of growth upon rewetting contrasted with  
269 density independence of mortality, supporting the hypothesis that population-level  
270 biological interactions, such as competition and predation, likely controlled the growth  
271 rates of taxa but not their death (Blazewicz et al., 2020).

272

273           A number of studies have shown differential sensitivity of soil bacterial taxa to dry-  
274 down and rewetting; this differential sensitivity is conserved at phylum and class  
275 phylogenetic groupings (Lennon et al., 2012; Placella et al., 2012; Barnard et al., 2013,  
276 2015; Engelhardt et al., 2018). This phylogenetic coherence reflects the evolutionary  
277 roots of microbial tolerance to drying and rewetting in microorganisms that are  
278 indigenous to and more common in semi-arid soil systems. The functional response of  
279 arid and semi-arid systems to dry-wet cycles can thus be expected to be deterministic and  
280 predictable (Averill et al., 2016). The two flagship phyla are Actinobacteria, which are  
281 commonly abundant in arid soils and include many taxa that are resistant to low moisture  
282 conditions (Goodfellow and Williams, 1983; Zvyagintsev et al., 2007) and Acidobacteria,  
283 a versatile group that can be adapted to changing environments (Eichorst et al., 2018);  
284 taxa from the Acidobacteria group have been found to dynamically track soil water  
285 conditions, flourishing rapidly upon rewetting (Placella et al., 2012; Barnard et al., 2013).  
286 Dry-down typically increases the relative abundance of the present or potentially active  
287 thick-walled, Gram-positive, high G+C content, spore-forming, and EPS-producing

288 bacterial groups (e.g. Actinobacteria, Firmicutes) but decreases that of thin-walled, Gram-  
289 negative or fast-growing groups such as Acidobacteria, Verrucomicrobia or Chloroflexi  
290 (Placella et al., 2012; Angel and Conrad, 2013; Barnard et al., 2013; Maestre et al., 2015;  
291 Zhou et al., 2016; Šťovíček et al., 2017a; Ochoa-Hueso et al., 2018). Upon rewetting,  
292 different bacterial groups respond on a variable timeframe that likely reflects their ability  
293 to have formed spores during the dry period, thus being potentially ready for a quick  
294 response and rapid growth (Keijser et al., 2007; Placella et al., 2012; Barnard et al., 2013;  
295 Sinai et al., 2015). Taxon-specific growth documented by quantitative stable isotope  
296 probing has shown that members of the Bacillales order of Firmicutes grew within 3h of  
297 rewetting a dry Mediterranean soil, followed in the first 24h by  $\beta$ -proteobacteria of the  
298 Burkholderia order (Blazewicz et al., 2020). Fungi generally display an overall greater  
299 resistance to desiccation-hydration cycles than bacteria (Bapiri et al., 2010; Curiel Yuste  
300 et al., 2011; Barnard et al., 2015), likely due to their hyphal network structure and  
301 frequent mutualistic strategies (de Boer et al., 2005), which complement other drought-  
302 resistance traits that can also be found in bacteria, such as production of extracellular  
303 polymeric substances (EPS) and heat-shock proteins (Crowther et al., 2014). As a  
304 consequence, the fungal community displays a higher stability than the overall bacterial  
305 community during dry-down and subsequent rewetting (de Vries et al., 2018).

306         In temperate climates, contrasting dry and wet conditions arise during a period of  
307 drought, i.e. water limitations outside the normal climatic envelope. Since the temperate  
308 soil biosphere may not be well-adapted to these extreme conditions, its response to  
309 drying and rewetting is expected to be more stochastic and less predictable than that of  
310 highly-adapted arid and semi-arid systems, although a trait-based phylogenetic  
311 framework could help predict microbial responses (Lennon et al., 2012; Amend et al.,  
312 2016). Drought legacy experiments have shown that in some systems having been

313 exposed to past drought conditions can shape the response of soil microbial communities  
314 to subsequent drought or rewetting (Bouskill et al., 2013; Göransson et al., 2013; Hawkes  
315 et al., 2017; Meisner et al., 2018), with consequences that can extend to soil processes  
316 (Evans and Wallenstein, 2012; Martiny et al., 2017) as well as plant communities (Lau and  
317 Lennon, 2012; Meisner et al., 2013; Kaisermann et al., 2017).

318         The intensity and duration of dry conditions determine the response of soils to  
319 rewetting (Zhang et al., 2019). After a severe dry period, soil rewetting triggers a larger  
320 CO<sub>2</sub> pulse (Xu et al., 2004; Cable et al., 2008; Göransson et al., 2013; Barnard et al., 2015),  
321 which is consistent with a greater loss of C in carbon-rich ecosystems that experience  
322 more pronounced dry-wet events (Canarini et al., 2017). Under extreme conditions (i.e.  
323 dry soil for a long period of time or large  $\Delta\psi$ ), maintaining metabolic functions upon  
324 rewetting may become more challenging than under more favorable conditions and there  
325 may be a greater frequency of microbial death and subsequent larger relative  
326 contribution of compatible solutes to the soil CO<sub>2</sub> pulse. However, the speed of dry-down  
327 should also be considered. When dry-down is slow, more compatible solutes accumulate  
328 in the soil relative to depolymerization products generated by exoenzymes (Warren,  
329 2016). In addition, microbial production of extracellular polymeric substances (EPS),  
330 such as exopolysaccharides, can both retain water during soil drying and slow down  
331 rewetting of the habitats of microbial cells. (Roberson and Firestone, 1992).

332         Maximum compatible solute concentration in soil microbes occurred at relatively  
333 high  $\psi$  (-5 MPa) under slow dry-down conditions (Warren, 2016), compared to the  
334 estimated -14 MPa at which microbial activity ceases in the soil (Manzoni et al., 2012).  
335 Thus, compatible solute accumulation can only protect indigenous soil organisms from  
336 dry down events of limited magnitude.

337           The physical effects of rewetting on soil aggregates are expected to become  
338 relevant once the point at which large soil aggregates become disrupted is reached (Lado-  
339 Montserrat et al., 2014). Rewetting aggregates with a large  $\Delta\psi$  would enable access to C  
340 pools that were previously inaccessible, i.e. occluded organic matter. How big an upshock,  
341 i.e. the size of  $\Delta\psi$ , is required to access occluded organic matter? As water travels down  
342 the soil profile, the vapor phase front likely influences microbial cell metabolism, but  
343 liquid water is required to disrupt soil aggregates. Does the disruption threshold depend  
344 on the size of  $\Delta\psi$  or is it an absolute threshold of  $\psi$  (i.e. soil water potential falling below  
345 the threshold during dry-down and rising above it upon rewetting)? While the dryness  
346 reached by the soil can play a role, the size of  $\Delta\psi$  seems to be the most relevant parameter  
347 (Xu et al., 2004; Chowdhury et al., 2011; Lado-Montserrat et al., 2014). Estimating this  
348 parameter could provide a metric of sensitivity of ecosystems to intense dry periods. Soil  
349 CO<sub>2</sub> emission rates before rewetting are significantly negatively correlated with the post-  
350 rewetting rates (Kim et al., 2012) and can be predicted from rewetting-related changes in  
351 soil moisture (Rey et al., 2017). Thus, the soil water content within the preceding years  
352 could possibly be used as a proxy to estimate the relative contribution of rewetting events  
353 to the overall C budget in systems that experience seasonally dry climatic conditions.  
354 Moreover, the speed of soil rewetting frames the impact of the event; this would depend  
355 on soil physico-chemical characteristics, among which texture (including preferential  
356 flow paths) and soil salinity are important (Cable et al., 2008; Chowdhury et al., 2011) as  
357 well as EPS content which can influence soil repellency as well as speed of rewetting  
358 (Seaton et al., 2019).

359           We propose that: (i) all the previously discussed substrates potentially contribute  
360 to soil CO<sub>2</sub> pulse upon rewetting, but that their relative contributions depend on climate,



361 soil type and magnitude of water potential upshock  $\Delta\psi$ ; and (ii) exceeding a threshold in  
362 dry-wet  $\Delta\psi$  is required to mobilize occluded organic matter (Fig. 1).

363

### 364 **Importance of plants**

365 Plants are the primary contributors to the quantity and quality of C entering soil  
366 and the size and composition of the available C pool controls the magnitude of the CO<sub>2</sub>  
367 pulse. Many of the studies investigating the nature of the C fueling the CO<sub>2</sub> pulse upon  
368 rewetting were undertaken in systems that were devoid of live plants at the time of  
369 rewetting (Borken and Matzner, 2009). This reflects the fact that wet-up studies, and the  
370  $\Delta\psi$  associated with substantial CO<sub>2</sub> pulses, require extremely dry soils, in which annual  
371 plants are generally no longer alive. However, the plants that were present during a  
372 growing period immediately preceding the dry-down may affect the microbial response  
373 to rewetting as: (i) labile C pools support CO<sub>2</sub> pulses ; (ii) above- and below-ground litter  
374 from semi-arid ecosystems can generate a large and labile pool of soil organic C that is  
375 present during the dry season ; and (iii) the presence of plants can impact the number and  
376 size of soil aggregates (Blankinship et al., 2016). Thus, plants may have been absent in  
377 many studies due either to the soil-centric focus of the researchers and the question, or  
378 due to the absence of living plants at the time of rewetting. For example, in Mediterranean  
379 systems the annual plant cover is often dead by the end of the dry season, when the first  
380 rains constitute the largest soil water potential upshocks.

381 Nevertheless, plants matter, whether dead or alive. Dry episodes can take place  
382 during the growing season without killing plant cover. In systems in which live plants are  
383 present, dry-wet cycling directly impacts plant-derived soil labile C inputs, both in their  
384 quantity, generally increasing exudation under moderate drought but having a more  
385 variable effect under intense drought (Preece and Peñuelas, 2016), and quality (Preece

386 and Peñuelas, 2016; Gargallo-Garriga et al., 2018), with consequences on ecosystem  
387 functioning (Oikawa et al., 2014; Canarini and Dijkstra, 2015; Williams and de Vries,  
388 2019). Dry-wet cycles can also affect plant N uptake, hydraulic redistribution (Fu et al.,  
389 2018) and trapping of windblown soil particles (Ravi et al., 2010), which all likely interact  
390 with major processes involved in the soil CO<sub>2</sub> pulse upon rewetting (Wang et al., 2015).  
391 Root exudation is of particular relevance, as it not only provides a direct labile C source  
392 for soil microorganisms, but can also contribute to shaping the root microbiome (Naylor  
393 and Coleman-Derr, 2017; Hartman and Tringe, 2019), a major driver of the soil CO<sub>2</sub> pulse  
394 upon rewetting.

395         Dry soils as well as those subject to infrequent watering events can hamper plant-  
396 microbial coupling by impeding the transfer of recent photo-assimilates from the roots to  
397 soil microorganisms (Ruehr et al., 2009; Fuchslueger et al., 2014; Engelhardt et al., 2018;  
398 Karlowsky et al., 2018). This may be due to reduced rhizodeposition rates (but see Preece  
399 and Peñuelas, 2016) or to challenging microbial access to rhizodeposits under diminished  
400 water film connectedness (Moyano et al., 2013; Fuchslueger et al., 2014; Tecon and Or,  
401 2016; von Rein et al., 2016; Karlowsky et al., 2018). The plant-microbial interaction  
402 component of the mechanisms underlying the soil CO<sub>2</sub> efflux pulse upon rewetting may  
403 also vary with depth (Engelhardt et al., 2018).

404         Few experiments have addressed rewetting events during the spring in  
405 Mediterranean systems, when the plants are still alive, actively growing and the high flux  
406 of rhizodeposits to the soil exerts a strong influence on soil microbial activity (Curiel Yuste  
407 et al., 2007; Ma et al., 2012). The seasonal component of microbial response to changes in  
408 water availability has been documented in several studies (Cruz-Martínez et al., 2009; Bell  
409 et al., 2014; Zhao et al., 2016). The plant-microbial interaction component of the soil CO<sub>2</sub>

410 pulse after rewetting may vary seasonally and experiments exploring rewetting after dry  
411 spring periods could provide a valuable perspective.

412 We propose that the origin of the C released upon soil rewetting (Fig. 2) is mainly  
413 controlled by three factors: the magnitude of the rewetting upshock ( $\Delta\psi$ ), soil physical  
414 characteristics, and ecosystem productivity (NEP). The  $\Delta\psi$  controls the pool of microbial-  
415 derived C, i.e. compatible solutes and dead cells. Soil physics controls pore connectivity,  
416 which in turn controls access to microbial- and plant-derived C. NEP controls the pool of  
417 plant-derived labile C which determines much of the soil enzyme pool.

418 Dry-wet cycles can impact soil C stabilization both positively and negatively  
419 (Bailey et al., 2019). A few dry-wet cycles increase the turnover of aggregates (i.e. as they  
420 are broken down then formed again), releasing inter-aggregate particulate organic matter  
421 and decreasing stabilization of fresh organic matter within the aggregate structure (Denef  
422 et al., 2001b). However, aggregates become slake-resistant with time, and more dry-wet  
423 cycles result in increased microaggregate stability (Denef et al., 2001a; Rahman et al.,  
424 2018). Dry-wet cycles increase microbial biomass C turnover, as microbial C lost through  
425 microbial death is replaced. Recent studies have proposed that enhanced microbial  
426 turnover under dry-wet cycles could result in an increased contribution of previously  
427 stable organic matter to microbial C (Lopez-Sangil et al., 2018; Schimel, 2018).

428

## 429 **Conclusion**

430 The large CO<sub>2</sub> pulse that is produced by rapid rewetting of very dry soil results  
431 from biological, physical and chemical mechanisms. The past 30+ years of research in this  
432 area provides an excellent example of integration across the subdisciplines of soil science.  
433 We suggest that significant future advances on the topic will be facilitated by greater  
434 inclusion and recognition of plant-microbe soil interactions.

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851 **Figure legends**

852

853 Figure 1. Proposed mechanisms fueling soil CO<sub>2</sub> efflux pulse upon rewetting.

854

855 Figure 2. Main drivers (gray) of the mechanisms releasing CO<sub>2</sub> upon rewetting a dry soil,

856 involving interactions between soil microorganisms (blue, center), plants (green, left) and

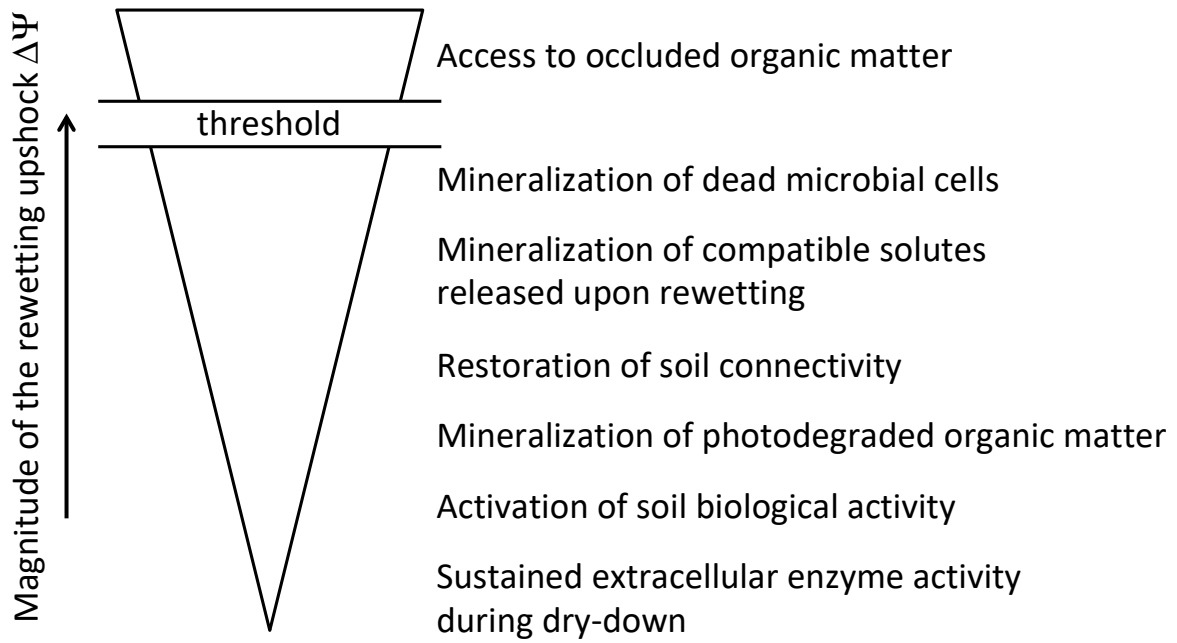
857 soil physico-chemical properties (red, right).



858 Figure 1

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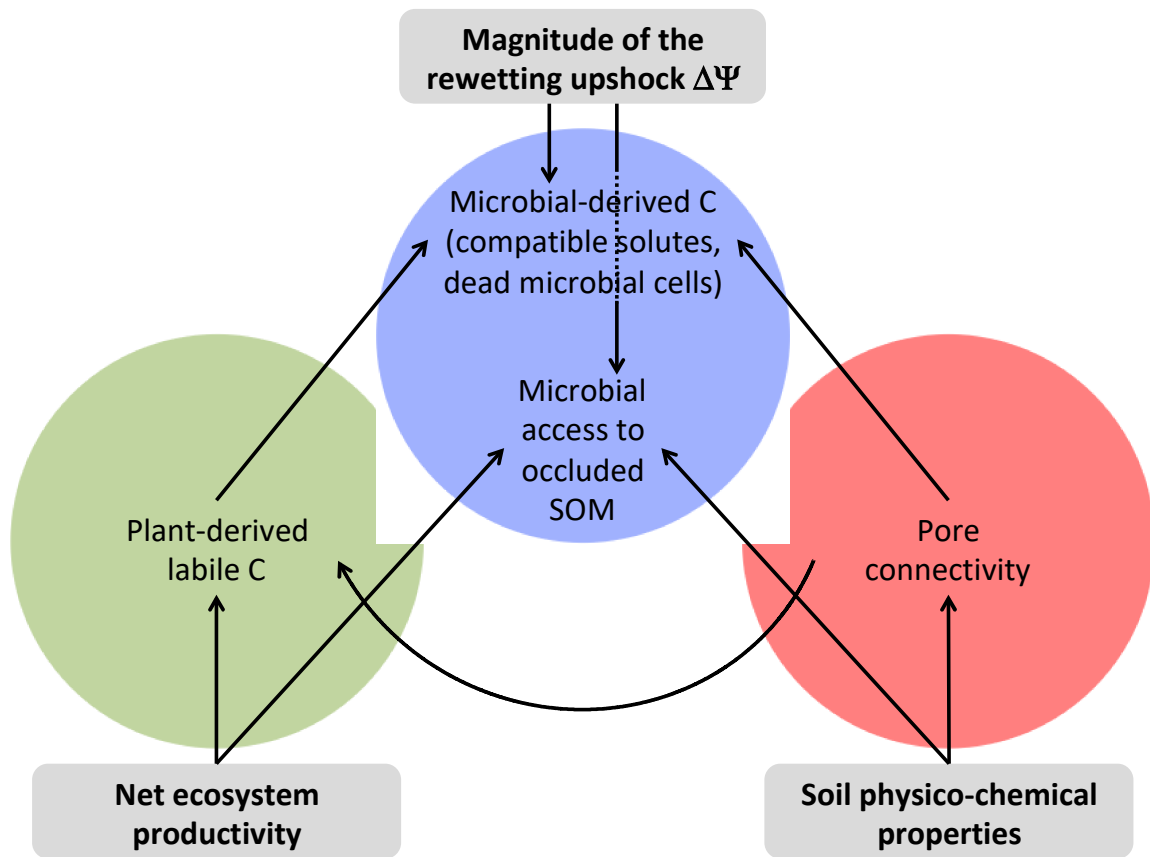
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862

863 Figure 2

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