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Rewetting of soil: revisiting the origin of soil CO₂ emissions

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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 CO₂ emissions, long-known as the Birch effect. In
24 arid and semi-arid systems, soil CO₂ 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 CO₂ 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 CO₂ pulse upon rewetting. The magnitude of the CO₂ 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 CO₂
37 pulses upon rewetting are likely to be modified by climate change. To understand and
38 predict the magnitude of soil CO₂ 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 CO₂ 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 (Prävālie, 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° and 45° 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° and 30° 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 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; Borke 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 CO_2 exchange of many terrestrial ecosystems
65 (Xu et al., 2004). In ecosystems that are characterized by distinct dry-wet seasons, the 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 CO₂ 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 CO₂ efflux pulse (Lado-Montserrat et al., 2014). Here we suggest that the addition of
97 liquid water to a very dry soil causes CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ pulse upon rewetting soil can be both abiotic and biotic.
129 Abiotic processes include solubilization of carbonates (depending on carbonate
130 concentration in soils), CO₂ displacement from the soil pores to the atmosphere by water,
131 as well as the quantitatively low degassing of CO₂ 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 CO₂ than do the
134 biotic processes, which are the main contributors of the soil CO₂ 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 CO₂ 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 CO₂ 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 CO₂
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 CO₂
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 CO₂ 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 CO₂ 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 CO₂ pulse upon rewetting
237 (Unger et al., 2010; Evans et al., 2016). Apart from carbonate solubilization, CO₂ 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 CO₂ pulse has been
264 measured using quantitative ¹⁸O 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 β -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 CO₂ 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 CO₂ 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 ψ (-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 ψ (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 CO₂ 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 CO₂ 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 CO₂
367 pulse. Many of the studies investigating the nature of the C fueling the CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂

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 CO₂ 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**

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853 Figure 1. Proposed mechanisms fueling soil CO₂ efflux pulse upon rewetting.

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855 Figure 2. Main drivers (gray) of the mechanisms releasing CO₂ upon rewetting a dry soil,

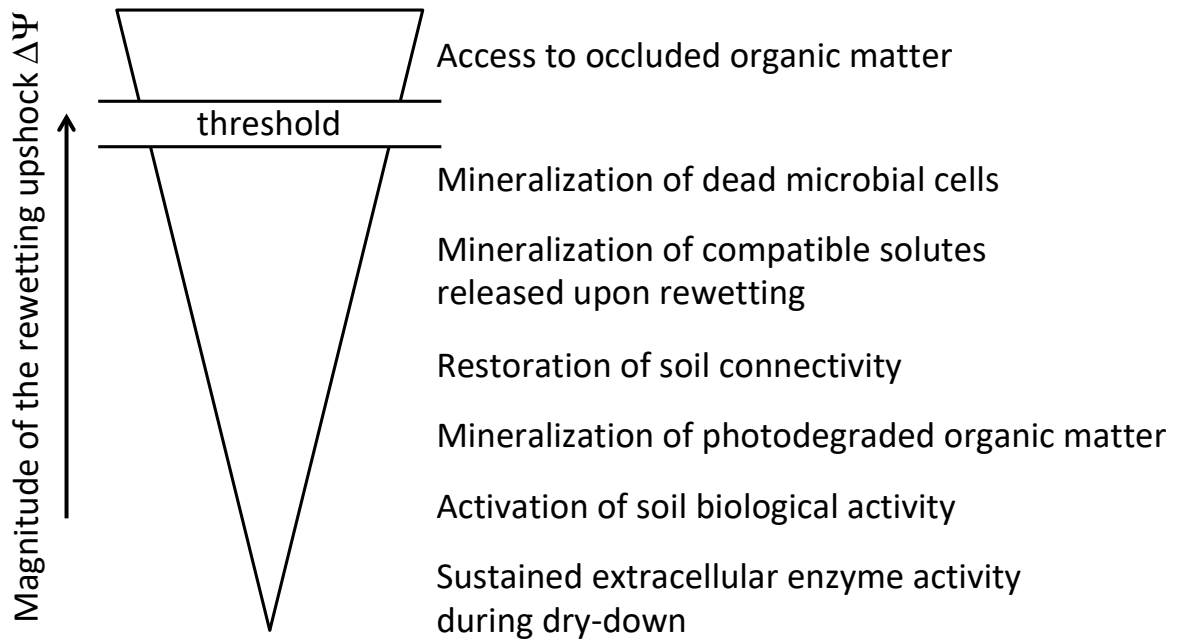
856 involving interactions between soil microorganisms (blue, center), plants (green, left) and

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

858 Figure 1

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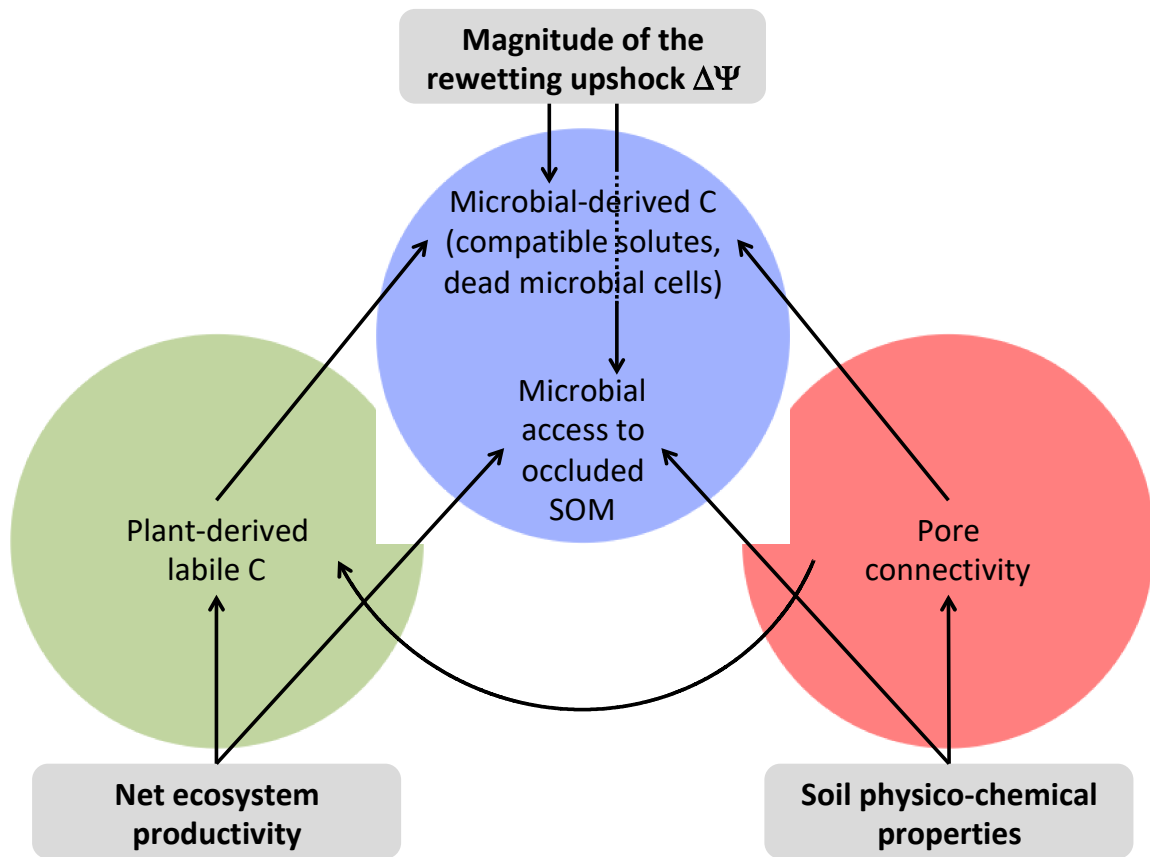
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863 Figure 2

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