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# The response of continental silicate rock weathering to the colonization of the continents by vascular plants in the Devonian

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**ABSTRACT.** The first forests appear on the continents during the Givetian stage of the Devonian. The fossil record shows that, by the end of the Devonian, vascular plants and forests were common and widespread in the wet lowlands. Although the impact of this major event on chemical weathering of the continents is reasonably known, the coeval change in physical erosion has never been explored. Here, we built a mathematical description of the coupled response of the physical erosion and chemical weathering on the continents, to the colonization by vascular plants over the course of the Devonian. This spatially-resolved erosion model is coupled to the GEOCLIM model to simulate the response of the global carbon and alkalinity cycles, and of climate, to the colonization phase. A set of simulations is described, assuming an increased weatherability of the continental surface, and a change in physical erosion which can be either a decrease or an increase in response to the spreading of vascular plants. We explore first the initial pre-colonization and the final post-colonization steady states of the surficial Earth system. Then, we simulate the transient states of the Earth system in response to theoretical randomized scenario for the colonization. We found that the pathways of the colonization have a major impact on the CO<sub>2</sub> history through the Devonian. Depending on the magnitude of the change in physical erodibility and chemical weatherability, and on the colonization scenario, atmospheric CO<sub>2</sub> evolution may display contrasting behavior: from a uniform CO<sub>2</sub> decrease over the Devonian, to more complex patterns characterized first by a global warming from the end of the Givetian into the Frasnian, and then by a final cooling, in first order agreement with the proxy data for CO<sub>2</sub> and reconstructed climate evolution.

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40

## 1. INTRODUCTION

41

### 1.1. *Devonian Atmospheric CO<sub>2</sub> and Plants*

42 In a seminal paper published in 1998, and following the mechanisms expounded in Algeo et al.  
43 (1995), Berner (1998) linked the atmospheric CO<sub>2</sub> decrease from the Early Devonian to the Late  
44 Carboniferous (Royer and others, 2007; Foster and other, 2017) to the colonization of the continents  
45 by the first vascular plants. Berner suggested that the development of deep roots resulted in a more  
46 efficient CO<sub>2</sub> consumption by silicate weathering through the mechanical breakdown of rocks and the  
47 production of respired CO<sub>2</sub> and organic acids in the soils. This activation of weathering would thus be  
48 driven by an increase in weatherability, which is defined as the product of the factors that affect rock  
49 chemical weathering other than climatic factors (air temperature and runoff, Kump and Arthur, 1997).  
50 This concept of weatherability is at the heart of the numerical models describing the evolution of the  
51 global carbon cycle at the geological timescale (Kump and Arthur, 1997; Berner, 2004, Lenton and  
52 others, 2018; Donnadieu and others, 2006; Royer and others, 2014; Joshi and others, 2019). It can be  
53 interpreted as a change in the strength of the negative feedback linking the weathering of the  
54 continental silicate rocks to the atmospheric CO<sub>2</sub> level (D'Antonio and others, 2020). Field studies  
55 confirm the existence of a weatherability change in the presence of plants (Moulton and others, 2000).  
56 The scenario of an enhanced weatherability during the Devonian is now largely accepted by the  
57 scientific community. For instance, Porder (2020) states that the spread of vascular plants drove a 40  
58 Myr decline in atmospheric CO<sub>2</sub> from 4000 ppmv to about 1000 ppmv.

59 Several recent studies raised concerns about the land plant scenario. Indeed, the timing of the  
60 colonization of the continents by vegetation has been re-evaluated. Molecular clock studies suggest  
61 that the colonization of the continents by primitive land plants started long before the Devonian, in the  
62 middle Cambrian or Early Ordovician (Morris and others, 2018), and microfossil evidence for the  
63 presence of land plants has been discovered in the Middle Ordovician (Rubinstein and others, 2010).  
64 However, there are no megafossils of bryophytes neither in the Ordovician nor in the Silurian (Driese  
65 and Mora, 2001; Edwards and others, 2015). Pre-Devonian fossil records show the existence of land  
66 plants limited in size (Edwards and others, 2015). Their potential impact on weathering processes  
67 remains difficult to assess. Microcosm laboratory experiments conducted on modern mosses suggest  
68 that bryophytes significantly enhance silicate weathering (Lenton and others, 2012). However, our  
69 poor knowledge of the spatial cover of Ordovician and Silurian bryophytes renders the extrapolation  
70 of such results at the global scale uncertain (Porada and others, 2016; Greb and others, 2006). These  
71 primitive plants were probably restricted to humid areas because of their homosporous reproduction  
72 necessitating free water for fertilization (Greb and others, 2006).

73 Whatever the impact of early bryophytes on the continental weatherability, a step increase in silicate  
74 rock weatherability must have followed the spread of vascular plants with deep root structures over  
75 the continents (D'Antonio and others, 2020}. Recently, Stein and others (2020) identified the oldest  
76 forest in the Middle Devonian (Givetian, between 387.7 and 382.7 Ma). Within this forest, some of  
77 the trees displayed a complex, modern-like root system, such as *Archeopteris*. The speed at which  
78 those big trees colonized the continental surfaces is not well constrained. The first forests rose in the  
79 Middle Devonian, and by the late Devonian (around 360 Ma), extensive "Carboniferous-style" forests  
80 had colonized large continental surfaces (Willis and McElwain, 2002).

81 Assuming the base of the Givetian stage as the starting date of the colonization (Stein and others,  
82 2020) and using the most recent compilation of atmospheric CO<sub>2</sub> proxy estimates (Foster and others,  
83 2017), it appears that an increase in atmospheric CO<sub>2</sub> first accompanied the spread of forests on land  
84 (from the Eifelian into the Givetian, Fig. 1), in agreement with the coeval low-latitude warming  
85 documented based on sedimentary apatite  $\delta^{18}\text{O}$  (Joachimski and others, 2009). Atmospheric CO<sub>2</sub>

86 subsequently fluctuated around ~1200 ppmv until the middle Frasnian and decreased down to 600  
87 ppm at the end of the Famennian (Foster and others, 2017). Then proxies are missing between 365 Ma  
88 and 345 Ma. At 340 Ma, 20 Myr after trees had become widely represented in the available  
89 fossil record, atmospheric CO<sub>2</sub> was as low as 300 ppm.

90

## 91 1.2. *The Importance of Physical Erosion*

92

93 Recent studies suggested that the link between the expansion of forests and atmospheric CO<sub>2</sub> ( $p\text{CO}_2$ )  
94 evolution may be more complex than the monotonic  $p\text{CO}_2$  decrease previously considered. New  
95 processes have been explored, such as the modification of the water cycle, requiring the development  
96 of process-based models. Lehir and others (2011) showed that the lowering of the continental albedo  
97 strongly modified the water cycle and the weathering rates. White and others (2020) have simulated  
98 the impact of vegetation on the continental water cycle over the Carboniferous and into the Permian.  
99 They showed that the rise in atmospheric oxygen during the late Carboniferous modified the  
100 atmospheric pressure, reducing the vegetation evapo-transpiration, ultimately increasing continental  
101 runoff rates and modifying the weathering rates. Ibarra and others (2019) built a model linking silicate  
102 weathering to a one-dimensional vapor transport model and showed that the growth of forests may  
103 have increased the strength of the silicate weathering feedback.

104 The contrast between the monotonic  $p\text{CO}_2$  drop predicted by previous modeling works and the  
105 complex  $p\text{CO}_2$  evolution based on proxy data suggests that rock weatherability may have been  
106 modulated by another factor not yet investigated. The physical erosion of the continents and its  
107 response to the expansion of plants might be one of those factors. The relationship between vegetation  
108 cover and landscape erosion is not straightforward, as illustrated by the few following examples.  
109 Surprisingly, abiotic environments, such as the surface of Mars, show landscape features similar to the  
110 vegetated Earth surface (Dietrich and Perron, 2006). But the difference between a biotic and abiotic  
111 world may lie in the greater occurrence of some landscape features in the presence of vegetation,  
112 compared to non-vegetated environments. On Earth, land plants can accelerate or buffer surface  
113 processes. Istanbuloglu and Bras (2005) suggested that vegetation can change the dominant erosion  
114 process from overland flow under abiotic conditions to land sliding in well-vegetated areas. Some  
115 case studies show that trees strongly inhibit erosion in mountainous areas (Vanacker and others,  
116 2010). In such environments, reforestation may reduce the fluxes of exported sediments by a factor of  
117 up to 45, compared to a barren ground. The presence of an evergreen vegetation in the Ecuadorian  
118 Andes strongly reduces erodibility (Ochoa and others, 2016). Based on a compilation of data covering  
119 Europe, Panagos and others (2015) calculated that the susceptibility to erosion in forested areas was  
120 about 100 times below the mean European value. A similar conclusion was reached by Garcia-Ruiz  
121 and others (2015) based on a worldwide database: forests and shrublands display the lowest erosion  
122 rates.

123 The question is why erosion rates are reduced in forested areas. One option could be an enhanced  
124 evapotranspiration and rainfall interception in the presence of trees, generating a decrease in runoff.  
125 However, Carriere and others (2020) challenged this hypothesis: they found that vegetation reduces  
126 the erosion rates by reducing the erodibility (defined as the susceptibility of the continental surfaces to  
127 erosion) (table 1), rather than by reducing the surface runoff. It has also been suggested that the  
128 impact of vascular plants on physical erodibility may depend on the considered time scale: vascular  
129 plants may stabilize river banks and promote single-thread channels (Davies and Gibling, 2010),  
130 decreasing erosion on decennial timescales, but potentially foster erosion on longer periods by  
131 focusing the river flow. Finally, two recent data compilations (Mishra and others, 2019; Starke and  
132 others, 2020) illustrate the variable effect of vegetation on erosion, such as initially proposed by

133 Langbein and Schumm (1958). Data from arid area show that the mechanical erosion strongly  
134 increases with increasing vegetation cover, because erosion is primarily driven by the corresponding  
135 increase in precipitation rate. Conversely mechanical erosion decreases with increasing vegetation  
136 cover in wetter areas because the protective role of vegetation dominates.

137 In the present contribution, we explore the consequences of the rise of the vascular plants on  
138 continental silicate weatherability. Although the rise of vascular plants also strongly modified the  
139 organic carbon cycle and the nutrient cycles (Algeo and Scheckler, 1998), the albedo, the rugosity and  
140 the evapo-transpiration of the continents, we deliberately focus on the inorganic part of the carbon  
141 cycle. Our goal is not to simulate all the processes at play, but rather to revisit how silicate weathering  
142 changed during the colonization when coupled to physical erosion.

143 In our modeling framework, we describe by "fully vegetated" continental surfaces upon which can be  
144 found vascular plants having the ability to change significantly the weatherability and erodibility of  
145 these surfaces. On the other hand, we qualify as "barren" continental surfaces without those vascular  
146 plants, though they may contain earlier forms of vegetation. We consider that all continental regions  
147 can be impacted by this transition from "barren" to "fully vegetated", including very dry areas and  
148 very cold regions. This simplification is arguable in terms of plant physiology, but from the modeling  
149 point of view, those regions are characterized by very low CO<sub>2</sub> consumption by silicate weathering  
150 anyway, because of unfavorable climatic conditions. Their contribution to the global CO<sub>2</sub>  
151 consumption by silicate weathering will remain negligible in any case. The connection between  
152 vascular plants and the calculated climate occurs only through the impact of plants on the continental  
153 weatherability and erodibility (table 1), and hence on atmospheric CO<sub>2</sub> concentration.

154 We will first simulate the steady-state of the surficial Earth system prior to the colonization of the  
155 continents by vascular plants, focusing on the impact of changes in weatherability and erodibility of  
156 the continents. Second, the post-colonization steady-state will be simulated and compared to the pre-  
157 colonization runs. Finally, the transient state from the pre- to the post-colonization steady-states will  
158 be explored.

159

## 160 2. MODEL DESCRIPTION

161 We develop a numerical model describing the coupling between physical erosion and chemical  
162 weathering, based on the model of Gabet and Mudd (2009) and West (2012), and we couple it with  
163 the deep time climate-carbon cycle model GEOCLIM (Donnadieu and others, 2006; Godd ris and  
164 others, 2014; Godd ris and others, 2017). The erosion/weathering model simulates three processes for  
165 each continental grid cell.

- 166 1. **The regolith production at the interface between the fresh bedrock and the regolith.**  
167 Modeling accurately the early stages of the bedrock weathering is complex. Regolith  
168 production is dependent on oxidation reactions able to break the bedrock, and releases  
169 unaltered minerals into the regolith (Navarre-Sitchler and others, 2015). Accordingly, we  
170 assume that this process does not consume CO<sub>2</sub>, and is dependent on temperature and on the  
171 availability of water at the bedrock interface.
- 172 2. **The removal of materials at the top of the regolith by physical erosion.** The physical  
173 erosion rate is simulated using a standard mathematical formulation used in most landscape  
174 models.
- 175 3. **The dissolution of primary minerals during their travel through the regolith, from their  
176 release at the bedrock/regolith interface to their removal by physical erosion at the top  
177 of the regolith.** The local chemical reaction rate of this dissolution at a given depth depends

178 on the amount of unweathered primary minerals left at that depth, and on climatic conditions.  
179 This process is the one consuming atmospheric CO<sub>2</sub>.

180 Introducing a mathematical description of the physical erosion in deep time models has profound  
181 implications regarding the climate-weathering feedback (Fig. 2). The classical negative feedback  
182 postulating that CO<sub>2</sub> consumption by weathering is increasing with enhanced greenhouse effect is still  
183 embedded in the model. But it is now connected too additional loops, generating a feedback either  
184 positive or negative. The dissolution rate of silicate minerals is made dependent on the physical  
185 erosion, which modifies the regolith thickness and production, and ultimately the depletion in primary  
186 minerals inside the continental regolith cover. This complexity cannot be unraveled without a  
187 numerical model.

188 The dynamic model is spatially distributed and solves a set of coupled equations for each continental  
189 grid cell and at each time step. The spatial resolution used for this study is 2.8° (longitude) x 1.4°  
190 (latitude). The model does not account for the lithology, because it cannot be constrained in the  
191 Paleozoic. We thus use a mean “bulk” lithology for the complete continental surfaces.

192 The first equation describes the time evolution of the regolith thickness:

$$\frac{dh}{dt} = P - E \quad (1)$$

193

194 where  $P$  (m/yr) represents the regolith production at the interface between the regolith and the  
195 unaltered bedrock, and  $E$  (m/yr) the removal of materials by physical erosion at the top of the regolith.  
196 This equation implicitly assumes that the weathering processes have no effect on regolith thickness  
197 (isovolumetric weathering approximation).  $P$  is assumed to be dependent on the regolith thickness  $h$   
198 through the soil production function  $f(h)$ .

$$P = P_0 \cdot f(h) \quad (2)$$

199

200 When the regolith thickness increases, less water can reach the regolith/bedrock interface and the  
201 regolith production decreases. Though this formulation was initially proposed for soils (Heimsath and  
202 others, 1997), the distinction between soil and regolith is not always explicit, and it has been widely  
203 used in numerical models to describe the production of regolith explicitly (e.g. Gabet and Mudd,  
204 2009; Carretier and others 2014; Braun and others, 2016). Several mathematical definitions of  $f(h)$  can  
205 be found in the literature (Humphrey and Wilkinson, 2007). We chose an exponential decay with  
206 thickness (Heimsath and others, 1997; Ferrier and Kirchner, 2008; Gabet and Mudd, 2009; Carretier  
207 and others, 2014):

$$f(h) = \exp\left(-\frac{h}{h_0}\right) \quad (3)$$

208

209  $h_0$  is the characteristic decay depth (table 2). The pre-exponential factor  $P_0$  (Eq. 2) is made dependent  
210 on air temperature  $T$  and runoff  $q$ , calculated as the difference precipitation minus evaporation  
211 (Carretier and others, 2014):

$$P_0 = f_W k_{rp} q e^{-(E_a/R)(1/T-1/T_0)} \quad (4)$$

212

213  $T_0$  is a reference temperature (293.15K),  $E_a$  is the apparent activation energy for granitic lithologies  
 214 (48200 J/mol: Oliva and others, 2003).  $R$  is the ideal gas constant and  $k_{rp}$  is the regolith production  
 215 calibration constant. The factor  $f_W$  simulates the impact of vascular plants on the regolith production  
 216 rate and on the weathering inside the regolith. This weatherability factor is set to 1 for modern  
 217 conditions (for the purpose of calibration). In the Devonian, its value on fully vegetated grid cell is  
 218 slightly lower, fixed at 0.87 (based on Berner, 2004, in the absence of angiosperms) in all the  
 219 presented scenarios. Its value prior to the colonization (“barren” grid cell) varies with the considered  
 220 scenario, but is always lower than 0.87 (Berner, 2004).

221 The physical erosion (m/yr) at the top of the regolith  $E$  (eq. 1) can be expressed as follows (Davy and  
 222 Lague, 2009):

$$E = f_E k_e q^m s^n \quad (5)$$

223

224 where  $s$  (m/m) is the prescribed local slope, and  $q$  (m<sup>3</sup>/yr) the local water runoff.  $k_e$  is a calibration  
 225 constant. The  $f_E$  factor represents the change in the erodibility related to the presence or absence of  
 226 vascular plants. It is set to 1 for modern conditions (for the purpose of calibration), as well as when  
 227 grid cells are fully vegetated. The value prior to the colonization by vascular plants is not known and  
 228 could be either greater or smaller than 1 as discussed in the previous section, depending on the  
 229 erodibility of barren continental surfaces. We refer to section 3 for a detailed discussion about the  
 230 values assigned to this parameter as a function of time.

231 The two other key equations of the dynamic regolith model define the abundance of primary mineral  
 232 phases within the regolith of each continental grid cell as a function of depth and time:

$$\frac{\partial x}{\partial t} = -P \cdot \frac{\partial x}{\partial z} - K \cdot x \cdot \tau^\sigma \quad (6)$$

233

$$\frac{\partial \tau}{\partial t} = -P \cdot \frac{\partial \tau}{\partial z} + 1 \quad (7)$$

234

235 where  $z$  (m) is the depth within the regolith.  $x$  (unitless) is the remaining fraction of primary minerals  
 236 at depth  $z$ , that is the density of remaining primary minerals (in kg per m<sup>3</sup> of regolith) at depth  $z$   
 237 divided by the primary density of minerals (in kg per m<sup>3</sup> of rock) in unweathered bedrock. This  
 238 definition is consistent as the model assumes the weathering to be isovolumetric: the dissolution of  
 239 primary phases does not affect  $z$ .  $\tau$  is the age of the primary mineral particles, that is the time elapsed  
 240 since the particles have left the bedrock/regolith interface and started to weather during their journey  
 241 towards the surface.  $K$  is the kinetic constant of the weathering reaction. This kinetic constant is

242 modulated by the age of the particles to the power  $\sigma$ .  $\sigma$  is negative, meaning that the reactivity of the  
 243 surfaces is decreasing with time, as secondary minerals progressively precipitate at the surface of the  
 244 primary mineral particles, limiting their weatherability.  $K$  is also made dependent on the runoff  $q$  and  
 245 on air temperature  $T$  (West, 2012):

$$K = f_W k_d (1 - e^{-k_w q}) e^{-(E_a/R)(1/T - 1/T_0)} \quad (8)$$

246

247 where  $k_d$  is the effective kinetic constant for the weathering of silicate rocks.  $k_w$  is a constant  
 248 describing the impact of the runoff on  $K$ .  $f_W$  is the same vegetation weatherability factor as in equation  
 249 4, as we assume that vascular plants have the same effect on mineral dissolution within the regolith  
 250 than on regolith production. Using the two equations (Eq. 6 and 7), it can be demonstrated that the  
 251 overall weathering rate and associated CO<sub>2</sub> consumption of each grid cell (mol/m<sup>2</sup>/yr) is equal to:

$$W = [BC]_{bedrock} \int_0^h K \tau^\sigma x dz \quad (9)$$

252

253 where  $[BC]_{bedrock}$  is the content of base cations (Ca and Mg) in bedrock, in mol/m<sup>3</sup>. Indeed, under the  
 254 isovolumetric assumption, the integral in equation 9 yields a volumetric weathering rate, in m<sup>3</sup> of  
 255 weathered minerals per m<sup>2</sup> per yr, that should be multiplied by bedrock density and its content of  
 256 cations (that boils down in the variable  $[BC]_{bedrock}$ ) to have a weathering rate in mol/m<sup>2</sup>/yr.

257 The products leaving the regolith no longer interact with the weathering model. Solutes are delivered  
 258 to the ocean by river systems quasi immediately (with respect to carbon residence time). As for solid  
 259 eroded products, their potential storage and “remote” weathering in floodplains is neglected by the  
 260 model.

261 This spatially resolved erosion/weathering model is coupled to the climate-carbon cycle model  
 262 GEOCLIM (Godd ris and Joachimski, 2004; Donnadieu and others, 2006; Godd ris and others, 2014;  
 263 Godd ris and others, 2017) (Fig. 2). At each time step of the transient numerical simulation,  
 264 GEOCLIM calculates the continental temperature and runoff fields based on a look-up table of  
 265 climatic fields simulated with a 3D-climate model at various  $p\text{CO}_2$  levels. These climatic fields have  
 266 been calculated using the FOAM ocean-atmosphere general circulation model (Donnadieu and others,  
 267 2006). These climatic fields are used by the weathering/erosion module to calculate the spatial  
 268 distributions of the regolith production rates, regolith weathering rates and physical erosion rates. The  
 269 regolith mass balance is then solved using the same spatial resolution (2.8 lon x 1.4 lat), which allows  
 270 the calculation of the spatial patterns of regolith thickness changes. The alkalinity generated by  
 271 weathering is released into the oceanic model (9 boxes describing the oceanic chemical composition  
 272 (Godd ris and Joachimski, 2004) where carbon is removed through sedimentation. GEOCLIM  
 273 calculates the new coeval  $p\text{CO}_2$  and the model moves towards the next time step. The resulting  
 274 coupled numerical model thus describes the coeval evolutions of climate, ocean biogeochemistry and  
 275 the erosion/weathering processes. The timestep of the simulations is equal to 0.05 years (about 20  
 276 days), a value constrained by the fastest processes simulated in GEOCLIM (the diffusion of CO<sub>2</sub> at  
 277 the ocean-atmosphere interface). However, the weathering module is updated only every 100  
 278 timesteps (about 5 years), and the timestep of the vascular plant colonization (see section 4.2) is 10  
 279 000 years.

280



281

### 282 3. BOUNDARY CONDITIONS AND PARAMETERS FOR THE STEADY-STATE 283 SIMULATIONS

284

285 We first calibrate the model on the present-day continental configuration, with an extensive  
286 vegetation cover. The vegetation factors  $f_W$  and  $f_E$  are set to 1 for present-day conditions, and we  
287 choose the set of model parameters generating the best agreement between the calculated weathering  
288 rates for a wide variety of large watersheds and the measured weathering rates from a published  
289 database (Gaillardet and others, 1999, following the method described in Maffre and others (2018),  
290 Table 2).

291 The Devonian simulations have been performed using the 350-360 Ma paleogeography from Golonka  
292 (2002) (Fig. 3). The paleogeography is held constant during the simulations. The solid Earth  
293 degassing is set to 6.8 Tmol(C)/yr, the value required to equilibrate the present-day CO<sub>2</sub> consumption  
294 by continental silicate weathering. We adopt a constant degassing in the past to limit the number of  
295 parameters, given the discrepancies existing between the various reconstructions available in the  
296 literature, mainly for more recent periods (Godd ris and Donnadieu, 2019). The altitude is fixed on  
297 each grid cell, and the slope is calculated from the present-day correlation between altitude and slope,  
298 following Godd ris and others (2017). The underlying assumption is that tectonic uplift balances  
299 erosion in every places.

300

301 Regarding the evolution of the  $f_W$  factor (Eq. 4 and 8) before, during and after the vascular plant  
302 colonization, two scenarios are explored. In the first scenario, the local weatherability is multiplied by  
303 3 when a grid element shifts from a barren state to fully vegetated conditions. This means that the  
304 local vegetation weatherability factor  $f_W$  increases from 0.29 prior to the colonization to 0.87 when the  
305 grid cell is colonized by vascular plants (based on Berner, 2004, in the absence of angiosperms) and  
306 the vegetation erodibility factor  $f_E$  is fixed at its modern value of 1. The alternative scenario, derived  
307 from the results of Ibarra and others (2019), considers that local weatherability is multiplied by 2  
308 during that transition ( $f_W$  increases from 0.43 to 0.87, Eq. 4 and 8).

309 The change in erodibility is not constrained (Eq. 5). For this reason, we performed a sensitivity study  
310 where the erodibility factor  $f_E$  is multiplied by 2, 1, 1/2, 1/4, and 1/8 when a grid element switches  
311 from barren to fully vegetated (that is,  $f_E$  changes, respectively, from 0.5, 1.0, 2.0, 4.0, and 8.0 to 1).  
312 We thus test 3 cases for which the susceptibility of the continents to physical erosion is greater for  
313 barren surfaces, one case study for which it is unchanged, and a last one for which barren continents  
314 are less erodible in the absence of vascular plants.

315 A limitation of our modeling framework is related to the water cycle. The GEOCLIM model  
316 calculates the water cycle using a 3-dimensional general circulation model (GCM) of the atmosphere  
317 and the ocean. The water cycle is thus physically resolved. But GEOCLIM cannot capture the changes  
318 in evapotranspiration and albedo associated with the expansion of vascular plants. Adding a feedback  
319 of the vegetation cover directly on the evapotranspiration conditions would necessitate the addition of  
320 one dimension to the climatic interpolation procedure, and hence multiply the number of GCM  
321 simulations. Such a procedure requires excessive computation time. This is the reason why the GCM  
322 runs have been performed assuming a prescribed distribution of the vegetation transpiration as a  
323 function of latitude, in all runs. We cannot account for the direct climatic impact of the vegetation,  
324 and we focus on the weathering and erosion changes. While previous numerical modeling work  
325 acknowledged the importance of changes in land surface properties associated with land plant

326 expansion, they also demonstrated that results are model-dependent and, consequently, poorly  
327 constrained (Le Hir and others, 2011; Brugger and others, 2019).

328 Finally, we define the Weathering Efficiency Index (WEI) as the ratio of the CO<sub>2</sub> consumption by  
329 weathering inside the regolith (W, Eq. 9) versus the maximum potential CO<sub>2</sub> consumption by  
330 weathering. The latter factor is equal to the regolith production (P, Eq. 2) multiplied by the base  
331 cation (BC) content of the bedrock.

$$WEI = \frac{W}{[BC]_{bedrock} \cdot P} \quad (10)$$

332

333 A WEI of 1 means that all primary minerals released from the bedrock through regolith production  
334 are fully weathered inside the regolith. There are no more primary minerals at the top of the regolith.  
335 A WEI of 1 is typical of the "supply-limited" weathering regime. Conversely, WEI values  
336 approaching zero mean that only a small fraction of the minerals released through regolith production  
337 is weathered inside the regolith, and the materials removed by physical erosion contain a lot of fresh  
338 unweathered minerals. "Kinetically-limited" weathering regimes are characterized by a WEI close to  
339 0.

340

341

## 4. RESULTS

342

343

### 4.1. *Steady-State Simulations*

344

345 We first run two sets of simulations until they reach steady-state, corresponding respectively to the  
346 world before the colonization by vascular plants ("barren") and the world when this colonization is  
347 complete ("fully vegetated"). Vascular plants are missing in the first series of runs, and they are  
348 assumed to have colonized the whole continental surface in the second series of simulations. These  
349 steady states are not dependent on the colonization scenario. The pattern of progressive spatial  
350 spreading of vascular plants on continental surfaces, whereby those surfaces go from barren  
351 everywhere to fully vegetated everywhere, has no impact on the pre- and post-colonization states (Fig.  
352 4). Converse, the pre and post colonization steady-states depend on the model parameters: the  
353 prescribed solid Earth degassing rate (held constant at the same value before and after the  
354 colonization) and on the model erodibility and weatherability for barren or fully vegetated conditions.  
355 Because the values of the vascular plants' parameters  $f_W$  and  $f_E$  are fixed in fully vegetated conditions  
356 (we only varied the barren conditions values), in our analysis of steady-state simulations, we use the  
357 fully vegetated values as the reference. In other words, we compare the pre-colonization "archaic"  
358 values to the post-colonization "modern" value.

359

#### 360 4.1.1. *Before the colonization*

361 Figure 5 shows the calculated steady-state  $p\text{CO}_2$  and surface temperature in the barren world as a  
362 function of the prescribed erodibility, assuming, over the entire continental surface, a lowering of the  
363 weatherability by a factor of 2 with respect to fully vegetated conditions, or by a factor of 3.

364 Using both pre-colonization weatherability  $f_W$  and erodibility  $f_E$  2 times lower than post-colonization  
365 values ( $f_W=0.43$ ,  $f_E = 0.5$ ), WEI equals 1 at steady-state for most of the continental grid cells (Fig. 6A).  
366 Because the erodibility is prescribed at a low value in the absence of vascular plants, materials are not  
367 efficiently removed by physical erosion and the spatially-distributed regolith thickens everywhere on  
368 Earth, at a rate depending on the local climate conditions. But as the regolith thickens, the soil  
369 production function decreases. Once reaching steady-state, the continents are covered by thick and  
370 depleted regolith as a result of the weak erodibility combined with the long residence time of the rock  
371 particles within the regolith (Fig. 7A). This long residence time allows weathering processes to  
372 operate at their maximum efficiency (WEI=1), but the CO<sub>2</sub> consumption is low. This setting is close  
373 to the transport-limited regime as defined by Stallard and Edmond (1983). High CO<sub>2</sub> levels are  
374 required to allow the global silicate weathering to balance the prescribed solid Earth degassing flux.

375 Increasing the prescribed erodibility prior to the advent of the vascular plants generates a decrease in  
376 the regolith thicknesses (Fig. 7B, 7C, and 7D), which counters the weathering inhibition (Fig. 6B and  
377 6C). As weathering reactions are now facilitated by a greater erosion, the balance between the global  
378 silicate weathering and the prescribed solid Earth degassing is achieved at lower CO<sub>2</sub> levels (Fig. 5).  
379 A value of 4 for pre-colonization  $f_E$  (i.e., erodibility is 4 times above the fully vegetated value) leads  
380 to a decrease in steady-state CO<sub>2</sub> level down to 1180 ppm (4.2 Pre-industrial Atmospheric Level, or  
381 PAL).

382 The decreasing trend of atmospheric CO<sub>2</sub> with increasing erodibility stops at a  $f_E$  of about 4 times the  
383 fully vegetated value. Above this threshold, the steady-state CO<sub>2</sub> rises with increasing  $f_E$  for barren  
384 lands (Fig. 5), while regolith thickness keeps decreasing (Fig. 7). When a very high erodibility is  
385 prescribed prior to the colonization ( $f_E = 8$ ), the regolith cover almost disappears (Fig. 7). The bedrock  
386 particles are removed by intense physical erosion before they are weathered. The calculated WEI  
387 stabilizes around 0.7 at best in restricted flat areas along the equator (Fig. 6C), corresponding to a  
388 calculated cation depletion of about 60%. Under such an intense physical erosion, weathering  
389 becomes inefficient because the fresh primary minerals are being removed before they experience a  
390 significant weathering. The weathering rates can only balance the prescribed solid Earth degassing  
391 rate under higher  $p\text{CO}_2$  level than when  $f_E=4$  (Fig. 5).

392 Mean temperatures (global, continental or sea surface), follow a pattern similar to  $p\text{CO}_2$  when plotted  
393 as a function of the pre-colonization erodibility  $f_E$ . (fig. 5B and D). Warmest pre-colonization  
394 temperatures are found for the lowest pre-colonization  $f_E$  (0.5), and minimum temperatures are  
395 simulated with  $f_E=4$ .

396 Model simulations using a pre-colonization weatherability factor  $f_W$  3 times lower than the fully  
397 vegetated conditions mimic the results of the pre-colonization runs with weatherability factor  $f_W$  2  
398 times lower fully vegetated one, but higher CO<sub>2</sub> levels are required to stabilize the global carbon cycle  
399 (Fig. 5C and 5D).

400

401 4.1.2. *After the colonization*

402

403 While we calculate a pre-colonization steady-state for each combination of  $f_W$  and  $f_E$  parameters, we  
404 can generate only one post-colonization state given that  $f_E$  and  $f_W$  are forced to be equal to 0.87 and 1  
405 respectively once the colonization achieved. The CO<sub>2</sub> level after the colonization stabilizes at 2.7 PAL  
406 (760 ppm). This CO<sub>2</sub> level is lower than all the tested pre-colonization cases, whether the pre-  
407 colonization erodibility is higher or lower than the fully vegetated one.

408 A striking difference between the pre-colonization and the post-colonization state is the latitudinal  
409 distribution of silicate rock weathering. For a prescribed pre-colonization erodibility equal to or  
410 greater than 4 times the post-colonization value, most of the weathering flux and associated CO<sub>2</sub>  
411 consumption is located in the low latitudes (Fig. 8). Indeed, the intense global erodibility makes the  
412 bedrock conversion into regolith fast enough for regolith to develop only along the equator where  
413 climate is warm and humid. In this environment, the model generates a regolith in which weathering  
414 reactions can occur. At higher latitudes, the erosion overtakes the weathering reactions. The material  
415 is removed by physical erosion before being significantly weathered. As discussed below, this  
416 behavior has a major impact on the calculated CO<sub>2</sub> and climate evolution during the colonization  
417 phase.

418

419

## 420 4.2. During the Colonization: Simulating the Transient State

421

### 422 4.2.1. Simulation design and sensitivity tests

423 The transient evolution of climate and carbon cycle once vascular plants start colonizing continents  
424 depends on the way the vascular plants spread on continental surfaces, until the continents are fully  
425 vegetated. Indeed, the pattern and timing in which continents get colonized affects weathering rates  
426 and hence the temporal evolution of pCO<sub>2</sub>. We refer to the pattern and timing of progressive spatial  
427 spreading of vascular plants on continental surfaces as the “colonization scenario”. Several  
428 colonization scenarios are presented hereinafter.

429 For the sake of clarity, we build our analysis in this section – and the following ones – on the changes  
430 in weatherability and erodibility following the transition from barren to fully vegetated. We thus  
431 define the vegetation enhancement factors  $\Delta f_w = f_w(\text{fully vegetated})/f_w(\text{barren})$ , and similarly for  $\Delta f_E$ .  
432 One should note that “ $\Delta$ ” is here meant for a ratio, and not a difference.

433 We build a simple cellular automaton to simulate the progressive expansion of the vascular plants on  
434 the continents. On each isolated continental block, we first choose arbitrarily a grid element where the  
435 colonization starts (Fig. 4). Then the change in weatherability and erodibility propagates according to  
436 the simple following rule: a naked neighbor of a grid element fully vegetated has a probability of 50%  
437 to be fully vegetated during the next time step. A new vegetation map is generated every 10 kyr.

438 As it was the case for the steady-state runs, here we present two sets of simulations, one assuming that  
439 vascular plant colonization increases the weatherability by a factor 2 ( $\Delta f_w = 2$ ), and the other by a  
440 factor of 3 ( $\Delta f_w = 3$ ). Each set includes three subsets of simulations, where the erodibility is  
441 unchanged ( $\Delta f_E = 1$ ), divided by 4 ( $\Delta f_E = 1/4$ ), and divided by 8 ( $\Delta f_E = 1/8$ ) respectively, when a  
442 continental grid element is fully vegetated. Finally, within each subset, three additional simulations  
443 allow to test the impact of the random propagation of the vascular plants on the continental surfaces,  
444 keeping the seeding points at the same location. This pattern is controlled by the cellular automaton  
445 and differs from one run to the other. Those colonization scenarios are labelled  $\alpha$ ,  $\beta$ , and  $\gamma$  (Fig. 4).

446 There are still large uncertainties about the colonization of dry uplands. Even if plants already  
447 developed the required adaptations for colonization of dry areas in the Silurian (Morris and others,  
448 2018), the question of the effective upland occupation by vascular plants remains open (Pawlik and  
449 others, 2020) This upland colonization might have occurred around the end of the Devonian (Willis  
450 and McElwain, 2016), or might have been delayed until the Carboniferous (Boyce and Lee, 2016).  
451 The exact timing and pattern of the colonization will be probably never known, because of the lack of  
452 fossils from dry areas. In the following, we will assume that the full colonization spans 30 million

453 years (the timespan from the Givetian to the Famennian), a duration that must be considered as a  
454 parameter.

455

#### 456 4.2.2. *Sensitivity of the Earth system to the colonization*

457 The following simulations have been performed using the  $\alpha$ ,  $\beta$ , and  $\gamma$  colonization scenario  
458 respectively (FDig. 4). When the weatherability is multiplied by 3 during the colonization ( $\Delta f_W = 3$ ),  
459 simulated  $p\text{CO}_2$  displays roughly the same temporal evolution whatever the prescribed change in  
460 erodibility and whatever the colonization scenario (Fig. 9A). The  $p\text{CO}_2$  decreases rapidly from very  
461 high values (between 4000 and more than 6000 ppm) down to the post-colonization steady-state value  
462 of 760 ppm. The change in weatherability is strong enough to overwhelm the effect of changing  
463 physical erodibility. This numerical solution, however, is not supported by available  $p\text{CO}_2$  proxy data.  
464 It implies very large  $\text{CO}_2$  levels prior to the colonization, while proxy data suggests a maximum  $p\text{CO}_2$   
465 of 1900 ppm in the Eifelian (Foster et al., 2017). Previous studies of the effect of the colonization on  
466 the carbon cycle are assuming a global decrease of the weatherability by a factor of 3 prior to the  
467 colonization (Berner, 2004). Our simulations suggest that this calculated  $\text{CO}_2$  decrease might be too  
468 large.

469

470 If weatherability is multiplied by 2 during the colonization phase ( $\Delta f_W = 2$ ), the global amplitude of  
471 the  $p\text{CO}_2$  changes is considerably reduced, in closer agreement with proxy data (Fig. 9B). Conversely  
472 to the previous results, changes in continental erodibility during the colonization lead to contrasting  
473  $p\text{CO}_2$  evolutions. The simulation with an unchanged erodibility during the colonization ( $\Delta f_E = 1$ )  
474 shows an overall decrease in atmospheric  $\text{CO}_2$ . In simulations  $\Delta f_E = 1/4$  and  $\Delta f_E = 1/8$ ,  $p\text{CO}_2$  increases  
475 during the early stages of the colonization, reaching a maximum just after the Givetian/Frasnian  
476 boundary, and subsequently decreases. The  $p\text{CO}_2$  simulated in all runs  $\Delta f_E = 1/4$  and  $\Delta f_E = 1/8$  (i.e.,  
477 using the colonization scenarios  $\alpha$ ,  $\beta$  or  $\gamma$ ) falls within the range of uncertainty of the  $\text{CO}_2$  proxy  
478 estimates. Consequently, these simulations are all equally plausible (Fig. 9B).

479

#### 480 4.2.3. *Analysis of the simulations with constant erodibility*

481

482 To decipher the respective influence of each parameters considered in this study, we first explore the  
483 dynamics of a simulation where erodibility does not change during the colonization ( $\Delta f_E = 1$ ,  $\Delta f_W = 2$   
484 with the  $\beta$  colonization scenario). Such run is somewhat similar to the simulations previously  
485 performed with the GEOCARB model family (e.g., Zhang et al., 2018), given that vascular plants  
486 generate a change in weatherability only, without impacting the physical erosion, with the notable  
487 differences that we account for the spatial distribution of the weathering rates, and we simulate the  
488 time evolution of the regolith thickness.

489

490 Simulation  $\Delta f_E = 1$ ,  $\Delta f_W = 2$  with the  $\beta$  colonization scenarios shows a general decrease in  $p\text{CO}_2$ .  
491 Starting a few hundred thousand years after the beginning of the colonization (Fig. 10A) and  
492 promoted by the increase in weatherability propagating on the continents in response to the expansion  
493 of vascular plants, the global  $\text{CO}_2$  consumption by weathering remains higher than the  $\text{CO}_2$  release by  
494 solid Earth degassing (Fig. 10B). The departure from equilibrium, however, is small (never exceeding  
495 0.2 Tmol/yr), which means that the weathering feedback is operating efficiently. The evolution of the  
496  $\text{CO}_2$  consumption by silicate weathering on each individual continent shows contrasting behaviors

497 (fig. 10C). Given their size, the two most important contributors to the global weathering flux are the  
498 Euramerica and Gondwana continents.

499 The silicate weathering CO<sub>2</sub> consumption stays remarkably constant over Euramerica for 7 million  
500 years after the start of the colonization (Fig. 10C). Then the colonization reaches the mountain range  
501 located close to the equator. The combination of more intense erosion linked to greater slopes with  
502 enhanced weatherability generates a marked increase in the Euramerica weathering flux (fig. 10C).  
503 The subsequent decrease in atmospheric CO<sub>2</sub> further cools the planet, forcing weathering on  
504 Gondwana to decrease.

505 Ten million years after the start of the colonization, Euramerica is fully vegetated in scenario β (Fig.  
506 4). The overall weatherability cannot increase anymore, and the growth of the regolith progressively  
507 inhibits weathering over Euramerica (Fig. 10C). The weathering of Euramerica shifts to a transport-  
508 limited mode. Conversely, weathering fluxes over Gondwana increase (Fig. 10C), because the  
509 continuous spreading of the vascular plants overcomes the effect of climate cooling on weathering  
510 fluxes. The contribution of each continent to the global weathering flux eventually converges towards  
511 the pre-perturbation spatial distribution, but at a much lower CO<sub>2</sub>.

512

#### 513 4.2.4. *Analysis of the simulations with a decreasing erodibility through the colonization*

514

515 We compare now the behavior of the carbon cycle in simulation ( $\Delta f_E = 1$ ,  $\Delta f_W = 2$ ), with erodibility  
516 insensitive to the colonization, with simulation where erodibility decreases by a factor of 4 on  
517 colonized grid cells ( $\Delta f_E = 1/4$ ,  $\Delta f_W = 2$ ). The colonization scenario β is used in each case.

518 The decrease in erodibility generates a positive excursion in  $p\text{CO}_2$  during the colonization phase. To  
519 provide an explanation for this puzzling behavior, we separated the general trend into three distinct  
520 phases.

- 521 • Phase 1. During the first ca. 2 to 3 million years of the colonization,  $p\text{CO}_2$  stays constant  
522 (Fig.10A, run  $\Delta f_E = 1/4$ ,  $\Delta f_W = 2$ ). Responding to the expansion of the vascular plants, the  
523 weathering rates (the flux per unit of land area) in the model grid cells instantaneously  
524 increase when the cells are colonized. In the equatorial band, hot spots of weathering appear  
525 as spikes in the silicate weathering curve of Euramerica (Fig. 10C, dashed lines). These  
526 hotspots vanish rapidly, within a few hundred thousand years after their colonization. During  
527 this time span, the regolith acts as a reservoir of cation-bearing minerals, but this reservoir is  
528 rapidly exhausted owing to the increased weatherability. This depletion of the regolith limits  
529 the weathering rates. As long as the fraction of the equatorial belt fully vegetated remains  
530 small, the overall weathering rates are not significantly affected, and so does  $p\text{CO}_2$ .
- 531 • Phase 2 As colonization proceeds and reduces the erodibility over increasing areas of  
532 Euramerica, the regolith thickness increases. The weathering rates are consequently  
533 progressively inhibited in the warm and humid equatorial belt, and after 2 to 3 million years,  
534  $p\text{CO}_2$  starts to rise.
- 535 • Phase 3. While this rise in CO<sub>2</sub> warms the climate, further inhibiting weathering in the  
536 equatorial region, it accelerates the weathering at higher latitudes together with the decrease  
537 in erosion associated with the colonization (Fig.11). As a consequence, the weathering at  
538 higher latitudes (around 40°S to 60°S) intensifies. Atmospheric CO<sub>2</sub> starts to decrease down  
539 to the post-colonization steady-state value of 760 ppm.

540

541 Figure 12 and 13 summarize the temporal evolution of the regolith thickness simulated in the ( $\Delta f_E = 1$ ,  
542  $\Delta f_W = 2$ ) and ( $\Delta f_E = 1/4$ ,  $\Delta f_W = 2$ ) simulations (both with colonization scenario  $\beta$ ). If erodibility does  
543 not change, the spatio-temporal pattern of the regolith thickness remains virtually unchanged: the  
544 equatorial region is covered by thick regoliths before, during and after the colonization, with a peak in  
545 regolith thickness at 10 million years (Fig. 12). After 10 million years, the regolith thickness starts to  
546 decrease, because the decrease in atmospheric CO<sub>2</sub> generates cooler and dryer conditions, reducing  
547 the efficiency of the regolith production. In the run ( $\Delta f_E = 1/4$ ,  $\Delta f_W = 2$ ), the flux of CO<sub>2</sub> consumption  
548 by silicate weathering is first located mainly along the equator, promoted by an intense weathering  
549 driven by a strong erosion, until ca. 3 million years after the start of the colonization. At that time, the  
550 regolith thickness starts to increase along the equator, and the weathering system shifts towards the  
551 modern geographic distribution (fig. 13).

552

553 The prescribed erodibility change  $\Delta f_E$  has important implications for the silicate weathering feedback  
554 (Walker and others, 1981). Indeed, the ( $\Delta f_E = 1/4$ ,  $\Delta f_W = 2$ ) simulation emphasizes the weakness of the  
555 silicate weathering negative feedback in the tropics, when the role of the regolith thickness is  
556 accounted for. Lower erosion rate due to lower erodibility ( $\Delta f_E = 1/4$ ) dramatically reduces chemical  
557 weathering rates in the tropics despite the increased weatherability ( $\Delta f_W = 2$ ). Hence, while  
558 Euramerican CO<sub>2</sub> consumption by silicate weathering rises during the colonization in simulation ( $\Delta f_E$   
559  $= 1$ ,  $\Delta f_W = 2$ ), it decreases by 20% in the simulation ( $\Delta f_E = 1/4$ ,  $\Delta f_W = 2$ ) (with colonization scenario  $\beta$ )  
560 between 0 and 10 million years (Fig. 10C). During a few million years, the tropics act as a powerful  
561 warming engine for Earth's climate. Without the presence of continents at higher latitude, the silicate  
562 weathering system may drive Earth's climate into a runaway greenhouse.

563

564 The behavior of weathering within equatorial Euramerica, where CO<sub>2</sub> consumption decreases with  
565 increasing CO<sub>2</sub>, is further investigated hereafter by comparing results obtained in simulation ( $\Delta f_E =$   
566  $1/4$ ,  $\Delta f_W = 2$ ) using the colonization scenario  $\alpha$ , on the one hand, and colonization scenarios  $\beta$  and  $\gamma$ ,  
567 on the other hand. The biggest contribution to the global CO<sub>2</sub> sink is located in Euramerica, especially  
568 prior to the colonization and during the early phases of the colonization. This implies that the global  
569 weathering CO<sub>2</sub> consumption is largely driven by Euramerica weathering. The  $p\text{CO}_2$  evolution  
570 simulated in scenarios  $\alpha$ ,  $\beta$  and  $\gamma$  are similar during the early stages of the colonization (Fig. 14).  
571  $p\text{CO}_2$  first stays constant, and then rises after 2 to 3 million years, for the reason exposed previously.  
572 Then, scenario  $\alpha$  generates a divergent story. After 4 million years, the rate of the CO<sub>2</sub> rise weakens,  
573 and after about 7 million years of colonization,  $p\text{CO}_2$  goes down in the  $\alpha$  run, while  $p\text{CO}_2$  still rises in  
574 scenarios  $\beta$  and  $\gamma$ . The only difference between these simulations is the pattern of the colonization in  
575 space and time. The colonization starts from the same seeding locations in each colonization scenario  
576 (on Euramerica, located on its Eastern equatorial border, Fig. 4) but the expansion is subsequently  
577 proceeding randomly. In scenarios  $\beta$  and  $\gamma$ , the colonization reaches the western border of equatorial  
578 Euramerica sooner than in scenario  $\alpha$ . At 8 million years, the warm and humid equatorial zone of  
579 Euramerica is almost wholly colonized in scenarios  $\beta$  and  $\gamma$ . Consequently, the weathering processes  
580 in this region (which is the main contributor to weathering) are strongly inhibited by the increasing  
581 regolith thickness. Conversely, in scenario  $\alpha$ , part of Euramerica is not fully vegetated at 8 million  
582 years as the colonization did not reach yet the western border of Euramerica. This region is thus still  
583 able to respond to climate change, with an unchanged erodibility factor  $f_E$  of 4 times the post-  
584 colonization efficiency. Owing to the global warming generated by the inhibition of weathering in the  
585 colonized equatorial grid cells outside of this region, the western part of Euramerica increases its  
586 consumption of atmospheric CO<sub>2</sub> under warmer and more humid climate. CO<sub>2</sub> is thus progressively  
587 removed from the atmosphere.

588 From a global perspective, the relationship between the total CO<sub>2</sub> consumption by silicate rock  
589 weathering and the change in atmospheric CO<sub>2</sub> is complex when physical erosion is accounted for.  
590 Indeed, when we assume that the colonization of the continents by vascular plants does not change the  
591 physical erodibility ( $Af_E = 1$ ,  $Af_W = 2$ ), the silicate weathering versus atmospheric CO<sub>2</sub> function  
592 displays an overall positive correlation between both variable (Fig. 15). But when we account for a  
593 decrease in erodibility through the colonization event ( $Af_E < 1$ ), the correlation is lost. During the  
594 early phases of the colonization, the global silicate weathering decreases with increasing CO<sub>2</sub> (Fig.  
595 15) because the shielding of the equatorial area limits the silicate weathering flux. But when the  
596 colonization starts to increase significantly the weathering at higher latitude, silicate weathering rises  
597 again with atmospheric CO<sub>2</sub>. Two tipping points can be identified. First, an inflexion in the silicate  
598 weathering vs CO<sub>2</sub> curve is calculated 5 million years after the beginning of the colonization event.  
599 This tipping point corresponds to the moment when silicate weathering become efficient at mid-  
600 latitude in response to the progressive expansion of vascular plants. The second tipping point occurs  
601 when the colonization is completed, 25 million years after the first tipping point. At that moment,  
602 weatherability ( $f_W$ ) and erodibility ( $f_E$ ) are held constant for all the continental grid cells, silicate  
603 weathering is not more forced and the model predicts the restoration of a classical weathering/CO<sub>2</sub>  
604 relationship.

605

606 Our numerical simulations thus strongly suggest that the colonization of the continents by vascular  
607 plants during most of the Devonian did not monotonically remove CO<sub>2</sub> from the atmosphere, in  
608 response to an enhanced weatherability. Simulations accounting for a decrease in erodibility of the  
609 continental surface show that  $p\text{CO}_2$  might have first risen, or oscillated, before starting to decrease.

610

## 611 5. LIMITATION AND ADDITIONAL THOUGHTS

612

613 Many studies have focused on the role played by mountain ranges on the evolution of the global  
614 carbon cycle. In the 90s, it has been repeatedly argued that the uplift of the Himalayan range was a  
615 powerful driver of the carbon cycle, by promoting physical erosion. The subsequent increase in  
616 regional silicate weathering rates was proposed as the culprit for the late Cenozoic cooling (Raymo,  
617 1991). Then Kump and Arthur (1997) defined the concept of weatherability. Mountain ranges are not  
618 boosting weathering fluxes, but they enhance the weatherability, forcing CO<sub>2</sub> to go down while the  
619 global carbon mass balance stays close to equilibrium. But this weatherability change is in fact a  
620 change in erodibility, which removes the regoliths and facilitates the dissolution of the fresh bedrock.  
621 Godd ris and others (2017) explored the role of erodibility change during the uplift and demise of the  
622 Central Pangean Mountains. It has also been suggested that mountainous regions reinforce the  
623 negative weathering feedback (West, 2012; Maher and Chamberlain, 2014). Recently, the role of  
624 mountain ranges on the global evolution of the carbon cycle has been repeatedly questioned. The  
625 burial of organic carbon exported from the ranges might be a powerful CO<sub>2</sub> sink (France-Lanord and  
626 Derry, 1997; Galy and others, 2007). Similarly, the release of sulfuric acid by the oxidation of  
627 sedimentary sulfur exposed in mountain ranges raises the importance of carbonate weathering, the  
628 mountains becoming a source of carbon at a timescale below the residence time of sulfur in the ocean-  
629 atmosphere system (Calmels and others, 2007; Torres and others, 2016). But all those processes are  
630 driven by the physical erosion in the specific case of active mountain ranges. The erodibility of the  
631 mountainous areas becomes the central piece of the climatic evolution of the Earth. For instance,  
632 using the formalism described here to simulate the physical erosion, Maffre and others (2021) have  
633 quantified the role played by the oxidation of sedimentary pyrite on the carbon cycle. Erodibility



634 being partly a function of climate, it paves the way for the integration of new feedback processes in  
635 global scale models.

636 This period of Earth history is critical because erodibility and weatherability are altered by two  
637 distinct, yet not independent processes. On the one hand, the release of organic acids and the below  
638 ground CO<sub>2</sub> release by the roots increases the weatherability, on the other, roots modify the erodibility  
639 by stabilizing the regolith. The coupling between the two processes occurs through the presence of  
640 vascular plants, but the relative amplitude of weatherability and erodibility changes are not precisely  
641 known, even for the present-day environment. This present uncertainty is even higher in the Devonian  
642 context, with extinct tree species (Pawlik and others, 2020). Nevertheless, we demonstrate that the  
643 Earth climate history from the middle to the late Devonian is heavily dependent on the relative  
644 importance of these two processes, and on vegetation colonization scenario.

645 Our results are also dependent on the positions of the "seeding" points. In the experiments, we  
646 prescribe arbitrarily one seeding point on each continent. Given that the three colonization scenarios  
647 (all with the same seeding point on each continent) have a strong impact on the atmospheric CO<sub>2</sub>  
648 evolution, the choice of the position of the seeding points will impact the time evolution of  
649 atmospheric CO<sub>2</sub>, because it modifies drastically the pattern of the colonization with time. This effect  
650 should be tested by multiplying the number of simulations to generate an ensemble of results that can  
651 be explored with adequate statistical methods. At this stage, this is beyond the objective of this study.  
652 But we perform a sensitivity analysis where we moved the seeding on the Gondwana continent from a  
653 tropical location to a high latitude site. We choose the Gondwana continent because its size will  
654 generate the maximum impact of the seeding point location (scenario  $\delta$ ). We re-run the simulations  
655 ( $\Delta f_E = 1$ ,  $\Delta f_W = 2$ ), ( $\Delta f_E = 1/4$ ,  $\Delta f_W = 2$ ), and ( $\Delta f_E = 1/8$ ,  $\Delta f_W = 2$ ). When erodibility does not change ( $\Delta f_E$   
656  $= 1$ ,  $\Delta f_W = 2$ ), the impact on the calculated atmospheric CO<sub>2</sub> evolution remains marginal. But when  
657  $\Delta f_E$  equals 1/4 or 1/8, the CO<sub>2</sub> shows a great sensitivity to the Gondwana seeding point (Fig. 16). We  
658 are a still generating rather constant CO<sub>2</sub> during the early phase of the colonization, and then a rise  
659 triggering a warmer climate later in the Frasnian, compared to the previous simulations.

660

661 Lastly, this is a theoretical study. We are not attempting at reproducing precisely the real evolution of  
662 the surficial environment during the colonization of the continents by vascular plants. Such an  
663 objective cannot be achieved for the following reasons: the timing is not well constrained, the  
664 scenario of the colonization is unknown, the position of the continents and their relief are held  
665 constant in the present work, the plants do not have a direct impact on the climate, and last but not  
666 least, our numerical model misses some key processes and feedbacks, despite its complexity. But we  
667 show that the colonization of the continental surfaces by vascular plants was probably not a long and  
668 quiet river, bringing the CO<sub>2</sub> from the high early Paleozoic levels down to the low Carboniferous level  
669 monotonically. And our study also highlights the importance of accounting for the spatial distribution  
670 of the weathering fluxes.

671

672

## 6. CONCLUSIONS

673

674 We used a modified version of the GEOCLIM climate-carbon cycle model to simulate the impact of  
675 the colonization of the continents by vascular plants during the Middle and Late Devonian. We  
676 accounted for the associated changes in weatherability and erodibility of the continental surfaces. This  
677 is the first attempt to simulate the coupled changes in the global carbon cycle including  $p\text{CO}_2$ ,  
678 climate, weathering processes (with a spatial resolution).

679 A first conclusion is that, whatever the change in erodibility, all simulations considering a 3-fold  
680 increase in weatherability due to the colonization by vascular plants, lead to a marked decrease in  
681 atmospheric CO<sub>2</sub> in response to the expansion of vascular plants in the Devonian. Such results align  
682 well with previous modeling studies (e.g., Berner, 2004). However, the amplitude of the simulated  
683 *p*CO<sub>2</sub> decrease is generally outside the range permitted by *p*CO<sub>2</sub> proxy data.

684 When considering a weaker increase in weatherability with colonization (i.e. a doubling), the  
685 temporal evolution of simulated *p*CO<sub>2</sub> becomes highly dependent on considered changes in physical  
686 erosion. If erodibility is kept the same, the *p*CO<sub>2</sub> decreases during the colonization. When a decrease  
687 in erodibility with colonization is considered, however, all simulations first generate a constant *p*CO<sub>2</sub>  
688 for about 3 million years after the beginning of the colonization, followed by a positive excursion. For  
689 instance, when erodibility is reduced by a factor of 4 or more, an ample positive excursion in *p*CO<sub>2</sub> is  
690 simulated. Assuming a colonization lasting 30Myrs, this *p*CO<sub>2</sub> excursion generally lasts about 10  
691 million years but its duration depends on the colonization scenario.

692 Whatever the change in erodibility considered, *p*CO<sub>2</sub> after the colonization is systematically lower  
693 than before the colonization. This is true for the range of change in erodibility tested here: from a  
694 decrease by a factor of 8 to an increase by a factor of 2 when continental areas transition from naked  
695 to fully vegetated.

696 A decreasing erodibility of the continental surface from barren to fully vegetated deeply alters the  
697 latitudinal distribution of weathering. Prior to the colonization, silicate weathering mostly takes place  
698 at equatorial latitudes (between 15°S to 15°N). During the colonization, this equatorial band shifts  
699 towards a transport limited mode, facilitated by the decrease in physical erodibility, the increase in  
700 weatherability, and a warm and humid climate. This induces decrease in CO<sub>2</sub> consumption by silicate  
701 weathering in the equatorial region, promoting atmospheric CO<sub>2</sub> rise. After a few million years, this  
702 inhibition of equatorial weathering is counteracted by the progressive increase in weathering at the  
703 mid-latitudes triggered by global climate warming. It is possible that this new spatial pattern of  
704 weathering impacted the efficiency of the weathering negative feedback stabilizing the Earth climate  
705 at the geological timescale.

706 In conclusion, the impact of vascular plants on the CO<sub>2</sub> consumption by silicate weathering cannot be  
707 described as a monotonic decrease in *p*CO<sub>2</sub> forced by an increasing weatherability. It appears that the  
708 concomitant change in erodibility is critical. The paleogeographic configuration is also a major  
709 controlling parameter, as is the sequence by which the environmental occupation of vascular plants  
710 expanded. All those three factors are not well constrained, and there is a possibility that they will  
711 never be known at the degree of confidence required to understand physically the Devonian evolution  
712 of the surficial Earth system.

713

714

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720

721

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949 APPENDIX 1: THE COLONIZATION SCENARIOS

950 Figure 16. Colonization of the continents by vascular plants (in each grid element turning green, the  
951 erodibility and weatherability is shifting from its pre-colonization value to its post-colonization value  
952 (see main text). These maps stand for scenario  $\alpha$ .

953 forest\_scenario\_vegdyn.pdf

954

955 Figure 17. Colonization of the continents by vascular plants (in each grid element turning green, the  
956 erodibility and weatherability is shifting from its pre-colonization value to its post-colonization value  
957 (see main text). These maps stand for scenario  $\beta$ .

958 forest\_scenario\_vegdyn2.pdf

959

960 Figure 18. Colonization of the continents by vascular plants (in each grid element turning green, the  
961 erodibility and weatherability is shifting from its pre-colonization value to its post-colonization value  
962 (see main text). These maps stand for scenario  $\gamma$ .

963 forest\_scenario\_vegdyn3.pdf

964

965 Figure 19. Colonization of the continents by vascular plants (in each grid element turning green, the  
966 erodibility and weatherability is shifting from its pre-colonization value to its post-colonization value  
967 (see main text). These maps stand for scenario HL (same scenario that  $\beta$  except that the position of the  
968 seeding points on Gondwana has been shifted to a higher latitude).

969 forest\_scenario\_vegdyn\_hl.pdf

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