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1 **Landmark Papers: No. 7**

2

3 **Smith, K.A., Ball, T., Conen, F., Dobbie, K.E., Massheder, J. & Rey, A.. 2003. Exchange**
4 **of greenhouse gases between soil and atmosphere: interactions of soil physical factors and**
5 **biological processes. European Journal of Soil Science, 54, 779–791.**

6

7 Commentary on the impact of Smith et al. (2003): by G. Guggenberger, B. Ludwig & M. Menon

8

9

10 **Introduction**

11 Smith et al. (2003) published their review on the interactions of soil physical factors and
12 biological processes controlling the exchange of greenhouse gases between soil and atmosphere
13 at a time when global change was already considered to be one of the most important challenges
14 of mankind (IPCC, 2001). In the Climate Change 2014 Synthesis Report (IPCC, 2014) a global
15 warming of 0.7°C between 1951 and 2010 was reported and further warming and long-lasting
16 changes in all components of the climate systems forecasted. Smith K.A. et al. (2003) and later
17 Smith P. et al. (2008) emphasized that about one third of CH₄ and two thirds of N₂O emitted
18 globally to the atmosphere per year derive from soil processes, while soil is considered a small
19 CO₂ sink, which may change with increasing warming (Crowther et al., 2016). This is reason
20 enough to analyse the processes that lead to this net emission of gases to the atmosphere. While
21 biological processes produce or consume these greenhouse gases, the size of the fluxes is
22 strongly controlled by soil physical factors. However, the controlling factors on the interaction
23 between the controlling physical factors and biological processes in the exchange of greenhouse
24 gases between the soil and atmosphere had not been widely considered. Keith Smith and his
25 co-authors were pioneering in this field (e.g. Smith, 1980; Ball et al., 1997a, Ball et al., 1997b;

26 Conen et al., 2000; Dobbie & Smith, 2001), which finally led to the review of Smith et al.
27 (2003).

28

29 Controlling factors for CO₂ emissions

30 Smith et al. (2003) summarized that the release of CO₂ by aerobic respiration can be described
31 by a non-linear function of temperature over a wide range of water contents. The link between
32 microbial processes and physical factors, in addition to availability of substrate and chemical
33 factors (e.g. soil pH), is of substantial importance because of the direct and indirect effects of
34 physical factors on the production of CO₂ by microorganisms and roots. The non-linear
35 response of CO₂ as a function of temperature has been confirmed in several recent studies (e.g.
36 Schaufler et al., 2010). The factors affected by water content that were discussed by Smith et
37 al. (2003) are also now well established; water is important for gas diffusivity (Ball, 2013) and
38 substrate supply to soil microorganisms (Schindlbacher et al., 2004). Notably, Schaufler et al.
39 (2010) reported that maximum CO₂ emissions from European soils under different land uses
40 occur at intermediate soil moisture, which accords well with the summarizing synthesis by
41 Smith et al. (2003).

42 Smith et al. (2003) reported a marked scatter of Q₁₀ values for CO₂ emissions and pointed
43 out the need for standardization and accurate interpretation of temperature responses of the
44 soil's CO₂ emissions at greater depths. They emphasized that for accurate determinations and
45 interpretations of Q₁₀ values, diurnal temperature changes, thermal conductivities and thermal
46 diffusivities of the soil need to be considered in greater detail in future studies. In fact, a later
47 study by Pavelka et al. (2007) also addressed this important issue and recommended
48 measurement of soil temperature at a very shallow soil depth to determine useable values of
49 Q₁₀, and suggested a procedure to standardize Q₁₀ values for soil temperatures measured at
50 different depths.

51

52 Controlling factors for N₂O emissions

53 For N₂O, Smith et al. (2003) focused on the important microbiological processes of nitrification
54 of ammonium and denitrification of nitrate in soil, and the governing processes for the
55 respective rates. In particular, they elucidated soil conditions, e.g. structure, wetness, O₂ content
56 of pores and soil depth, being responsible for the release of N₂O to the atmosphere or further
57 reduction to N₂. Nitrate ammonification and nitrifier denitrification as additional processes
58 leading to the formation of N₂O have been discussed since in greater detail by Baggs & Phillipot
59 (2010) and Smith (2017). The merit of the review by Smith et al. (2003) lies again in the
60 important emphasis of the link between microbial processes and physical factors in addition to
61 other factors, such as substrate availability and chemical factors such as soil pH (e.g. Weslien
62 et al., 2009). This link is crucial for an understanding and prognosis of N₂O emissions.

63 Smith et al. (2003) emphasized that the anaerobic volume is affected by increases in the
64 water-filled pore space (WFPS), where an increase in WFPS may also result in an exponential
65 increase in N₂O emissions. There is still some controversy about which physical soil property
66 is most useful for estimating N₂O emissions; for example the ratio of gas diffusivity within the
67 soil to that in free air, the degree of aggregation and compaction, matric potential, WFPS and
68 volumetric water content (for a discussion see Ball, 2013 and Smith, 2017). Smith et al. (2003)
69 indicated that N₂O emissions also increase markedly with temperature. They attributed this to
70 increases in the anaerobic volume fraction. An increase in temperature results in an increase in
71 the size of the anaerobic zones because of increased respiration, which causes larger gradients
72 in O₂. In addition, increased temperatures are also likely to lead to increased rates of
73 denitrification per unit anaerobic volume. Both increases then favour a dramatic increase in
74 N₂O emissions. In fact, the concept of anaerobic zones is a key feature of the process-based
75 DNDC (denitrification-decomposition) model, for which there are several versions for different
76 land uses. This model has a kinetic scheme for the anaerobic volumetric fraction (an ‘anaerobic
77 balloon’) that is implemented to calculate the anaerobic fraction of soil in a given soil layer in

78 relation to O₂ diffusion and the respiratory activity of soil micro-organisms and roots (for a
79 summary of the DNDC model see Gilhespy et al., 2014). Overall, there is no doubt that soil
80 temperature and soil moisture are important for explaining much of the temporal variation in
81 N₂O emissions within a site (e.g. Pilegaard et al. 2006).

82

83 Controlling factors for CH₄ emissions

84 For CH₄ production and transport, Smith et al. (2003) reported that ebullition and diffusion
85 through the aerenchyma of rice and plants in natural wetlands contribute substantially to the
86 emission of CH₄ and that the proportion of the emissions taking place by each pathway varies
87 seasonally.. The oxidation of atmospheric CH₄ to CO₂ is controlled by gas diffusivity, whereas
88 the effect of temperature is small (Smith et al., 2003). Ball (2013) suggested that the control of
89 gas diffusivity on the oxidation of CH₄ might not hold for all sites and that the effect of pH,
90 moisture, temperature, and nitrogen and type of organic matter and content might be
91 pronounced. The role of nitrogen as a regulatory factor of CH₄ oxidation has been addressed in
92 detail by Bodelier & Laanbroek (2004), who discussed the inhibiting role of additions of
93 nitrogenous fertilizer. The effect of WFPS on CH₄ oxidation may be seen as a hump-shaped
94 function where the optimum oxidation occurs at 20–50% WFPS. At smaller water contents,
95 desiccation stress and at larger water contents diffusion limitation might be inhibiting CH₄
96 oxidation (Dunfield, 2007). Thus, moist, well-aerated soil favours CH₄ oxidation and CO₂
97 exchange (Ball, 2013).

98

99 Soil structure, microbial communities and greenhouse gas emissions

100 Smith et al. (2003) emphasized that although the greenhouse gases are produced by microbial
101 processes, the size of their fluxes between soil and atmosphere depends largely on soil physical
102 factors. The transport of gases within the soil and the gas exchange between soil and atmosphere
103 is a function of gas diffusivity, which depends on the air-filled porosity or, inversely, with the

104 WFPS. Most soils develop a three-dimensional architecture with pedogenesis, which is
105 characterized by the aggregate size distribution. The distribution of aggregates largely controls
106 almost every process in soil. This refers to the air-filled porosity or WFPS at a given matric
107 potential (Ball, 2013) as well as to the distribution of microbial populations in soil (Nunan et
108 al., 2003). Therefore, soil structure controls the habitat of the actors involved in the production
109 of greenhouse gases and determines the diffusion of O₂ and dissolved organic matter (DOM) to
110 fuel aerobic microbes. Consequently, inter- and intra-aggregate pore space needs to be
111 considered. Sey et al. (2008) compared the greenhouse gas emissions from various aggregate
112 size classes (<0.25 mm, 0.25–2 mm and 2–6 mm) and from 2-mm sieved bulk soil at different
113 WFPS (20, 40, 80 and 80%). They found that denitrification was responsible for 95% of N₂O
114 emissions in microaggregates, whereas nitrification was responsible for 97–99% of N₂O
115 production in macroaggregates. This inferred that diffusion of O₂ was largely inhibited in
116 microaggregates when the WFPS was 80%, whereas macroaggregates maintained aerobic
117 conditions.

118 The interrelations between soil structure and greenhouse gas emissions can be readily
119 investigated when the natural soil structure and size distribution of aggregates are disrupted due
120 to external forces (e.g. compaction), which in turn can alter the pore size distribution and
121 hydraulic properties (Menon et al., 2015). Beare et al. (2009) showed that the production of
122 N₂O was 67 times greater in compacted than uncompacted soil at field moisture contents, and
123 they demonstrated the effect of soil moisture on emissions of N₂O and CO₂. Deurer et al. (2012)
124 reported enhanced carbon sequestration under the wheel tracks, probably because of reduced
125 microbial decomposition of organic matter. Bessou et al. (2010) also found that compacted soil
126 had smaller emissions of CO₂, but at the same time larger N₂O emissions by inducing anoxic
127 conditions favourable for denitrification activity.

128 Experiments with compacted soil also help to elucidate the relation between microbial
129 communities and greenhouse gas emissions depending on soil physical factors. So Nadian et

130 al. (1998) reported a significant decline in vesicular-arbuscular mycorrhizal fungi biomass at
131 higher bulk density, and Peacock et al. (2001) found a significant reduction in microbial
132 biomass for heavy traffic treatments. Schnurr-Pütz et al. (2006) observed that fungi, in
133 particular, are negatively affected by soil compaction, whereas denitrifiers and methanogens
134 appear to be more prominent. From that, the links between soil physical properties and
135 greenhouse gas emissions can be conceptualized as in Fig. 1.

136

137 New developments in linking soil physical factors to biological processes

138 In their landmark paper on the interactions of soil physical factors and biological processes,
139 Smith et al. (2003) focus on gas diffusivity, which affects soil aeration and the capacity of the
140 soil microbial community to produce or consume CO₂, N₂O and CH₄. The concept of hotspots
141 and hot moments (Kuzyakov & Blagodatskaya, 2015) adds the supply of the organic substrates,
142 which is also linked partly to soil physical factors. Transport of the labile OM sources to the
143 microbial community occurs largely through biotic activities such as the release of root
144 exudates (Jones et al. 2004) and the detritus of soil animals (Schrader et al. 2007), but also as
145 DOM leached from the O and A horizons (Qualls & Haines 1992). Translocation of DOM to
146 the subsoil depends strongly on the flow paths in soil and on soil structure and precipitation
147 events (Leinemann et al. 2016). Because DOM is mainly translocated in the inter-aggregate
148 pore space of the soil, it is retained on aggregate surfaces, which are enriched in OM (Amelung
149 et al. 2002), thus creating a hotspot. At the same time, the inter-aggregate pore space usually
150 enables good aeration, leading to the release of CO₂ with microbial decomposition of the
151 substrate. In otherwise aerobic soil, strong microenvironments may exist that are important
152 sources of N₂O and CH₄ (Keiluweit et al. 2016). Hotspots of denitrification and methanogenesis
153 in the intra-aggregate pore space results from slow diffusion of O₂, whereas in the rhizosphere
154 this is caused by the inflow of very available OM from root exudation (Henry et al. 2008). This,
155 once again, emphasizes the complex interplay of soil physical factors and biological processes

156 in the production of greenhouse gases in soil and their exchange between soil and atmosphere
157 (Smith et al. 2003).

158

159 Methodological progress

160 The landmark paper of Smith et al. (2003) on these interactions also triggered substantially the
161 methodological development with respect to the visualization of pores of different size, to
162 measurement of microbial activity and the resulting O₂ and CO₂ partial pressures at small
163 scales, and the development of physical and biophysical models. In the last decade much
164 progress in the understanding of soil structure and the associated pore-space architecture has
165 been? gained by X-ray computed tomography (CT), which enables an in-situ and real-time 3-
166 D mapping at scales of a few microns. Measured properties include porosity, pore-size
167 distribution, tortuosity and topology (Naveed et al. 2013; Vogel et al. 2010). Peth et al. (2014)
168 showed that synchrotron-based X-ray CT in combination with osmium staining is not only
169 suitable for describing soil structure, but also for identifying the location of organic matter in
170 soil, e.g. in the intra-aggregate pore space. Neutron radiography emerged as a useful method to
171 map the water distribution within soil and its temporal changes (Oswald et al. 2008; Carminati
172 et al. 2010), whereas the 2-D distribution of oxygen concentration can be analysed by
173 fluorescence imaging with planar optodes (Blossfeld et al. 2011). Rudolph-Mohr et al. (2017)
174 emphasized the great potential of combining neutron radiography with fluorescence imaging
175 to investigate the effect of different soil moisture conditions on the oxygen patterns in soil. Such
176 analyses may provide important input parameters for geometry-based mechanistic models.

177 Keith Smith also pioneered modelling of microbial respiration and denitrification at the
178 aggregate scale by systematically incorporating factors such as oxygen supply and nitrogen
179 concentration (Smith, 1980). Ebrahimi & Or (2015, 2016) have built on that and developed a
180 3-D pore-scale model that simulates the aerobic and anaerobic microbial communities within
181 aggregates together with rates of production of N₂O and CO₂ along the aggregate radius. This

182 model considers substrate and oxygen diffusion processes and is integrated with individual cell-
183 based models that link soil physical processes with microbial community dynamics. Ebrahimi
184 & Or (2016) upscaled this modelling framework to quantify depth-resolved rates of production
185 of CO₂ and N₂O depending on small-scale environmental conditions. In a very recent model,
186 this approach was used to quantify methane production in thawing permafrost soil, based on
187 the microbial activity dynamics in pore networks with? consideration of transport dynamics and
188 physiological aspects of the cells (Ebrahimi & Orr, 2017).

189

190 **Conclusions**

191 Smith and co-authors expressed hope that their review would demonstrate the key roles played
192 by soil physical factors in controlling the biological processes responsible for the exchange of
193 greenhouse gases between soil and atmosphere. Indeed, the authors convincingly built a bridge
194 between soil physics and soil biology. From this landmark publication and some other
195 manuscripts, soil biophysics has developed as an emerging field within the soil sciences. Inter-
196 and intra-aggregate pore architecture is decisive in the control of the availability of O₂ and
197 organic substrates to microorganisms. It is thus of utmost importance not only for the
198 production of the different greenhouse gases, but also for organic matter stabilization and biotic
199 redox processes associated with mineral weathering and mineral transformation. The effect of
200 biota on soil physical factors has also received increasing interest recently. This concerns, for
201 example, the formation of aggregates by living and dead organic agents, which affects soil
202 structure and associated pore architecture, or the rhizosphere, where water uptake by the roots
203 strongly modifies the WFPS. Novel instrumental and modelling approaches will allow an
204 understanding of the multiple interactions between soil physical and biotic processes in soil in
205 relation to soil functioning and ecosystem services. This is only possible by crossing the
206 boundaries in soils science, which is what this landmark paper emphasized.

207

208 **References**

- 209 Amelung, W., Kaiser, K., Kammerer, G. & Sauer, G. 2002. Organic carbon at soil particle
210 surfaces—Evidence from X-ray photoelectron spectroscopy and surface abrasion. *Soil*
211 *Science Society of America Journal*, **66**, 1526–1530.
- 212 Baggs, E. & Phillipot, L. 2010. Microbial terrestrial pathways to nitrous oxide. In: *Nitrous*
213 *Oxide and Climate Change* (ed. K.A. Smith), pp. 4–35. Earthscan, London.
- 214 Ball, B.C. 2013. Soil structure and greenhouse gas emissions: a synthesis of 20 years of
215 experimentation. *European Journal of Soil Science*, **64**, 357–373.
- 216 Ball, B.C., Dobbie, K.E., Parker, J.P.O. & Smith, K.A. 1997a. The influence of gas transport
217 and porosity on methane oxidation in soils. *Journal of Geophysical Research*, **102**, 23309–
218 23317.
- 219 Ball, B.C., Smith, K.A., Klemmedtsson, L., Brumme, R., Sitaula, B.K., Hansen, S. et al. 1997b.
220 The influence of soil gas transport properties on methane oxidation in a selection of northern
221 European soils. *Journal of Geophysical Research*, **53**, 29–39.
- 222 Benckiser, G., Schartel, T. & Weiske, A. 2015. Control of NO₃⁻ and N₂O emission in
223 agroecosystems: a review. *Agronomy for Sustainable Development*, **35**, 1059–1074.
- 224 Bessou, C., Mary, B., Leonard, J., Roussel, M., Grehan, E. & Gabrielle, B. 2010. Modelling
225 soil compaction impacts on nitrous oxide emissions in arable fields. *European Journal of*
226 *Soil Science*, **61**, 348–363.
- 227 Blossfeld, S., Gansert, D., Thiele, B., Kuhn, A.J. & Lösch, R. 2011. The dynamics of oxygen
228 concentration, pH value, and organic acids in the rhizosphere of *Juncus* spp. *Soil Biology &*
229 *Biochemistry*, **43**, 1186–1197.
- 230 Bodelier, P.L.E. & Laanbroek, H.J. 2004. Nitrogen as a regulatory factor of methane oxidation
231 in soils and sediments. *FEMS Microbiology Ecology*, **47**, 265–277.
- 232 Carminati, A., Moradi, A.B., Vetterlein, D., Vontobel, P., Lehmann, E., Weller, U., et al. 2010.
233 Dynamics of soil water content in the rhizosphere. *Plant and Soil*, **332**, 163–176.

234 Conen, F., Dobbie, K.E. & Smith, K.A. 2000. Predicting N₂O emissions from agricultural land
235 through related soil parameters. *Global Change Biology*, **6**, 417–426.

236 Crowther, T.W., Todd-Brown, K.E.O., Rowe, C.W., Wieder, W.R., Carey, J.C., Machmuller,
237 M.B. et al. 2016. Quantifying global soil carbon losses in response to warming. *Nature*, 540,
238 104–108.

239 Dobbie, K.E. & Smith, K.A. 2001. The effects of temperature, water-filled pore space and land
240 use on N₂O emissions from an imperfectly drained gleysol. *European Journal of Soil*
241 *Science*, **52**, 667–673.

242 Dunfield, P.F. 2007. The soil methane sink. In: *Greenhouse Gas Sinks* (eds D.S. Reay, C.N.
243 Hewitt, K.A. Smith & J. Grace), pp. 152–157. CAB International, Wallingford, UK.

244 Ebrahimi, A. & Or, D. 2015. Hydration and diffusion processes shape microbial community
245 organization and function in model soil aggregates. *Water Resources Research*, **51**, 9804–
246 9827.

247 Ebrahimi, A. & Or, D. 2016. Microbial community dynamics in soil aggregates shape
248 biogeochemical gas fluxes from soil profiles—Upscaling an aggregate biophysical model.
249 *Global Change Biology*, **22**, 3141–3156.

250 Ebrahimi, A. & Or, D. 2017. Mechanistic modeling of microbial interactions at pore to profile
251 scale resolve methane emission dynamics from permafrost soil. *Journal of Geophysical*
252 *Research: Biogeosciences*, **122**, 1216–1238.

253 Gilhespy, S.L., Anthony, S., Cardenas, L., Chadwick, D., del Prado, A., Li, C.S., Misselbrook
254 T. et al. 2014. First 20 years of DNDC (DeNitrification DeComposition): model evolution.
255 *Ecological Modelling*, **292**, 51–62.

256 Henry, S., Texier, S., Hallet, S., Bru, D., Dambreville, C., Chèneby, D. et al. 2008.
257 Disentangling the rhizosphere effect on nitrate reducers and denitrifiers: insight into the role
258 of root exudates. *Environmental Microbiology*, **10**, 3082–3092.

259 IPCC. 2001. Climate Change 2001: The Scientific Basis. Contribution of Working Group I to
260 the Third Assessment Report of the Intergovernmental Panel on Climate Change (eds J.T.
261 Houghton, Y. Ding, D.J. Griggs, M. Noguer, P.J. van der Linden, X. Dai et al.) Cambridge
262 University Press, Cambridge, United Kingdom and New York, NY, USA, .

263 IPCC. 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II
264 and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change
265 (eds Core Writing Team, R.K. Pauchauri & L.A. Meyer). IPCC, Geneva, Switzerland.

266 Jones, D.L., Hodge, A. & Kuzyakov, Y. 2004. Plant and mycorrhizal regulation of
267 rhizodeposition. *New Phytologist*, **163**, 459–480.

268 Keiluweit, M., Nico, P.S., Kleber, M. & Fendorf, S. 2016. Are oxygen limitations under
269 recognized regulators of organic carbon turnover in upland soils? *Biogeochemistry*, **127**,
270 157–171.

271 Leinemann, T., Mikutta, R., Kalbitz, K., Schaarschmidt, F. & Guggenberger, G. 2016. Small
272 scale variability of vertical water and dissolved organic matter fluxes in sandy Cambisol
273 subsoils as revealed by segmented suction plates. *Biogeochemistry*, **131**, 1–15.

274 Menon, M., Jia, X., Lair, G.J., Fraj, P.H. & Bland, A. 2015. Analysing the impact of compaction
275 of soil aggregates using X-ray microtomography and water flow simulations. *Soil & Tillage
276 Research*, **150**, 147–157.

277 Nadian, H., Smith, S.E., Alston, A.M., Murray, R.S. & Siebert, B.D. 1998. Effects of soil
278 compaction on phosphorus uptake and growth of *Trifolium subterraneum* colonized by four
279 species of vesicular-arbuscular mycorrhizal fungi. *New Phytologist*, **140**, 155–165.

280 Naveed, M., Moldrup, P., Arthur, E., Wildenschild, D., Eden, M., Lamande, M. et al. 2013.
281 Revealing soil structure and functional macroporosity along a clay gradient using X-ray
282 computed tomography. *Soil Science Society of America Journal*, **77**, 403–411.

283 Nunan, N., Wu, K., Young, I.M., Crawford, J.W. & Ritz, K. 2003. Spatial distribution of
284 bacterial communities and their relationships with the micro-architecture of soils. *FEMS*
285 *Microbiology Ecology*, **44**, 203–215.

286 Oswald, S.E., Menon, M., Carminati, A., Vontobel, P., Lehmann, E. & Schulin, R. 2008.
287 Quantitative imaging of infiltration, root growth, and root water uptake via neutron
288 radiography. *Vadose Zone Journal*, **7**, 1035–1047.

289 Pavelka, M., Acosta, M., Marek, M.V., Kutsch, W. & Janous, D. 2007. Dependence of the Q_{10}
290 values on the depth of the soil temperature measuring point. *Plant and Soil*, **292**, 171–179

291 Peth, S., Chenu, C., Leblond, N., Mordhorst, A., Garnier, P., Nunan, N. et al. 2014. Localization
292 of soil organic matter in soil aggregates using synchrotron-based X-ray microtomography.
293 *Soil Biology & Biochemistry*, **78**, 189–194.

294 Pilegaard, K., Skiba, U., Ambus, P., Beier, C., Brüeggemann, N., Butterbach-Bahl, K. et al.
295 2006. Factors controlling regional differences in forest soil emission of nitrogen oxides (NO
296 and N₂O). *Biogeosciences*, **3**, 651–661.

297 Qualls, R.G. & Haines, B.L. 1992. Biodegradability of dissolved organic matter in forest
298 throughfall, soil solution, and stream water. *Soil Science Society of America Journal*, **56**,
299 578–586.

300 Rudolph-Mohr, N., Tötze, C., Kardjilov, N. & Oswald, S.E. 2017. Mapping water, oxygen,
301 and pH dynamics in the rhizosphere of young maize roots. *Journal of Plant Nutrition and*
302 *Soil Science*, **180**, 336–346.

303 Schaufler, G., Kitzler, B., Schindlbacher, A., Skiba, U., Sutton, M.A. & Zechmeister-
304 Boltenstern, S. 2010. Greenhouse gas emissions from European soils under different land
305 use: effects of soil moisture and temperature. *European Journal of Soil Science*, **61**, 683–
306 696.

307 Schindlbacher, A., Zechmeister-Boltenstern, S. & Butterbach-Bahl, K. 2004. Effects of soil
308 moisture and temperature on NO, NO₂, and N₂O emissions from European forest soils.
309 *Journal of Geophysical Research*, **109**, 1–12.

310 Sey, B.K., Maceur, A.M., Wahlen, J.K., Gregorich, E.G. & Rochette, P. 2008. Small-scale
311 heterogeneity in carbon dioxide, nitrous oxide and methane production from aggregates of a
312 cultivated sandy-loam soil. *Soil Biology & Biochemistry*, **40**, 2468–2473.

313 Smith, K.A. 1980. A model of the extent of anaerobic zones in aggregated soils, and its potential
314 application to estimates of denitrification. *Journal of Soil Science*, **31**, 263–277.

315 Smith, K.A., 2017. Changing views of nitrous oxide emissions from agricultural soil: key
316 controlling processes and assessment at different spatial scales. *European Journal of Soil
317 Science*, **68**, 137–155.

318 Smith, K.A., Ball, T., Conen, F., Dobbie, K.E., Massheder, J. & Rey, A. 2003. Exchange of
319 greenhouse gases between soil and atmosphere: interactions of soil physical factors and
320 biological processes. *European Journal of Soil Science*, **54**, 779–791.

321 Smith, P., Fang, C., Dawson, J.J.C. & Moncrieff, J.B. 2008. Impact of global warming on soil
322 organic carbon. *Advances in Agronomy*, **97**, 1–43.

323 Tiunov, A.V. & Scheu, S. 2000. Microbial biomass, biovolume and respiration in *Lumbricus*
324 *terrestris* L. cast material of different age. *Soil Biology & Biochemistry*, **32**, 265–275.

325 Schnurr-Pütz, S., Bååth, E., Guggenberger, G., Drake, H. & Küsel, K. 2006. Compaction of
326 forest soil by logging machinery favours occurrence of prokaryotes. *FEMS Microbiology
327 Ecology*, **58**, 503–516.

328 Vogel, H.-J., Weller, U. & Schlüter, S. 2010. Quantification of soil structure based on
329 Minkowski function. *Computational Geosciences*, **36**, 1236–1245.

330
331
332

333 **Figure**

334

335 Figure 1. Conceptual model on the link between soil physical properties and greenhouse gas
336 emission depending on soil compaction (Menon and Bland, unpublished). Soil compaction
337 leads to changes in soil structure (e.g. porosity), which will affect the flow of air and water,
338 and thereby create a more anaerobic environment in soil. This may lead to a shift in the
339 relative abundance and functions of the microbial population, shown here as effects on the
340 C and N cycles. Abundance of nitrifiers and aerobic degraders are given by dashed lines and
341 abundance of denitrifiers and methanogens are given by solid lines.

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