

1 **Land inclination controls CO₂ and N₂O fluxes, but not CH₄ uptake, from a**
2 **temperate upland forest soil**

3 Lauren M. Gillespie¹, Nathalie Y. Triches², Diego Abalos³, Peter Finke⁴, Sophie Zechmeister-
4 Boltenstern¹, Stephan Glatzel⁵, Eugenio Díaz-Pinés¹

5 ¹ Institute of Soil Research, University of Natural Resources and Life Sciences, Vienna (BOKU), Peter-
6 Jordan-Straße 82, 1190, Vienna, Austria.

7 ² Department of Environment, Faculty of Bioscience Engineering, Ghent University, Coupure links 653,
8 B-9000, Ghent, Belgium. Present address: Max Planck Research Institute for Biogeochemistry, Hans-
9 Knöll- Straße 10, 07745, Jena, Germany.

10 ³ Department of Agroecology, iCLIMATE, Aarhus University, Blichers Allé 20, Tjele, 8830, Denmark.

11 ⁴ Department of Environment, Research group of soilscape genesis, Ghent University, Coupure links
12 653, B-9000, Ghent, Belgium.

13 ⁵ University of Vienna, Department of Geography and Regional Research, Universitätsstraße 7, 1010
14 Vienna, Austria.

15

16 **Abstract**

17 Inclination and spatial variability in soil and litter properties influence soil greenhouse gas
18 (GHG) fluxes, and thus on-going climate change, but their relationship in forest ecosystems is
19 poorly understood. To elucidate this, we explored the effect of inclination, distance to a stream,
20 soil moisture, soil temperature, and other soil and litter properties on soil-atmosphere fluxes of
21 carbon dioxide (CO₂), methane (CH₄), and nitrous oxide (N₂O) with automated static chambers
22 in a temperate upland forest in Eastern Austria. We hypothesised that soil CO₂ emissions and
23 CH₄ uptake are higher in sloped locations with lower soil moisture content, whereas soil N₂O
24 emissions are higher in flat, wetter locations. During the measurement period, soil CO₂
25 emissions were significantly higher on flat locations ($p < 0.05$), and increased with increasing
26 soil temperature ($p < 0.001$) and decreasing soil moisture ($p < 0.001$). The soil acted as a CH₄

27 sink, and CH₄ uptake was not significantly related to inclination. However, CH₄ uptake was
28 significantly higher at locations furthest away from the stream compared to at the stream ($p <$
29 0.001), and positively related to litter weight and soil C content ($p < 0.01$). N₂O fluxes were
30 significantly higher on flat locations and further away from the stream ($p < 0.05$), and increased
31 with increasing soil moisture ($p < 0.001$), soil temperature ($p < 0.001$) and litter depth ($p <$
32 0.05). Overall, this study underlines the importance of inclination and the resulting soil and
33 litter properties in predicting GHG fluxes from forest soils and therefore their potential source-
34 sink balance.

35

36 **Keywords:** slope inclination, soil greenhouse gas fluxes, carbon dioxide, methane, nitrous
37 oxide, soil moisture, forest litter

38

39 **Introduction**

40 Forests play a crucial role in the global climate by emitting and consuming the greenhouse gases
41 (GHGs) carbon dioxide (CO₂), methane (CH₄), and nitrous oxide (N₂O) (IPCC, 2022). They
42 store a large amount of carbon (C) in the vegetation and soil organic matter and can be effective
43 CO₂ sinks (Pan et al., 2011). Soil microorganisms also take up atmospheric C through the
44 oxidisation of CH₄ during methanotrophy (Le Mer and Roger, 2001; Hiltbrunner et al., 2012).
45 However, forest soils also emit substantial quantities of CO₂ (Webster et al., 2008), which, in
46 aerobic conditions, is mainly released by root respiration and microbial respiration during
47 decomposition (Cronan, 2018; Zechmeister-Boltenstern et al., 2018). N₂O is produced by soil
48 microorganisms, mainly during nitrification and denitrification (Butterbach-Bahl et al., 2013).
49 In aerobic conditions, bacteria convert ammonium to nitrite and further to nitrate during
50 nitrification. In anoxic conditions, nitrate is then used as an alternative electron acceptor instead
51 of O₂ and reduced to N₂ during denitrification (Butterbach-Bahl et al., 2014). Under most
52 conditions, these processes occur simultaneously and usually result in a net atmospheric

53 emission of N₂O (Ambus, 1998). Conversely, net N₂O uptake has been reported from forest
54 soils, especially since monitoring instrumentation has become sensitive enough to measure very
55 low fluxes (Savage et al., 2014; Subke et al., 2021). Net N₂O uptake (from the atmosphere into
56 the soil) is a complex process closely tied to N₂O consumption (within the soil) that is driven
57 principally by denitrifying bacteria (Liu et al., 2022).

58 Temporal and spatial variations in soil CO₂, CH₄, and N₂O fluxes are driven mostly by changes
59 in soil temperature and soil moisture (Raich and Potter, 1995; Davidson et al., 1998; Le Mer
60 and Roger, 2001; Butterbach-Bahl et al., 2014). Rising temperatures accelerate microbial
61 activities and, consequently, the production and emission of N₂O and CO₂ (Butterbach-Bahl et
62 al., 2013). Elevated soil respiration could lead to a depletion of O₂, which also results in
63 increased N₂O from denitrification (Butterbach-Bahl et al., 2013). Contrarily, CH₄ uptake
64 appears to be less sensitive to temperature changes than CO₂ and N₂O fluxes (Hanson and
65 Hanson, 1996). Soil moisture has a major influence on all GHG fluxes by regulating O₂ and
66 substrate availability to soil microorganisms and influencing the diffusion of gases within the
67 soil matrix (Butterbach-Bahl et al., 2014; Schimel, 2018). Indeed, soil microbial activity
68 decreases as soils become water saturated (Davidson et al., 2012). Soil moisture further affects
69 fluxes since diffusion coefficients of GHG in air are approximately 10⁴ times larger than in
70 water (Marrero and Mason, 1972).

71 Inclination and distance to a water source influence some of the most important drivers of soil
72 GHG fluxes. For example, soil moisture content changes on small scales at different
73 inclinations through accumulation, runoff, and leaching of precipitation water (Burt and
74 Butcher, 1985; Lookingbill and Urban, 2004; Lin et al., 2006). Inclination also modifies other
75 important drivers of soil GHG fluxes, such as the hydrological transport of nutrients (Hairston
76 and Grigal, 1994), litter accumulation (Butler et al., 1986), soil aeration, soil texture, soil pH,
77 and substrate availability (soil C and N), usually resulting in a high GHG spatial variability
78 (e.g., Fierer and Jackson, 2006; Thomas and Packham, 2007). Flat locations by a water source

79 are also at higher risk to be influenced by flooding and subsequent changes to the soil properties
80 and soil microbial community (Ou et al., 2019; Unger et al., 2009). Forest litter in particular
81 can have a major impact on the exchange of GHGs by adding nutrients to the soil, acting as a
82 physical barrier (i.e., holding gases in the soil rather than releasing them into the atmosphere)
83 or influencing the water and heat exchange between soil and atmosphere (Leitner et al., 2016;
84 Walkiewicz et al., 2021).

85 Studies on the effect of inclination on GHG fluxes from temperate upland forest soils are
86 particularly rare. Some studies reported higher soil CO₂ emissions on sloped compared to flat
87 locations, associated with warmer air and soil temperatures and lower soil moisture contents,
88 favouring faster diffusion rates though not so low as to impede microbial activity (Yu et al.,
89 2008; Warner et al., 2018). Conversely, no effect of topography on soil CO₂ emissions has also
90 been reported in a laboratory study from a montane tropical forest (Arias-Navarro et al., 2017).
91 With regard to CH₄, relatively little is known on how inclination and its influence on chemical
92 and physical soil properties may affect CH₄ fluxes (Warner et al., 2018). Soil CH₄ uptake is
93 highly variable in space and time and appears to be highest on dry slopes (Hiltbrunner et al.,
94 2012; Yu et al., 2021), even though it is assumed that temperate upland forest soils take up CH₄
95 irrespective of the inclination (Lamprea Pineda et al., 2021). Effects of inclination on N₂O
96 fluxes are also contradictory. Some studies show increased N₂O emissions with higher soil
97 water content at flat locations (Davidson et al., 2000; Lamprea Pineda et al., 2021), whereas
98 others show a higher emission in aerated soils on slopes (Yu et al., 2008, 2021). Assessing the
99 impact of inclination on soil GHGs therefore remains a challenging task.

100 In this study, we aim to improve the understanding of the effects of inclination and distance to
101 a stream on the emission and uptake of GHGs in a temperate upland forest soil in Eastern
102 Austria. We monitored soil CO₂, CH₄, and N₂O fluxes with automated chambers over six
103 months for two different inclinations and at four distances from a stream in a deciduous forest.
104 We tested three hypotheses: 1) Soil CO₂ emissions are higher in sloped than flat locations

105 because of the inclination and the lower soil moisture content at sloped locations; 2) Soil CH₄
106 uptake is higher in sloped than flat locations because of the inclination and the lower soil
107 moisture content at sloped locations; and 3) Soil N₂O emissions are lower in sloped than flat
108 locations because of the inclination and the higher soil moisture content at flat locations.

109

110 **Methods**

111 *Study site and experimental design*

112 This study was conducted within the framework of the “Long-Term Ecosystem and socio-
113 ecological Research Infrastructure - Carbon, Water and Nitrogen” (LTER-CWN) project
114 (further information is available at <https://www.lter-austria.at/en/cwn-sites/>). The BOKU
115 University Forest “Rosalia Lehrforst” (47°42’25.35” N / 16°16’36.62” E) is one of the
116 associated sites and served as the site for our study (see Fürst et al., 2021) for more information).
117 At the site, European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) H. Karst.)
118 are the dominant tree species, but alluvial forest species (*Alnus spp.* Mill, *Fraxinus excelsior*
119 L.) are also present next to the study location. The elevation is around 400 m a.s.l. and the
120 dominant soil type is pseudo-gleyic Cambisol (Schad, 2016).

121 We used the GasFluxTrailer (explained below) to measure soil GHG fluxes from 17 June to 24
122 November 2020. We positioned 16 chambers linearly in groups of four at four different
123 distances from a small forest stream: 0.5 m, 5 m, 10 m, and 15 m (Fig. S1). Adjacent trees to
124 the chambers were *F. sylvatica* and *P. abies*. These distances served as first treatment effect
125 and are hereafter referred to as chamber group (CG): CG0.5, CG5, CG10, and CG15. These
126 distances were chosen because they were expected to cover a decreasing soil moisture gradient
127 from CG0.5 towards CG15. To measure this gradient, one Em50 (METER Group, Inc. Pullman,
128 WA; USA) was connected to four ECH2O 5 TM volumetric water content and temperature
129 sensors (METER Group). One sensor was installed per CG approximately one meter away from
130 the outer chamber (Fig S.1). As a second treatment effect, the distances were also chosen so

131 that the CGs were set up at two different inclinations. CG0.5 and CG5 were located at flat
132 (average 1°; the slope at these distances did not exceed 2°), CG10 and CG15 at sloped locations
133 (average 35°; west-facing).

134 For meteorological information, we used the precipitation (OTT Pluvio L weighing rain gauge)
135 and air temperature (air temperature and humidity sensor TR1) data recorded at 30 min intervals
136 by the weather station “Mehlbeerleiten”, located approximately 100 m north-west of the site
137 (Diaz-Pines and Gasch, 2021; Fürst et al., 2021).

138

139 *Gas flux measurements: GasFluxTrailer*

140 An automated and mobile measuring system was used, termed the GasFluxTrailer. It consists
141 of a mobile trailer estimating soil-atmosphere GHG exchange rates of CH₄, CO₂, and N₂O. The
142 GasFluxTrailer connects with the chambers, and it controls the sampling of each individual
143 chamber (i.e., the opening and closing and gas sampling) and recording of the gas
144 concentrations. The 16 automated, static, non-steady-state, non-flow-through chambers
145 (Pumpanen et al., 2004) with an area of 0.5 m × 0.5 m and height of 0.15 m are made of
146 stainless-steel and placed on stainless-steel frames of the same area. They are equipped with
147 fans to ensure homogenous air mixing. The gas analysers are a G2301 (PICARRO Inc., Santa
148 Clara, USA), measuring concentrations of CO₂ and CH₄, and a G5131i (PICARRO Inc.),
149 estimating N₂O concentrations. The software used to run automatic sequences is the IDASw
150 Recorder 4.5.0., developed by the Institute of Meteorology and Climate Research Atmospheric
151 Environmental Research (IMK-IFU) in Germany.

152

153 *Field and laboratory measurements*

154 We inserted the chamber frames 5 cm deep into the soil approximately one month before the
155 measuring campaign to avoid additional soil CO₂ release from cut roots, affecting our
156 measurements (Davidson et al., 2002). For each measurement estimate, a chamber was closed

157 for 10 min, which, thanks to the highly sensitive instruments used here, was sufficient time to
158 measure gas concentrations changes, including low N₂O fluxes (Harris et al., 2021). The closing
159 and opening was done successively; thus one full cycle of all 16 chambers took 160 minutes.
160 We calculated fluxes with a linear regression approach according to Butterbach-Bahl et al.
161 (2011). This was justified with short chamber closure times and a relatively large chamber size
162 (Hutchinson and Mosier, 1981). Positive flux values indicate gas emission from the soil, and
163 negative values indicate net uptake. To ensure the system was running and working correctly,
164 we controlled the GHG flux measurements on-site every week and three-four times a week
165 remotely. There were no inundations or significant drying/rewetting events during the
166 observation period.

167 Close to each of the 16 chambers, a litter and soil sample was collected in December 2021. The
168 litter depth was measured first, before disturbing the litter and topsoil by placing a 0.2 m × 0.2
169 m frame on the ground at this location. The litter was then collected within this frame, dried at
170 65°C for 7 days, and weighed. After litter collection and removal of organic layer, two soil
171 cores (stainless steel core, 7 cm diameter, 7 cm depth) were taken from the topsoil mineral layer
172 for analyses of pH, C and N content, and soil texture. C and N contents (%) were determined
173 by dry combustion on 1.6 mg of soil using the Austrian standard ÖNORM L 1080 (ÖNORM,
174 2013). Particle size analysis was conducted using the pipette method on 10 g of soil according
175 to the Austrian standard ÖNORM L 1061 (ÖNORM, 2002), after the organic material had been
176 burned off in an oven at 550 °C, to determine soil texture (%). In short, sieved soil (<2 mm) is
177 agitated in a volume of water, and a pipette is used to sample a defined volume at a defined
178 depth at specific times after which the samples are dried to determine clay and silt contents.
179 The remaining soil is then sieved (63 µm) to determine sand content. Soil pH was measured on
180 5 g of soil with 0.01 M CaCl₂ using the Austrian standard ÖNORM L 1083 (ÖNORM, 2006).
181 Because the soil was relatively rocky, we calculated the soil bulk density (BD, g cm⁻³) including
182 the coarse (stone) fraction as:

183
$$BD \text{ with stones} = \frac{\text{dry soil weight}}{\text{core volume}}$$

184 where dry soil weight is the weight of the soil in the core after oven drying in g and core volume
185 is the volume of the core in cm³.

186 We calculated the total porosity (Φ) using the bulk density and an estimated soil particle density,
187 obtained by a weighted average of the specific weights of mineral material (2.65 g cm⁻³) and
188 organic matter (1.45 g cm⁻³). We took into account the organic matter content because it was
189 relatively high, i.e., between 8 and 27 %.

190

191 *Data processing and statistics*

192 We quality-controlled the CO₂, CH₄, and N₂O flux data using the determination coefficient (R-
193 squared, R²) values between GHG concentrations and the time after chamber closure. For CO₂
194 and CH₄, we filtered the data with R² > 0.8 and a visual plausibility check based on expert
195 knowledge. For N₂O, R² > 0.8 was applied only if fluxes were > 5 μg N₂O-N m⁻² h⁻¹. For low
196 flux rates (< 5 μg N₂O-N m⁻² h⁻¹), we did not remove values with R² < 0.8 if corresponding CO₂
197 fluxes were valid. We kept these measurements in the dataset, because the low R² values were
198 due to fluxes below the detection limit of the system; however, the measurement itself remained
199 valid as indicated by plausible CO₂ fluxes, and as elaborated in Parkin et al. (2012). Through
200 this quality control, we found that two chambers did not produce any reliable measurements
201 from 24 September onwards. August data for all chambers was excluded due to malfunctioning
202 of the equipment that was not initially detected. Furthermore, all the data from one chamber
203 (chamber 13) were also not used for the analysis because of a failure in the chamber gas
204 sampling. After data quality screening, there were 125 measurement days included in analysis
205 for CO₂ and CH₄, and 85 days for N₂O.

206 All statistical analyses were performed with R (version 4.0.4; R Core Team, 2022). All data
207 was visually and statistically checked for normality (Levene's test) and homoscedasticity before

208 testing for statistical differences. Since the original data was not normally distributed, CO₂ and
209 N₂O fluxes were log-transformed. To homogenise the data from the gas flux analysers and the
210 soil temperature and soil moisture sensors, we rounded all gas flux data to 3-hour intervals
211 (00:00, 03:00, 06:00, 09:00, 12:00, 15:00, 18:00, 21:00), corresponding to the approximate gas
212 flux measurement cycle duration. Soil temperature and soil moisture data was available every
213 30 min and was thus also aggregated for the same 3-hour intervals. For the statistical analyses,
214 we ran linear mixed-effect models (LMM) using the “lmer” function from the lme4 package
215 (version 1.1-27; Bates et al., 2015), the “lmerTest” package (version 3.1-3; Kuznetsova et al.,
216 2017), and the “optimx” function from the optimx package (version 2021-6.12; Nash and
217 Varadhan, 2011). Models were selected according to the guidelines of Zuur et al. (2009). For
218 the null models, soil temperature, soil moisture, and inclination or distance from the stream
219 (i.e., 0.5 m to 15 m away from the stream, CG0.5 – CG15) were included as fixed effects, with
220 an interaction between soil temperature and soil moisture. Sampling date and chamber number
221 were included as random effects. Sampling date was included as a random variable since we
222 were not exploring temporal changes and since there were multiple observations per day.
223 Inclination and distance were not included in the same model because they were highly
224 correlated. We therefore separated our treatments in “inclination” and “distance”, resulting in
225 two LMM models per GHG. We then created a model, using the original model structure,
226 including each soil or litter characteristic individually as an additional explanatory variable.
227 The model Akaike Information Criteria (AIC) were then compared using ANOVA. Finally,
228 we selected the model with the lowest AIC value if it was significantly different from the null
229 model. This was done for each gas-inclination or distance combination. To obtain the
230 conditional and marginal R² of the models, the “r2_nakagawa” function from the performance
231 package was used (version 0.7.3; Nakagawa et al., 2017).

232

233 **Results**

234 Over the measurement period (June–November 2020, 161 days), the mean air temperature was
 235 12.30°C and cumulative precipitation was 561 mm. The average volumetric water content, here
 236 referred to as ‘soil moisture’, was $0.22 \pm 0.07 \text{ m}^3 \text{ m}^{-3}$, with wetter soils in flat
 237 ($0.28 \pm 0.04 \text{ m}^3 \text{ m}^{-3}$) compared to sloped locations ($0.17 \pm 0.02 \text{ m}^3 \text{ m}^{-3}$; Fig. S2). The mean soil
 238 temperature was $12.85 \pm 2.62^\circ\text{C}$, with no significant difference between flat and sloped
 239 locations. The wettest and warmest location was at CG5 ($0.31 \pm 0.03 \text{ m}^3 \text{ m}^{-3}$ and $13.62 \pm 2.54^\circ\text{C}$;
 240 Fig. S2). Changes in soil moisture and soil temperature were strongly related to variation of
 241 precipitation and air temperature (Fig. S3). Furthermore, the interaction between soil moisture
 242 and soil temperature was significant in all models ($p < 0.001$), showing a decrease in soil
 243 moisture with increasing soil temperature. Litter depth and weight were much lower at CG0.5
 244 than at all other CGs (Table 1). Soil N and C contents and organic matter content were lowest
 245 at CG0.5 and highest at CG10, but C:N ratios were similar at all CGs (Table 1). Bulk density
 246 was low ($0.6\text{--}0.8 \text{ g cm}^{-3}$) at all distances. Soil pH was considerably higher at CG0.5 compared
 247 to all other CGs (Table 1). The soil in flat locations was sandier, whereas the sloped locations
 248 were more clayey (Table 1).

249 **Table 1:** Average value and standard error of litter and soil parameters at each distance from
 250 the stream. “CG” indicates chamber group, with the numbers 0.5, 5, 10, and 15 defining the
 251 distance to the stream (m). Different letters indicate differences between distances (Dunn
 252 multiple comparison test after Kruskal–Wallis test, $p < 0.05$) for each variable.

Variable	Unit	Chamber group			
		CG0.5	CG5	CG10	CG15
Litter depth	cm	4.4 ± 0.7^a	7.0 ± 1.2^{ab}	8.5 ± 1.0^b	8.0 ± 1.4^b
Litter weight	g m^{-2}	147.7 ± 23.1^a	311.8 ± 47.0^{ab}	358.5 ± 100.0^{ab}	622.2 ± 362.1^b
Soil N content	%	0.25 ± 0.06^a	0.39 ± 0.09^{ab}	0.6 ± 0.26^b	0.42 ± 0.18^{ab}
Soil C content	%	4.12 ± 0.78^a	6.35 ± 1.65^{ab}	10.15 ± 4.8^b	7.85 ± 4.29^{ab}
Soil C:N ratio	-	16.56 ± 1.35^a	16.24 ± 0.81^a	17.07 ± 1.81^a	18.23 ± 1.99^a
Bulk density*	g cm^{-3}	0.81 ± 0.15^a	0.73 ± 0.12^a	0.6 ± 0.11^a	0.81 ± 0.08^a
Volumetric stone content	%	7.59 ± 8.4^a	7.84 ± 2.57^a	10.79 ± 2.78^a	13.16 ± 2.24^a
Porosity†	-	0.75 ± 0.01^a	0.79 ± 0.03^{ab}	0.87 ± 0.04^b	0.80 ± 0.02^{ab}
Organic material (OM)	%	9.25 ± 1.4^a	13.87 ± 3.73^{ab}	20.86 ± 8.01^b	16.70 ± 7.02^{ab}
Soil pH	-	5.57 ± 0.65^a	4.00 ± 0.34^{ab}	4.01 ± 0.34^{ab}	3.78 ± 0.31^b

Sand content	%	598.970 ± 7.5 ^a	52.0 ± 9.5 ^a	40.6 ± 3.7 ^a	41.6 ± 4.4 ^a
Silt content	%	38.5 ± 7.7 ^a	45.1 ± 8.5 ^a	53.1 ± 4.5 ^a	52.0 ± 5.0 ^a
Clay content	%	2.5 ± 0.3 ^a	2.9 ± 1.4 ^a	6.3 ± 1.4 ^b	6.5 ± 0.7 ^{ab}

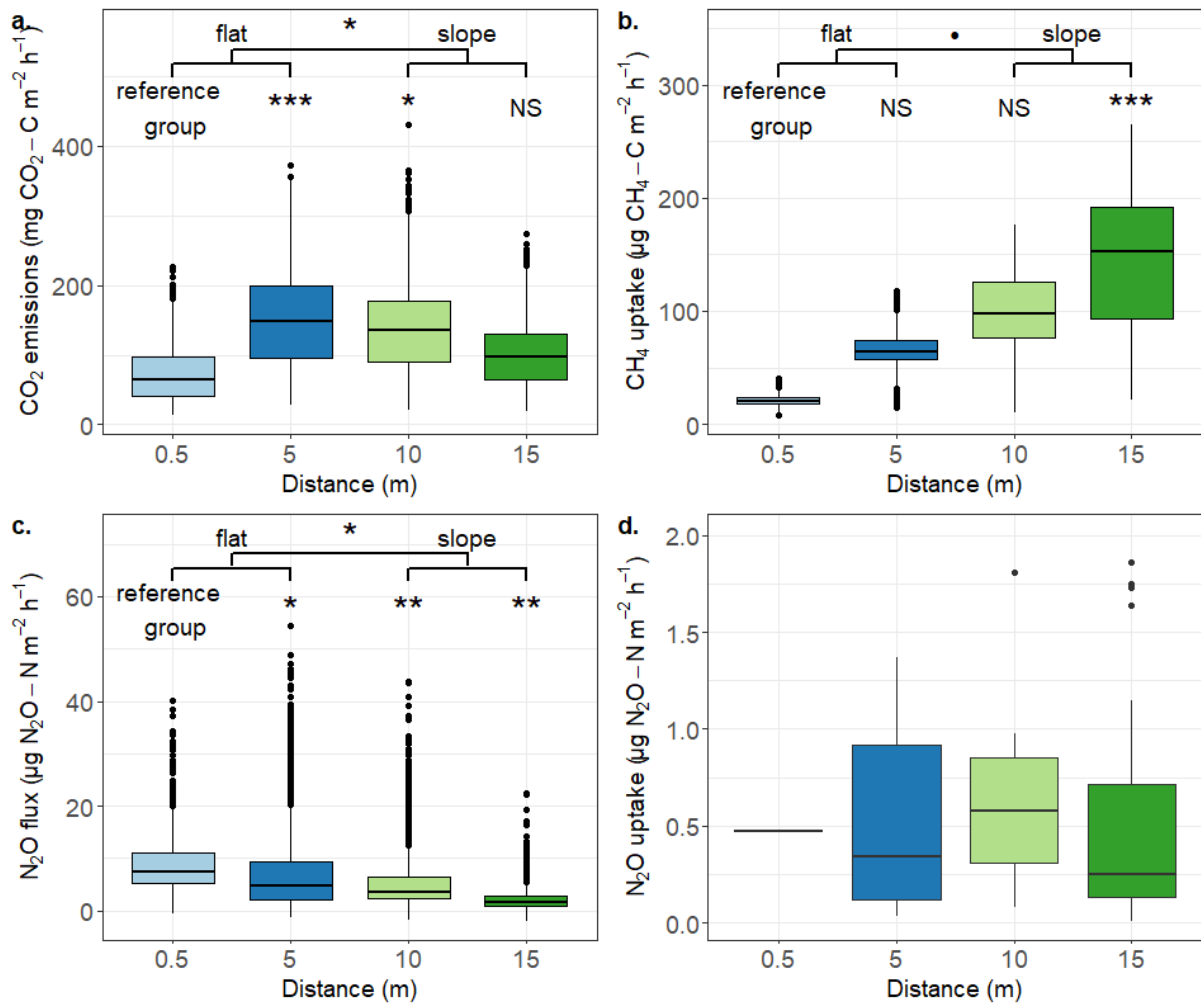
*with coarse material

†without coarse material

253

254 *Soil CO₂ emissions*

255 The average soil CO₂ emissions during the observation period were
256 116.2 ± 61.5 mg CO₂-C m⁻² h⁻¹, with flat and sloped locations emitting 113.6 ± 66.7 and
257 118.6 ± 56.3 mg CO₂-C m⁻² h⁻¹, respectively (Table 2, Fig. 1a). The soil CO₂ emission pattern
258 was bell-curved with increasing distance from the stream, with the lowest emissions at CG0.5,
259 the highest emissions at CG5 and CG10, and relatively low emissions at CG15 as compared to
260 CG10 (Table 2, Fig. 1a). Our analysis showed a significant inclination effect on soil CO₂
261 emissions ($p < 0.05$); furthermore, we found a significant difference between emissions at
262 CG0.5 and CG5 ($p < 0.001$), as well as between CG0.5 and CG10 ($p < 0.05$, Table 2).



264

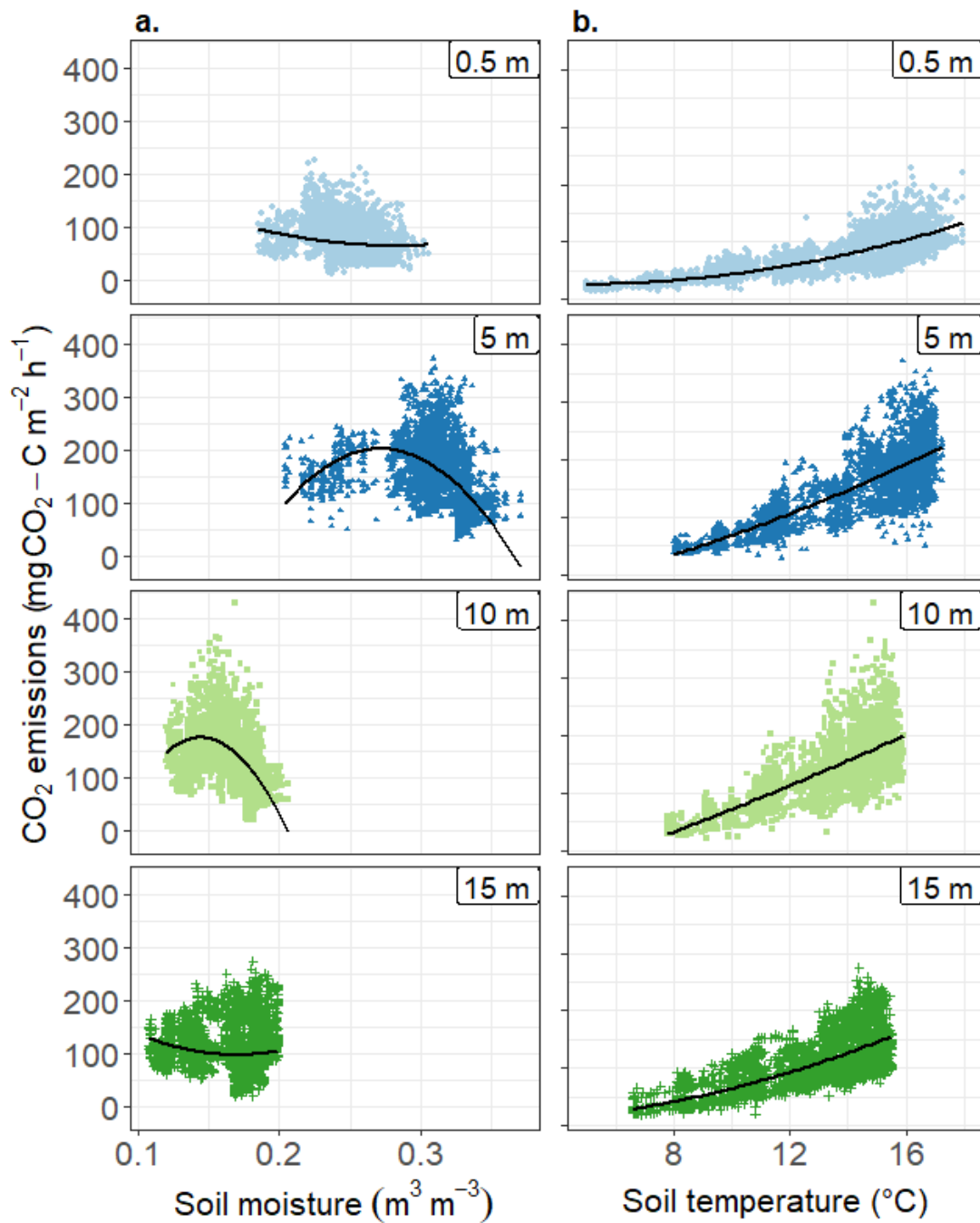
265 **Figure 1:** a. CO₂ emissions (mg CO₂-C m⁻² h⁻¹), b. CH₄ uptake (µg CH₄-C m⁻² h⁻¹), c. N₂O flux
 266 (µg N₂O-N m⁻² h⁻¹), and d. N₂O uptake (µg N₂O-N m⁻² h⁻¹) at four distances from a stream: 0.5
 267 m, 5 m, 10 m, and 15 m (i.e., Chamber Groups: CG0.5, CG5, CG10, and CG15). Blue indicates
 268 flat locations, and green indicates sloped locations. Statistical significances are from the
 269 'distance model' (linear mixed model, LMM) for the differences between the four distances
 270 and the 'inclination model' for the differences between the flat and slope positions associated
 271 with each gas (Table 1, 2, 3); no LMM was run for N₂O uptake. Non-significance is indicated
 272 by 'NS' and *p*-values are coded as *p* < 0.1 '.', *p* < 0.05 '*', *p* < 0.01 '**', and *p* < 0.001 '***'.

273

274 **Table 2:** LMM results exploring the relationship between inclination (flat compared to slope)
 275 or distance (m), soil moisture ($\text{m}^3 \text{m}^{-3}$), soil temperature ($^{\circ}\text{C}$), soil moisture:soil temperature
 276 interaction, soil pH, and volumetric stone content on soil CO_2 emissions ($\text{mg CO}_2\text{-C m}^{-2} \text{h}^{-1}$).
 277 Soil pH and volumetric stone content are included because the LMM models including these
 278 variables had AIC values statistically smaller than the null model. $R^2\text{m}$ indicates marginal R^2 ,
 279 and $R^2\text{c}$ indicates conditional R^2 values. P -values are coded as: $p < 0.05$ ‘*’, $p < 0.01$ ‘***’, and
 280 $p < 0.001$ ‘****’.

CO₂ emissions	$R^2\text{c}= 0.91$		$R^2\text{m}= 0.28$		AIC= -9475.99	
Inclination – pH	Estimate	Std. Error	df	t value	Pr(> t)	
Soil moisture	-1.48	0.18	11330.00	-8.22	< 2E-16	***
Soil temperature	0.06	4.55E-03	9060.00	14.08	< 2E-16	***
Inclination (slope)	-0.41	0.17	12.20	-2.42	0.03	*
Moisture:temperature	-0.05	0.01	11410.00	-4.35	1.40E-05	***
Soil pH	-0.41	0.12	12.00	-3.33	6.02E-03	**
CO₂ emissions	$R^2\text{c}= 0.91$		$R^2\text{m}= 0.42$		AIC= -9474.05	
Distance – stone content	Estimate	Std. Error	df	t value	Pr(> t)	
Soil moisture	-1.49	0.18	11300.00	-8.26	< 2E-16	***
Soil temperature	0.06	4.55E-03	9060.00	14.07	< 2E-16	***
Distance 5 m	0.86	0.16	10.10	5.52	2.49E-04	***
Distance 10 m	0.43	0.16	10.10	2.76	0.02	*
Distance 15 m	0.14	0.16	10.10	0.86	0.41	
Moisture:temperature	-0.05	0.01	11400.00	-4.35	1.39E-05	***
Volumetric stone content	0.02	0.01	10.00	1.76	0.11	

281
 282 Both model results showed a significant negative correlation between soil CO_2 emissions and
 283 soil moisture ($p < 0.001$, Table 2). This pattern was more distinct looking at the CGs at the
 284 different distances (Fig. 2a). A significant positive correlation between CO_2 emissions and soil
 285 temperature was found ($p < 0.001$, Table 2, Fig. 2b). The interaction between soil moisture and
 286 temperature, namely soil moisture decreasing with increasing soil temperature, was shown to
 287 correlate negatively with CO_2 emissions ($p < 0.001$, Table 2). According to “inclination” model
 288 results, CO_2 emissions also decreased with increasing soil pH when comparing flat to sloped
 289 locations ($p < 0.01$, Table 2).



290

291 **Figure 2:** Relationship between soil CO₂ emissions (mg CO₂-C m⁻² h⁻¹) and **a.** soil moisture
 292 (m³ m⁻³), and **b.** soil temperature (°C) by distance from the stream (0.5 m, 5 m, 10 m, 15 m).

293 Flat locations are indicated in blue (0.5 m and 5 m) and sloped locations in green (10 m and 15
 294 m). The fitted lines show the linear regression on geometrically distributed data using the

295 “geom_smooth” function (method = “lm”) from ggplot2. The R² for these regressions are

296 shown in Table 2.

297
 298
 299
 300
 301
 302
 303
 304
 305
 306
 307
 308
 309
 310
 311
 312
 313
 314
 315
 316

Soil CH₄ uptake

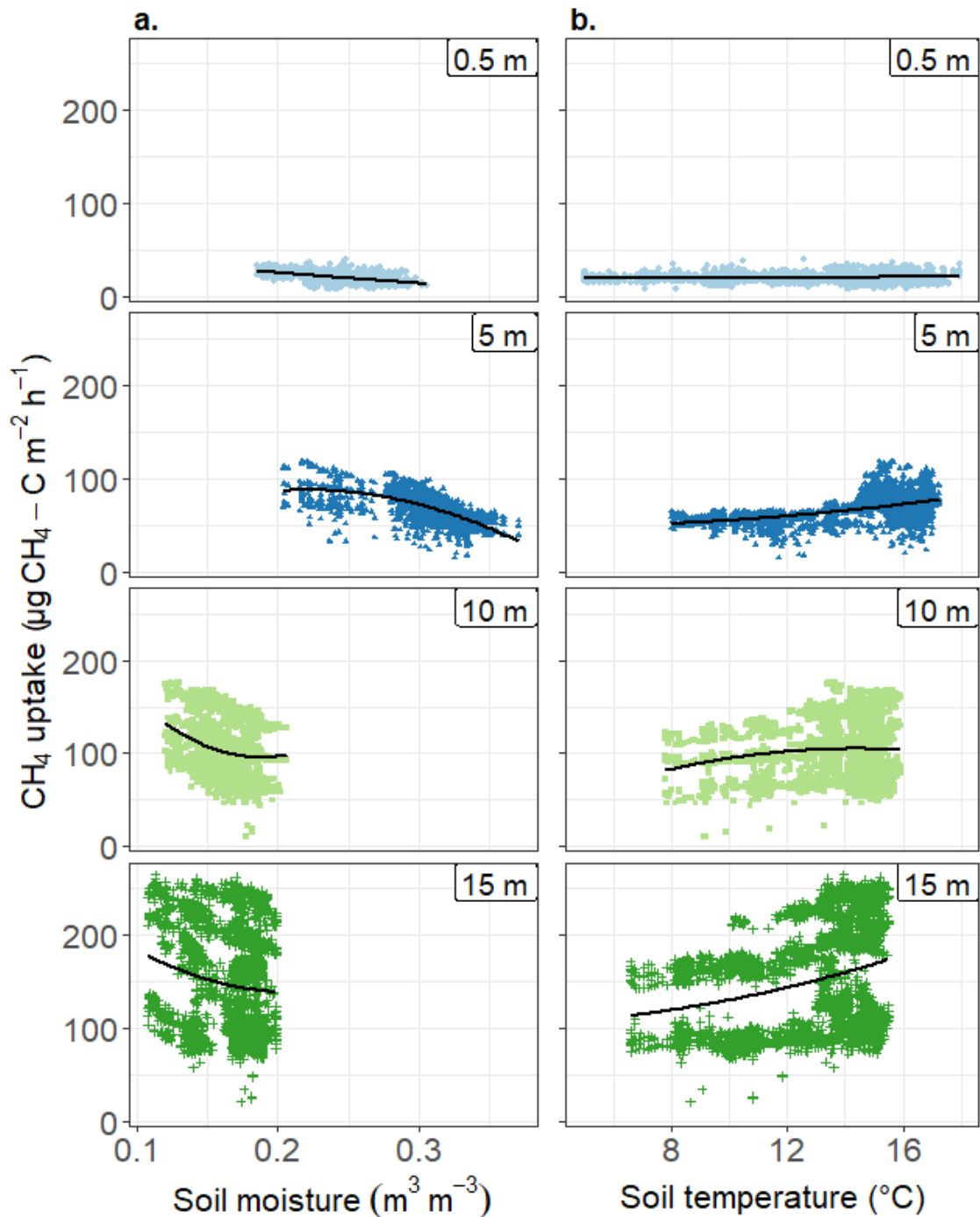
The soil showed an average CH₄ uptake of 88.5 ± 58.0 μg CH₄-C m⁻² h⁻¹, with uptake 180 % higher in sloped as compared to flat locations (126.9 ± 51.3 and 45.0 ± 25.3 μg CH₄-C m⁻² h⁻¹, respectively; Fig. 1b). Average CH₄ uptake increased by approximately 40 μg CH₄-C m⁻² h⁻¹ per 5 m distance further away from the stream (Fig. 1b). However, the “inclination” model showed only marginally significant differences between the CH₄ uptake at flat and sloped locations (*p* < 0.1, Table 3). Litter weight was positively correlated with the CH₄ uptake at flat and sloped locations (*p* < 0.001). The “distance” model showed a significant difference between the locations at the stream (CG0.5) and furthest away (CG15; *p* < 0.001, Table 3) and a positive correlation between soil C content and CH₄ uptake at all CGs (*p* < 0.01, Table 3).

Table 3: LMM results exploring the relationship between inclination (flat compared to slope) or distance (m), soil moisture (m³ m⁻³), soil temperature (°C), soil moisture:soil temperature interaction, litter weight (g), and soil C content effects on soil CH₄ uptake (μg CH₄-C m⁻² h⁻¹). Litter weight and soil C content are included because the LMM models including these variables had AIC values statistically smaller than the null model. R²m indicates marginal R², and R²c indicates conditional R² values. *P*-values are coded as: *p* < 0.1 ‘.’, *p* < 0.05 ‘*’, *p* < 0.01 ‘**’, and *p* < 0.001 ‘***’.

CH₄ uptake	R ² c= 0.97		R ² m= 0.67		AIC= 88007.79	
Inclination – Litter weight	Estimate	Std. Error	df	t value	Pr(> t)	
Soil moisture	173.06	12.81	11318.95	13.51	< 2E-16	***
Soil temperature	-2.52	0.33	10140.69	-7.71	1.43E-14	***
Inclination (slope)	30.51	15.49	12.11	1.97	0.07	.
Moisture:temperature	-14.73	0.80	11406.27	-18.34	< 2E-16	***
Litter weight	0.80	0.16	12.00	4.92	3.54E-4	***
CH₄ uptake	R ² c= 0.97		R ² m= 0.70		AIC= 87987.56	

Distance – Soil C content	Estimate	Std. Error	df	t value	Pr(> t)	
Soil moisture	172.71	12.81	11313.21	13.48	< 2E-16	***
Soil temperature	-2.52	0.33	10139.66	-7.71	1.41E-14	***
Distance 5 m	31.93	18.74	10.02	1.70	0.12	
Distance 10 m	24.10	22.20	10.02	1.09	0.30	
Distance 15 m	93.49	19.82	10.02	4.72	8.15E-04	***
Moisture:temperature	-14.73	0.80	11406.02	-18.34	< 2E-16	***
Soil C content	7.82	2.04	10.00	3.83	3.3E-03	**

317
318 Both “inclination” and “distance” model results show a significant, positive correlation between
319 soil moisture and CH₄ uptake ($p < 0.001$), and a significant, negative correlation between soil
320 temperature and CH₄ uptake ($p < 0.001$, Table 3). These patterns could, however, not be
321 confirmed visually (Fig. 3). Like for CO₂ emissions, the soil moisture:soil temperature
322 interaction, namely soil moisture decreasing with increasing soil temperature, was significant
323 ($p < 0.001$, Table 3). According to the “inclination” model results, litter weight was positively
324 correlated with the CH₄ uptake at flat and sloped locations ($p < 0.001$). The “distance” model
325 showed that higher soil C content resulted in a higher CH₄ uptake at all CGs ($p < 0.01$, Table
326 3).



327
 328 **Figure 3:** Relationship between CH₄ uptake (μg CH₄-C m⁻² h⁻¹) and **a.** soil moisture (m³ m⁻³),
 329 and **b.** soil temperature (°C) by distance from the stream (0.5 m, 5 m, 10 m, 15 m). Flat locations
 330 are indicated in blue (0.5 m and 5 m) and sloped locations in green (10 m and 15 m). The fitted
 331 lines show the linear regression on geometrically distributed data using the “geom_smooth”
 332 function (method = “lm”) from ggplot2. The R² for these regressions are shown in Table 3.

333

334 *Soil N₂O flux*

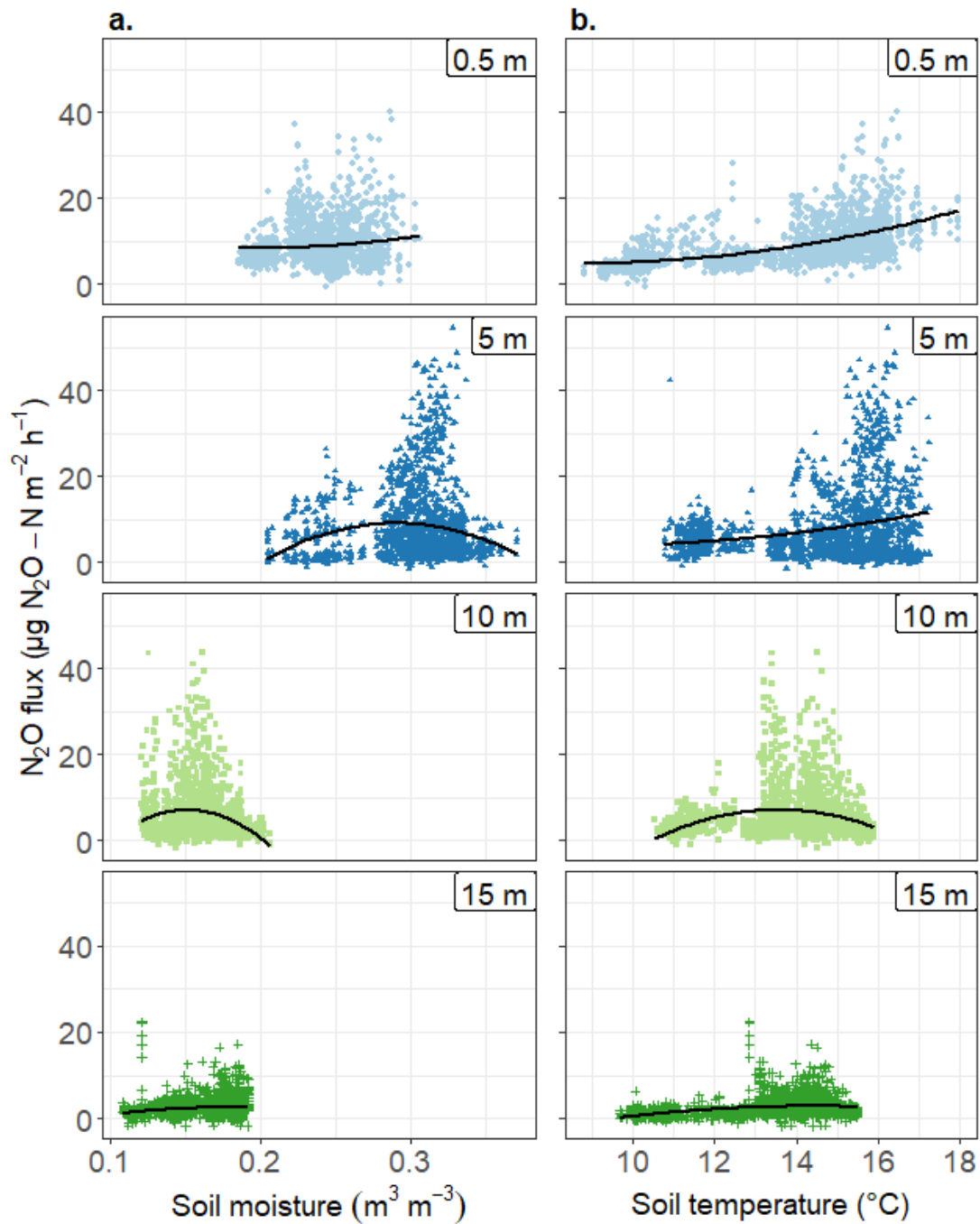
335 The soil had an average N₂O emission of $5.9 \pm 6.3 \mu\text{g N}_2\text{O-N m}^{-2} \text{ h}^{-1}$, with flat locations having
 336 120% higher fluxes than sloped (8.4 ± 7.2 and $3.8 \pm 4.5 \mu\text{g N}_2\text{O-N m}^{-2} \text{ h}^{-1}$, respectively;
 337 Fig. 1c). The “inclination” model results showed significantly decreasing N₂O emissions on
 338 sloped locations compared to flat locations ($p < 0.05$, Table 3). This was supported by the
 339 “distance” model results, with significantly decreasing emissions from CG0.5 towards CG15
 340 (Fig. 1c, Table 4).

341 **Table 4:** LMM results exploring the relationship between inclination (flat compared to sloped)
 342 or distance (m), soil moisture ($\text{m}^3 \text{ m}^{-3}$), soil temperature ($^{\circ}\text{C}$), soil moisture:soil temperature
 343 interaction, and litter depth (cm) on soil N₂O emissions ($\mu\text{g N}_2\text{O-N m}^{-2} \text{ h}^{-1}$). Litter depth is
 344 included because the LMM model including this variable had an AIC value statistically smaller
 345 than the null model. R²m indicates marginal R², and R²c indicates conditional R² values. *P*-
 346 values are coded as: $p < 0.05$ ‘*’, $p < 0.01$ ‘**’, and $p < 0.001$ ‘***’.

N₂O emissions	R ² c= 0.79		R ² m= 0.21		AIC= 4993.94	
Inclination	Estimate	Std. Error	df	t value	Pr(> t)	
Soil moisture	7.75	0.62	7660.60	12.46	< 2E-16	***
Soil temperature	0.16	0.01	3119.98	11.42	< 2E-16	***
Inclination (slope)	-0.62	0.23	13.61	-2.71	0.02	*
Moisture:temperature	-0.58	0.04	7445.77	-14.07	< 2E-16	***
N₂O emissions	R ² c= 0.80		R ² m= 0.39		AIC= 4995.59	
Distance – Litter depth	Estimate	Std. Error	df	t value	Pr(> t)	
Soil moisture	7.74	0.62	7650.00	12.45	< 2E-16	***
Soil temperature	0.16	0.01	3120.00	11.40	< 2E-16	***
Distance 5 m	-0.82	0.35	10.10	-2.35	0.04	*
Distance 10 m	-1.51	0.45	10.00	-3.36	7.24E-03	**
Distance 15 m	-1.81	0.42	10.10	-4.36	1.42E-03	**
Moisture:temperature	-0.58	0.04	7440.00	-14.04	< 2E-16	***
Litter depth	0.25	0.09	9.99	2.70	0.02	*

347 We found significant positive correlations between N₂O emissions and both soil moisture and
 348 soil temperature in both the “inclination” and “distance” model ($p < 0.001$, Table 3). The
 349 correlation between N₂O emissions and soil moisture appeared bell-curved at CG5 and CG10
 350

351 (Fig. 4a). The correlation between N₂O emissions and soil temperature appeared bell-curved at
352 CG10 (Fig. 4b). As for CO₂ and CH₄ fluxes, the soil moisture:soil temperature interaction
353 resulted in significantly decreasing N₂O emissions across all CGs and both the flat and sloped
354 locations. Similar to the “inclination” model results for CH₄ uptake, the N₂O “distance” model
355 showed that a higher litter depth resulted in increasing N₂O emissions at all CGs ($p < 0.05$).



356

357 **Figure 4:** Relationship between N₂O fluxes (μg N₂O-N m⁻² h⁻¹) and **a.** soil moisture (m³ m⁻³),
 358 and **b.** soil temperature (°C) by distance from the stream (0.5 m, 5 m, 10 m, 15 m). Flat locations
 359 are indicated in blue (0.5 m and 5 m) and sloped locations in green (10 m and 15 m). The fitted
 360 lines show the linear regression on geometrically distributed data using the “geom_smooth”
 361 function (method = “lm”) from ggplot2. The R² for these regressions are shown in Table 4.

362

363 Over the 85-day measurement period, we detected episodes of N₂O uptake at eleven chambers.
364 The measured uptake rates averaged $0.51 \pm 0.48 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$. N₂O uptake occurred
365 predominantly in sloped locations (number of observations: 65 sloped, 16 flat), notably at CG15
366 (50 observations; Fig. 1d), and predominantly later in the measurement period (September to
367 November).

368

369 **Discussion**

370 *Soil CO₂ emissions*

371 The soil CO₂ emissions estimated in this study are similar to those from studies in nearby
372 forests, with $115.7 \text{ mg CO}_2\text{-C m}^{-2} \text{h}^{-1}$ and $113.0 \text{ mg CO}_2\text{-C m}^{-2} \text{h}^{-1}$ emitted in Rosalia (Leitner
373 et al., 2016) and at Schottenwald, near Vienna, respectively (Hahn et al., 2000). The values we
374 measured are only slightly lower than the average soil CO₂ emission from 18 different forest
375 ecosystems amongst Europe (Janssens et al., 2001). However, other studies in comparable
376 beech and spruce stands in France (Epron et al., 1999) and Germany have found values up to
377 50% lower (Luo et al., 2012). Apart from differences in measurement methods and seasons, it
378 is very likely that most of the differences can be explained by variations in soil moisture (e.g.,
379 Hanson et al., 1993) and temperature (e.g., Lloyd and Taylor, 1994), as discussed in the
380 following section.

381

382 *Effect of inclination and distance to a stream on soil CO₂ emissions*

383 Model results showed a significant negative effect of inclination, with lower soil CO₂ emissions
384 on sloped locations. This is contrary to our first hypothesis and to the findings of studies from
385 temperate and boreal forests in North America (Creed et al., 2013; Warner et al., 2018), where
386 soil CO₂ emissions were highest in sloped locations compared to ridge and flat locations, while
387 a subtropical forest in Puerto Rico showed only a weak relation between CO₂ fluxes and
388 topographic variation (Quebbeman et al., 2022). However, our results suggest that higher CO₂

389 emissions at flat locations were mainly driven by CG5, where we observed the highest CO₂
390 emissions. Being at the foot hill of the slope, CG5 likely received a large water and nutrient
391 input from the steep slope as compared to the other distances and had optimal conditions for
392 soil microbial activity. A soil texture favourable to microbial activity (enough clay to retain
393 moisture and enough sand to allow sufficient volatile substrate and O₂ access) could lead to
394 such a peak, but the clay content was not significantly different between CG0.5, CG5, and
395 CG15 nor was the sand significantly different at any distance. The effect of soil moisture on
396 CO₂ emissions was different across the CGs: at CG10, where we recorded the second-highest
397 emissions, soil moisture was as low as at CG15. It is possible that the high porosity at CG10
398 enabled an easier diffusion of CO₂ from the soil matrix to the atmosphere. However, even
399 though we found highest emissions at the wettest CG, our overall results showed higher CO₂
400 emissions with decreasing soil moisture, probably due to the negative correlation between soil
401 moisture and soil temperature. Indeed, the strong interaction between soil moisture and
402 temperature, seen in the model results for all three gases, restricts our ability to draw firm
403 conclusions for these variables individually. Consistent over all CGs, we found that CO₂
404 emissions increased with increasing soil temperature, in agreement with findings from, e.g.,
405 temperate Norway spruce and beech forests in Europe (Epron et al., 1999; Hahn et al., 2000;
406 Buchmann, 2000; Luo et al., 2012), where most temporal variations in the soil CO₂ flux could
407 be explained by soil temperature. The spatial variability of soil moisture and soil temperature
408 itself may be an effect of a different slope, its exposition and the direction from where the rain
409 comes. This influences the amount of rain reaching the soil surface and the evapotranspiration
410 of the forest, which results in a differing water balance. Compared to sites in North America
411 (Creed et al., 2013; Warner et al., 2018) and Germany (Buchmann, 2000), and considering the
412 exposition of the slope (Finke 2022, personal communication), our site is likely drier.

413 We suggest that the effect of inclination and distance to the stream were closely interacting with
414 indirect effects on soil properties and resulted in different soil CO₂ emissions than we expected,

415 notably at CG5. For example, CO₂ emissions were significantly lower at CG0.5 than all other
416 CGs, and soil pH was the highest at this distance, probably due to the close proximity to the
417 forest stream with a higher pH value or root-mediated changes in the pH (Hinsinger et al., 2003;
418 Fürst et al., 2021). Higher soil pH (> 5) can increase soil CO₂ fluxes by stimulating autotrophic
419 respiration from living roots and heterotrophic respiration from soil microorganisms (Reth et
420 al., 2005; Aciego Pietri and Brookes, 2008). However, our model results suggest increasing
421 CO₂ emissions with low soil pH values. We suggest that this is due to the chemistry in the soil,
422 namely the dominating carbonate species (Finke 2022, personal communication). At a low soil
423 pH, carbonic acid (H₂CO₃) dominates over carbonate (CO₃²⁻), and carbonic acid might release
424 CO₂. At high pH, carbonate dominates, which can hinder CO₂ emissions. We encourage
425 researchers to analyse their sites covering a wider range of microbial communities, roots, and
426 soil nutrients, which might give further insight on whether soil pH directly or indirectly
427 influences soil CO₂ emissions on a topological and moisture gradient. Overall, inclination likely
428 had an indirect effect on the CO₂ emissions at our study site through its influence on soil
429 moisture and soil properties at the base of the slope (GC5) where the highest emissions were
430 measured.

431

432 *CH₄ uptake*

433 The soil CH₄ uptake at our site was considerably higher than values reported from other studies
434 in the same forest (Leitner et al., 2016), in forests near Vienna (Hahn et al., 2000), and in
435 Germany (Born et al., 1990; Brumme and Borken, 1999). These differing values support the
436 findings in forest ecosystems across Northern Europe, where temperate forest soils showed CH₄
437 uptake rates with a widely varying range between 1-165 µg CH₄-C m⁻² h⁻¹ (Smith et al., 2000).
438 The uptake on our sloped locations (126.9 ± 51.3 µg CH₄-C m⁻² h⁻¹) falls on the upper end of
439 this range. Different measurement methods, involving the use of manual chambers and gas
440 chromatography in nearby plots (see Leitner et al., 2016) compared to automated chambers and

441 laser-based gas analysers in our study, could explain the dissimilar values obtained in the same
442 forest ecosystem. In addition, the measurement period of this study did not cover the entire
443 year, which may give rise to the differences between this study and previous studies conducted
444 at the same site. As for soil CO₂ emissions, spatial variability resulting from the exposition of
445 the slope, and the differences in soil moisture and soil temperature, might be other reason for
446 our high values. Because the soils at our site are relatively dry, this might have favoured the
447 uptake of soil CH₄.

448

449 *Effect of inclination and distance to a stream on soil CH₄ uptake*

450 Opposite to our second hypothesis, soil CH₄ uptake was not significantly correlated with
451 inclination. This is opposite to the findings of other studies that did find an inclination effect.
452 However, the studies are not in agreement as to where uptake is higher: in a subtropical forest
453 in Puerto Rico, higher CH₄ uptake on ridges was found as compared to in valleys (Quebbeman
454 et al., 2022); in a temperate forest in Maryland, USA, CH₄ uptake was higher in transition zones
455 than uplands, and valley bottoms were occasionally large net sources (Warner et al., 2018); and
456 in a tropical forest in China, hillslopes were found to be hotspots for CH₄ uptake, while the
457 slope foot and groundwater discharge zone contributed less (Yu et al., 2021). Nonetheless, soil
458 CH₄ uptake was significantly higher at CG15 compared to CG0.5, suggesting that the distance
459 to the stream did have an effect on CH₄ uptake; the two other distances were potentially not far
460 enough from the stream for them to have a significant effect on the soil moisture, soil
461 temperature, and soil parameters that would lead to an effect on the CH₄ uptake. With
462 significant positive correlations between both litter weight and soil C content with CH₄ uptake,
463 we suggest that soil C content and litter regulated CH₄ uptake over distance. In agreement with
464 our findings, Warner et al. (2018) found a higher CH₄ uptake on locations with high C content
465 in a temperate forest landscape in Maryland, USA. Litter can hinder water from precipitation
466 to easily enter into the soil (Walkiewicz et al., 2021). Since there was more litter on sloped than

467 on flat locations, the litter could have stored the rainfall water, thus keeping the mineral soils
468 underneath drier at sloped locations, as has been reported in other studies (Borken and Beese,
469 2006; Wang et al., 2013). We therefore suggest that inclination modulated the soil CH₄ uptake
470 through its influence on weight and depth of the litter layer, and that inclination *per se* was not
471 the main driver of CH₄ uptake at our site. Instead, the weight and depth of the litter layer and
472 the soil C content had the largest effect on the CH₄ uptake.

473 In our study, both models showed higher CH₄ uptake rates with increasing soil moisture and
474 decreasing soil temperature. This does not only contradict findings from other forests (e.g.,
475 Adamsen and King, 1993; Castro et al., 1995) but cannot be distinguished visually (Fig. 3). It
476 is possible that our models produced ambiguous results for soil moisture and temperature,
477 because they were unavoidably associated in our studied *in situ* system; both variables are
478 influenced by inclination and distance to a stream concurrently and this thus limits our ability
479 to draw firm conclusions about either variable separately. Running a LMM with one variable
480 or the other did not help resolve this ambiguity. A long-term study in a German forest, also
481 found that soil moisture and soil temperature only weakly correlated with CH₄ uptake and were
482 not able to find a suitable empirical model for CH₄ (Luo et al., 2012). The lack of clear
483 relationships between soil moisture and soil temperature with CH₄ uptake confirms that litter
484 and soil C content were the best predictors of CH₄ uptake at our site.

485

486 *Soil N₂O fluxes*

487 The soil N₂O emissions from our site were very similar to the rates reported 200 m further
488 upslope from this study (Leitner et al., 2016) and in deciduous forests near Vienna (Pilegaard
489 et al., 2006), with values between 5.4 and 6.4 μg N₂O-N m⁻² h⁻¹, respectively. They are also
490 comparable to the average N₂O emissions from soils in seven European coniferous forests
491 (Pilegaard et al., 2006), but lower than N₂O emission estimates in forests subjected to high N
492 deposition rates in Europe (Hahn et al., 2000; Luo et al., 2012; Gundersen et al., 2012),

493 suggesting that N deposition was not a significant driver for the N₂O emissions at our study
494 site. In addition to data on low N₂O emissions, we provide a new dataset from a temperate
495 upland forest soil with reliable N₂O uptake measurements, highlighting the possibility of upland
496 forest soils acting as N₂O sink (Wrage et al., 2004; Savage et al., 2014). With the GasFluxTrailer
497 being a robust, state-of-the-art instrument and a total of 7670 N₂O flux observations, 81
498 observations indicating uptake, we are confident that the N₂O uptake we measured is not
499 instrumental noise (see Cowan et al., 2014).

500

501 *Effect of inclination and distance to a stream on soil N₂O emissions*

502 In agreement with our third hypothesis, N₂O emissions were significantly lower in sloped
503 locations with lower soil moisture content, which was also found by other forest soil studies in
504 France (Vilain et al., 2012), Kenya (Arias-Navarro et al., 2017), Australia (Butterbach-Bahl et
505 al., 2004), and Ecuador (Lamprea Pineda et al., 2021); although, this is opposite to the findings
506 in forests in China (Yu et al., 2021) and in Puerto Rico (Quebbeman et al., 2022). Furthermore,
507 N₂O emissions in flat positions increased with increasing soil temperature. Our findings
508 therefore could support the hypothesis that inclination influences N₂O emissions from
509 temperate upland forest soils. However, this soil temperature effect should be interpreted with
510 caution considering the concurrent, significant soil moisture:soil temperature interaction, which
511 could influence the significance of individual effects. N₂O emissions further decreased
512 significantly with increasing distance to the stream. The decrease of N₂O emissions from CG0.5
513 to CG15 might also be a consequence of the higher litter depth at these distances. The quantity
514 and quality of the litter input has been shown to influence N₂O emissions from forests (Ambus
515 et al., 2006; Pilegaard et al., 2006; Walkiewicz et al., 2021), especially when coniferous needle
516 litter is compared with deciduous leaf litter. Moreover, tree species have been found to exert a
517 strong control on N cycling in forests (Lovett et al., 2004). We suggest that the thick, mostly
518 deciduous leaf litter layer provided a physical barrier that hindered rainfall water to easily reach

519 the soil matrix and thus affected N₂O emissions indirectly by reducing soil moisture, which is
520 in line with what we suggested for the CH₄ uptake. Our conclusions, however, are not consistent
521 with a study conducted at another site in Rosalia, where removal of litter led to lowered N₂O
522 emissions (Leitner et al., 2016). This site was, however, a pure mature beech stand. Because it
523 is unclear how much of the total soil N₂O emissions resulted from the litter layer, we suggest
524 that further studies repeat litter removal versus control experiments to quantify the magnitude
525 of N₂O emissions resulting from litter. We propose that for our site, a large fraction of the N
526 remained stored in the litter layer and was not released as N₂O (Eickenscheidt and Brumme,
527 2013).

528

529 **Conclusion**

530 With the state-of-the-art technology used in this study, our dataset allows a detailed look at the
531 influence of inclination, distance to a stream, soil moisture, soil temperature, and other soil and
532 litter properties on soil CO₂, CH₄, and N₂O fluxes in a temperate upland forest in Eastern
533 Austria. Our study provides evidence of the complex interactions between inclination and
534 distance to a stream, and the resulting small-scale changes of soil and litter properties within an
535 upland forest ecosystem. We suggest that soil CO₂ emissions were likely indirectly affected by
536 inclination through its influence on soil moisture and soil properties. Contrary to our
537 expectations, soil CO₂ emissions were lower in sloped locations where soil moisture content
538 was lower. Our study site was a large CH₄ sink over the whole measurement period, with higher
539 soil CH₄ uptake rates on the locations furthest away from the stream. Because inclination was
540 not significantly related to the uptake of CH₄, we suggest that it was not a direct driver of CH₄
541 uptake at our site. Instead of soil moisture, which is commonly cited as the main driver of CH₄
542 fluxes, we found that soil C content and litter depth and weight were likely the main drivers of
543 CH₄ uptake. Our study showed a clear, significant influence of inclination and distance to the
544 stream on soil N₂O emissions from a temperate upland forest ecosystem, which was to some

545 extent regulated by litter depth. We showed that the impact of inclination and distance to a
546 stream on GHG fluxes is driven by multiple direct and indirect effects, highlighting the need to
547 consider small-scale differences as controlling factor for future GHG flux studies to improve
548 future GHG balance predictions in forest ecosystems.

549

550 **Statements and Declarations**

551 **Funding**

552 This work has been financially supported by the Austrian Research Promotion Agency (FFG),
553 project “LTER-CWN: Long-Term Ecosystem Research Infrastructure for Carbon, Water and
554 Nitrogen” (858024), by the Austrian Climate Research Program, 12th Call
555 (KR19AC0K17557, “EXAFOR”) and by the European Commission (H2020 Project eLTER
556 PLUS, Number 871128)

557

558 **Conflicts of interest/Competing interests**

559 The authors have no conflicts of interest to declare.

560

561 **Authors' contributions**

562 E.D.-P designed the experiment and collected and pre-processed the data.

563 L.G. and N.T. analysed the data, assisted by D.A, P.F, and E.D-P.

564 L.G. conducted the final statistics and finalised the figures.

565 N.T. and L.G wrote the manuscript with extensive comments from E.D.-P.

566 D.A, P.F, S.G. and S.Z.-B. edited the manuscript.

567 E.D.-P., S.Z.-B., and S.G., were responsible for infrastructure development in the LTER-

568 CWN project.

569 S.Z.-B. and S.G. were responsible for funding acquisition.

570

571 **Availability of data and material**

572 The gas flux data and soil and litter parameter data are stored in the online repository B2Share
573 and can be shared upon request. The meteorological data is open access on the online
574 repository B2Share: <http://doi.org/10.34730/f883fa7ae62648debd6e172448cfbc9b>.

575

576 **Code availability**

577 The code can be provided upon request.

578

579

580 **References**

581 Aciego Pietri, J. C. and Brookes, P. C.: Nitrogen mineralisation along a pH gradient of a silty
582 loam UK soil, *Soil Biol Biochem*, 40, 797–802, <https://doi.org/10.1016/j.soilbio.2007.10.014>,
583 2008.

584 Adamsen, A. P. S. and King, G. M.: Methane Consumption in Temperate and Subarctic
585 Forest Soils: Rates, Vertical Zonation, and Responses to Water and Nitrogen, *Appl Environ*
586 *Microbiol*, 59, 485–490, <https://doi.org/10.1128/aem.59.2.485-490.1993>, 1993.

587 Ambus, P.: Nitrous oxide production by denitrification and nitrification in temperate forest,
588 grassland and agricultural soils, *Eur J Soil Sci*, 49, 495–502, <https://doi.org/10.1046/j.1365-2389.1998.4930495.x>, 1998.

590 Ambus, P., Zechmeister-Boltenstern, S., and Butterbach-Bahl, K.: Sources of nitrous oxide
591 emitted from European forest soils, *Biogeosciences*, 3, 135–145, <https://doi.org/10.5194/bg-3-135-2006>, 2006.

593 Arias-Navarro, C., Díaz-Pinés, E., Klatt, S., Brandt, P., Rufino, M. C., Butterbach-Bahl, K.,
594 and Verchot, L. V: Spatial variability of soil N₂O and CO₂ fluxes in different topographic
595 positions in a tropical montane forest in Kenya, *J Geophys Res Biogeosci*, 122, 514–527,
596 <https://doi.org/10.1002/2016JG003667>, 2017.

597 Bates, D., Mächler, M., Bolker, B., and Walker, S.: Fitting Linear Mixed-Effects Models
598 using lme4, *J Stat Softw*, 67, 1–48, 2015.

599 Borken, W. and Beese, F.: Methane and nitrous oxide fluxes of soils in pure and mixed stands
600 of European beech and Norway spruce, *Eur J Soil Sci*, 57, 617–625,
601 <https://doi.org/10.1111/j.1365-2389.2005.00752.x>, 2006.

602 Born, M., Dorr, H., and Levin, I.: Methane consumption in aerated soils of the temperate
603 zone, *Tellus B*, 42, 2–8, <https://doi.org/10.1034/j.1600-0889.1990.00002.x>, 1990.

604 Brumme, R. and Borken, W.: Site variation in methane oxidation as affected by atmospheric
605 deposition and type of temperate forest ecosystem, *Global Biogeochem Cycles*, 13, 493–501,
606 <https://doi.org/10.1029/1998GB900017>, 1999.

607 Buchmann, N.: Biotic and abiotic factors controlling soil respiration rates in *Picea abies*
608 stands, *Soil Biol Biochem*, 32, 1625–1635, [https://doi.org/10.1016/S0038-0717\(00\)00077-8](https://doi.org/10.1016/S0038-0717(00)00077-8),
609 2000.

610 Burt, T. P. and Butcher, D. P.: Topographic controls of soil moisture distributions, *Journal of*
611 *Soil Science*, 36, 469–486, <https://doi.org/10.1111/j.1365-2389.1985.tb00351.x>, 1985.

612 Butler, J., Goetz, H., and Richardson, J. L.: Vegetation and Soil-Landscape Relationships in
613 the North Dakota Badlands, *American Midland Naturalist*, 116, 378,
614 <https://doi.org/10.2307/2425746>, 1986.

615 Butterbach-Bahl, K., Kock, M., Willibald, G., Hewett, B., Buhagiar, S., Papen, H., and Kiese,
616 R.: Temporal variations of fluxes of NO, NO₂, N₂O, CO₂, and CH₄ in a tropical rain forest
617 ecosystem, *Global Biogeochem Cycles*, 18, n/a-n/a, <https://doi.org/10.1029/2004GB002243>,
618 2004.

619 Butterbach-bahl, K., Kiese, R., and Liu, C.: Chapter eighteen - Measurements of Biosphere–
620 Atmosphere Exchange of CH₄ in Terrestrial Ecosystems, in: *Methods in Enzymology*, vol.
621 495, Elsevier Inc., 271–287, [https://doi.org/https://doi.org/10.1016/B978-0-12-386905-](https://doi.org/https://doi.org/10.1016/B978-0-12-386905-0.00018-8)
622 [0.00018-8](https://doi.org/https://doi.org/10.1016/B978-0-12-386905-0.00018-8), 2011.

623 Butterbach-Bahl, K., Baggs, E. M., Dannenmann, M., Kiese, R., and Zechmeister-
624 Boltenstern, S.: Nitrous oxide emissions from soils: how well do we understand the processes
625 and their controls?, *Philosophical Transactions of the Royal Society B: Biological Sciences*,
626 368, 20130122, <https://doi.org/10.1098/rstb.2013.0122>, 2013.

627 Butterbach-Bahl, K., Diaz-Pines, E., and Dannenmann, M.: Soil Trace Gas Emissions and
628 Climate Change, in: *Global Environmental Change*, Springer Netherlands, Dordrecht, 325–
629 334, https://doi.org/10.1007/978-94-007-5784-4_4, 2014.

630 Castro, M. S., Steudler, P. A., Melillo, J. M., Aber, J. D., and Bowden, R. D.: Factors
631 controlling atmospheric methane consumption by temperate forest soils, *Global Biogeochem*
632 *Cycles*, 9, 1–10, <https://doi.org/10.1029/94GB02651>, 1995.

633 Cowan, N. J., Famulari, D., Levy, P. E., Anderson, M., Reay, D. S., and Skiba, U. M.:
634 Investigating uptake of N₂O in agricultural soils using a high-precision dynamic chamber
635 method, *Atmos Meas Tech*, 7, 4455–4462, <https://doi.org/10.5194/amt-7-4455-2014>, 2014.

636 Creed, I. F., Webster, K. L., Braun, G. L., Bourbonnière, R. A., and Beall, F. D.:
637 Topographically regulated traps of dissolved organic carbon create hotspots of soil carbon
638 dioxide efflux in forests, *Biogeochemistry*, 112, 149–164, [https://doi.org/10.1007/s10533-](https://doi.org/10.1007/s10533-012-9713-4)
639 [012-9713-4](https://doi.org/10.1007/s10533-012-9713-4), 2013.

640 Cronan, C. S.: *Ecosystem Biogeochemistry*, Springer International Publishing, Cham,
641 <https://doi.org/10.1007/978-3-319-66444-6>, 2018.

642 Davidson, E. A., Keller, M., Erickson, H. E., Verchot, L. V, and Veldkamp, E.: Testing a
643 Conceptual Model of Soil Emissions of Nitrous and Nitric Oxides, *Bioscience*, 50, 667,
644 [https://doi.org/10.1641/0006-3568\(2000\)050\[0667:tacmos\]2.0.co;2](https://doi.org/10.1641/0006-3568(2000)050[0667:tacmos]2.0.co;2), 2000.

645 Davidson, E. A., Savage, K., Verchot, L. V., and Navarro, R.: Minimizing artifacts and biases
646 in chamber-based measurements of soil respiration, *Agric For Meteorol*, 113, 21–37,
647 [https://doi.org/10.1016/S0168-1923\(02\)00100-4](https://doi.org/10.1016/S0168-1923(02)00100-4), 2002.

648 Davidson, E. A., Samanta, S., Caramori, S. S., and Savage, K.: The Dual Arrhenius and
649 Michaelis-Menten kinetics model for decomposition of soil organic matter at hourly to
650 seasonal time scales, *Glob Chang Biol*, 18, 371–384, [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2486.2011.02546.x)
651 [2486.2011.02546.x](https://doi.org/10.1111/j.1365-2486.2011.02546.x), 2012.

652 Davidson, EriC. A., Belk, E., and Boone, R. D.: Soil water content and temperature as
653 independent or confounded factors controlling soil respiration in a temperate mixed hardwood
654 forest, *Glob Chang Biol*, 4, 217–227, <https://doi.org/10.1046/j.1365-2486.1998.00128.x>,
655 1998.

656 Diaz-Pines, E. and Gasch, J.: Rosalia Lehrforst Austria - Meteorological Data 2001-2020,
657 <https://doi.org/10.23728/b2share.681966be29a34f3ebc6015ac255ab143>, 2021.

658 Eickenscheidt, N. and Brumme, R.: Contribution of ¹⁵N-labelled leaf litter to N turnover,
659 nitrous oxide emissions and N sequestration in a beech forest during eleven years, *Plant Soil*,
660 362, 67–77, <https://doi.org/10.1007/s11104-012-1245-0>, 2013.

661 Epron, D., Farque, L., Lucot, É., and Badot, P.-M.: Soil CO₂ efflux in a beech forest:
662 dependence on soil temperature and soil water content, *Ann For Sci*, 56, 221–226,
663 <https://doi.org/10.1051/forest:19990304>, 1999.

664 Fierer, N. and Jackson, R. B.: The diversity and biogeography of soil bacterial communities,
665 *Proc Natl Acad Sci U S A*, 103, 626–631, <https://doi.org/10.1073/pnas.0507535103>, 2006.

666 Fürst, J., Nachtnebel, H. P., Gasch, J., Nolz, R., Stockinger, M. P., Stumpp, C., and Schulz,
667 K.: Rosalia: an experimental research site to study hydrological processes in a forest
668 catchment, *Earth Syst Sci Data*, 13, 4019–4034, <https://doi.org/10.5194/essd-13-4019-2021>,
669 2021.

670 Gundersen, P., Christiansen, J. R., Alberti, G., Brüggemann, N., Castaldi, S., Gasche, R.,
671 Kitzler, B., Klemedtsson, L., Lobo-do-Vale, R., Moldan, F., Rütting, T., Schleppei, P.,
672 Weslien, P., and Zechmeister-Boltenstern, S.: The response of methane and nitrous oxide
673 fluxes to forest change in Europe, *Biogeosciences*, 9, 3999–4012, <https://doi.org/10.5194/bg-9-3999-2012>, 2012.

675 Hahn, M., Gartner, K., and Zechmeister-Boltenstern, S.: Greenhouse gas emissions (N₂O,
676 CO₂ and CH₄) from three forest soils near Vienna (Austria) with different water and nitrogen
677 regimes, *Die Bodenkultur*, 2, 115–125, 2000.

678 Hairston, A. B. and Grigal, D. F.: Topographic variation in soil water and nitrogen for two
679 forested landforms in Minnesota, USA, *Geoderma*, 64, 125–138,
680 [https://doi.org/10.1016/0016-7061\(94\)90093-0](https://doi.org/10.1016/0016-7061(94)90093-0), 1994.

681 Hanson, P. J., Wullschleger, S. D., Bohlman, S. A., and Todd, D. E.: Seasonal and
682 topographic patterns of forest floor CO₂ efflux from an upland oak forest, *Tree Physiol*, 13,
683 1–15, <https://doi.org/10.1093/treephys/13.1.1>, 1993.

684 Hanson, R. S. and Hanson, T. E.: Methanotrophic bacteria, *Microbiol Rev*, 60, 439–471,
685 <https://doi.org/10.1128/mr.60.2.439-471.1996>, 1996.

686 Harris, E., Diaz-Pines, E., Stoll, E., Schloter, M., Schulz, S., Duffner, C., Li, K., Moore, K.
687 L., Ingrisch, J., Reinthaler, D., Zechmeister-Boltenstern, S., Glatzel, S., Brüggemann, N., and
688 Bahn, M.: Denitrifying pathways dominate nitrous oxide emissions from managed grassland
689 during drought and rewetting, *Sci Adv*, 7, eabb7118, <https://doi.org/10.1126/sciadv.abb7118>,
690 2021.

691 Hiltbrunner, D., Zimmermann, S., Karbin, S., Hagedorn, F., and Niklaus, P. A.: Increasing
692 soil methane sink along a 120-year afforestation chronosequence is driven by soil moisture,
693 *Glob Chang Biol*, 18, 3664–3671, <https://doi.org/10.1111/j.1365-2486.2012.02798.x>, 2012.

694 Hinsinger, P., Plassard, C., Tang, C., and Jaillard, B.: Origins of root-mediated pH changes in
695 the rhizosphere and their responses to environmental constraints: A review, *Plant Soil*, 248,
696 43–59, <https://doi.org/10.1023/A:1022371130939>, 2003.

697 Hutchinson, G. L. and Mosier, A. R.: Improved Soil Cover Method for Field Measurement of
698 Nitrous Oxide Fluxes, *Soil Science Society of America Journal*, 45, 311–316,
699 <https://doi.org/10.2136/sssaj1981.03615995004500020017x>, 1981.

700 IPCC: IPCC, 2022: Climate Change 2022: Impacts, Adaptation, and Vulnerability.
701 Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental
702 Panel on Climate Change, Cambridge University Press. Cambridge University Press,
703 Cambridge, UK and New York, <https://doi.org/10.1017/9781009325844>, 2022.

704 Janssens, I. A., Lankreijer, H., Matteucci, G., Kowalski, A. S., Buchmann, N., Epron, D.,
705 Pilegaard, K., Kutsch, W., Longdoz, B., Grünwald, T., Montagnani, L., Dore, S., Rebmann,
706 C., Moors, E. J., Grelle, A., Rannik, Ü., Morgenstern, K., Oltchev, S., Clement, R.,
707 Guðmundsson, J., Minerbi, S., Berbigier, P., Ibrom, A., Moncrieff, J., Aubinet, M.,
708 Bernhofer, C., Jensen, N. O., Vesala, T., Granier, A., Schulze, E.-D., Lindroth, A., Dolman,
709 A. J., Jarvis, P. G., Ceulemans, R., and Valentini, R.: Productivity overshadows temperature
710 in determining soil and ecosystem respiration across European forests, *Glob Chang Biol*, 7,
711 269–278, <https://doi.org/10.1046/j.1365-2486.2001.00412.x>, 2001.

712 Kuznetsova, A., Brockhoff, P. B., and Christensen, R. H. B.: lmerTest Package: Tests in
713 Linear Mixed Effects Models, *J Stat Softw*, 82, <https://doi.org/10.18637/jss.v082.i13>, 2017.

714 Lamprea Pineda, P. A., Bauters, M., Verbeeck, H., Baez, S., Barthel, M., Bodé, S., and
715 Boeckx, P.: Ideas and perspectives: Patterns of soil CO₂, CH₄, and N₂O fluxes along an
716 altitudinal gradient - A pilot study from an Ecuadorian neotropical montane forest,
717 *Biogeosciences*, 18, 413–421, <https://doi.org/10.5194/bg-18-413-2021>, 2021.

718 Leitner, S., Sae-Tun, O., Kranzinger, L., Zechmeister-Boltenstern, S., and Zimmermann, M.:
719 Contribution of litter layer to soil greenhouse gas emissions in a temperate beech forest, *Plant
720 Soil*, 403, 455–469, <https://doi.org/10.1007/s11104-015-2771-3>, 2016.

721 Lin, H. S., Kogelmann, W., Walker, C., and Bruns, M. A.: Soil moisture patterns in a forested
722 catchment: A hydrogeological perspective, *Geoderma*, 131, 345–368,
723 <https://doi.org/10.1016/j.geoderma.2005.03.013>, 2006.

724 Liu, H., Li, Y., Pan, B., Zheng, X., Yu, J., Ding, H., and Zhang, Y.: Pathways of soil N₂O
725 uptake, consumption, and its driving factors: a review, *Environmental Science and Pollution
726 Research*, 29, 30850–30864, <https://doi.org/10.1007/s11356-022-18619-y>, 2022.

727 Lloyd, J. and Taylor, J. A.: On the Temperature Dependence of Soil Respiration, *Funct Ecol*,
728 8, 315, <https://doi.org/10.2307/2389824>, 1994.

729 Lookingbill, T. and Urban, D.: An empirical approach towards improved spatial estimates of
730 soil moisture for vegetation analysis, *Landsc Ecol*, 19, 417–433,
731 <https://doi.org/10.1023/B:LAND.0000030451.29571.8b>, 2004.

732 Lovett, G. M., Weathers, K. C., Arthur, M. A., and Schultz, J. C.: Nitrogen cycling in a
733 northern hardwood forest: Do species matter?, *Biogeochemistry*, 67, 289–308,
734 <https://doi.org/10.1023/B:BIOG.0000015786.65466.f5>, 2004.

735 Luo, G. J., Brüggemann, N., Wolf, B., Gasche, R., Grote, R., and Butterbach-Bahl, K.:
736 Decadal variability of soil CO₂, NO, N₂O, and CH₄ fluxes at the Höglwald Forest, Germany,
737 *Biogeosciences*, 9, 1741–1763, <https://doi.org/10.5194/bg-9-1741-2012>, 2012.

738 Marrero, T. R. and Mason, E. A.: Gaseous Diffusion Coefficients, *J Phys Chem Ref Data*, 1,
739 3–118, <https://doi.org/10.1063/1.3253094>, 1972.

740 Le Mer, J. and Roger, P.: Production, oxidation, emission and consumption of methane by
741 soils: A review, *Eur J Soil Biol*, 37, 25–50, [https://doi.org/10.1016/S1164-5563\(01\)01067-6](https://doi.org/10.1016/S1164-5563(01)01067-6),
742 2001.

743 Nakagawa, S., Johnson, P. C. D., and Schielzeth, H.: The coefficient of determination R² and
744 intra-class correlation coefficient from generalized linear mixed-effects models revisited and
745 expanded, *J R Soc Interface*, 14, 20170213, <https://doi.org/10.1098/rsif.2017.0213>, 2017.

746 Nash, J. C. and Varadhan, R.: Unifying Optimization Algorithms to Aid Software System
747 Users: optimx for R, *J Stat Softw*, 43, <https://doi.org/10.18637/jss.v043.i09>, 2011.

748 ÖNORM: ÖNORM L 1061. Physical determination of grain size distribution of soils less than
749 2 mm particle size, Austrian Standards Institute, Vienna, 2002.

750 ÖNORM: ÖNORM L 1083. Chemical analyses of soils - Determination of acidity (pH value),
751 Austrian Standards Institute, Vienna, 2006.

752 ÖNORM: ÖNORM L 1080. Chemical Analyses of Soils—Determination of Organic Carbon
753 by Dry Combustion with and without Consideration of Carbonates, Austrian Standards
754 Institute, Vienna, 2013.

755 Ou, Y., Rousseau, A. N., Wang, L., Yan, B., Gumiere, T., and Zhu, H.: Identification of the
756 alteration of riparian wetland on soil properties, enzyme activities and microbial communities
757 following extreme flooding, *Geoderma*, 337, 825–833,
758 <https://doi.org/10.1016/j.geoderma.2018.10.032>, 2019.

759 Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L.,
760 Shvidenko, A., Lewis, S. L., Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S. W.,
761 McGuire, A. D., Piao, S., Rautiainen, A., Sitch, S., and Hayes, D.: A Large and Persistent

762 Carbon Sink in the World's Forests, *Science* (1979), 333, 988–993,
763 <https://doi.org/10.1126/science.1201609>, 2011.

764 Parkin, T. B., Venterea, R. T., and Hargreaves, S. K.: Calculating the Detection Limits of
765 Chamber-based Soil Greenhouse Gas Flux Measurements, *J Environ Qual*, 41, 705–715,
766 <https://doi.org/10.2134/jeq2011.0394>, 2012.

767 Pilegaard, K., Skiba, U., Ambus, P., Beier, C., Brüggemann, N., Butterbach-Bahl, K., Dick,
768 J., Dorsey, J., Duyzer, J., Gallagher, M., Gasche, R., Horvath, L., Kitzler, B., Leip, A.,
769 Pihlatie, M. K., Rosenkranz, P., Seufert, G., Vesala, T., Westrate, H., and Zechmeister-
770 Boltenstern, S.: Factors controlling regional differences in forest soil emission of nitrogen
771 oxides (NO and N₂O), *Biogeosciences*, 3, 651–661, <https://doi.org/10.5194/bg-3-651-2006>,
772 2006.

773 Pumpanen, J., Kolari, P., Ilvesniemi, H., Minkkinen, K., Vesala, T., Niinistö, S., Lohila, A.,
774 Larmola, T., Morero, M., Pihlatie, M., Janssens, I., Yuste, J. C., Grünzweig, J. M., Reth, S.,
775 Subke, J.-A., Savage, K., Kutsch, W., Østreg, G., Ziegler, W., Anthoni, P., Lindroth, A., and
776 Hari, P.: Comparison of different chamber techniques for measuring soil CO₂ efflux, *Agric
777 For Meteorol*, 123, 159–176, <https://doi.org/10.1016/j.agrformet.2003.12.001>, 2004.

778 Quebbeman, A. W., Menge, D. N. L., Zimmerman, J., and Uriarte, M.: Spatial Variation in
779 Soil Greenhouse Gas Fluxes in a Subtropical Forest, *Ecosystems*, 25,
780 <https://doi.org/10.1007/s10021-021-0067>, 2022.

781 Raich, J. W. and Potter, C. S.: Global patterns of carbon dioxide emissions from soils, *Global
782 Biogeochem Cycles*, 9, 23–36, <https://doi.org/10.1029/94GB02723>, 1995.

783 R Core Team: R: A language and environment for statistical computing. R Foundation for
784 Statistical Computing, R Foundation for Statistical Computing, Vienna, Austria, 2022.

785 Reth, S., Reichstein, M., and Falge, E.: The effect of soil water content, soil temperature, soil
786 pH-value and the root mass on soil CO₂ efflux – A modified model, *Plant Soil*, 268, 21–33,
787 <https://doi.org/10.1007/s11104-005-0175-5>, 2005.

788 Savage, K., Phillips, R., and Davidson, E.: High temporal frequency measurements of
789 greenhouse gas emissions from soils, *Biogeosciences*, 11, 2709–2720,
790 <https://doi.org/10.5194/bg-11-2709-2014>, 2014.

791 Schad, P.: The International Soil Classification System WRB, Third Edition, 2014, in:
792 Springer Water, Springer International Publishing, 563–571, https://doi.org/10.1007/978-3-319-24409-9_25, 2016.

794 Schimel, J. P.: Life in Dry Soils: Effects of drought on soil microbial communities and
795 processes, *Annu Rev Ecol Evol Syst*, 49, 409–432, <https://doi.org/10.1146/annurev-ecolsys-110617-062614>, 2018.

797 Smith, K. A., Dobbie, K. E., Ball, B. C., Bakken, L. R., Sitaula, B. K., Hansen, S., Brumme,
798 R., Borken, W., Christensen, S., Priemé, A., Fowler, D., Macdonald, J. A., Skiba, U.,
799 Klemedtsson, L., Kasimir-Klemedtsson, A., Degórska, A., and Orlanski, P.: Oxidation of
800 atmospheric methane in Northern European soils, comparison with other ecosystems, and
801 uncertainties in the global terrestrial sink, *Glob Chang Biol*, 6, 791–803,
802 <https://doi.org/10.1046/j.1365-2486.2000.00356.x>, 2000.

803 Subke, J.-A., Kutzbach, L., and Risk, D.: Soil Chamber Measurements, in: Springer
804 Handbook of Atmospheric Measurements, Springer International Publishing, 1603–1624,
805 https://doi.org/10.1007/978-3-030-52171-4_60, 2021.

806 Thomas, P. A. and Packham, J. R.: Ecology of woodlands and forests: Description, dynamics
807 and diversity, 1–528 pp., <https://doi.org/10.1017/CBO9780511805578>, 2007.

808 Unger, I. M., Motavalli, P. P., and Muzika, R.-M.: Changes in soil chemical properties with
809 flooding: A field laboratory approach, *Agric Ecosyst Environ*, 131, 105–110,
810 <https://doi.org/10.1016/j.agee.2008.09.013>, 2009.

811 Vilain, G., Garnier, J., Passy, P., Silvestre, M., and Billen, G.: Budget of N₂O emissions at the
812 watershed scale: role of land cover and topography (the Orgeval basin, France),
813 *Biogeosciences*, 9, 1085–1097, <https://doi.org/10.5194/bg-9-1085-2012>, 2012.

814 Walkiewicz, A., Rafalska, A., Bulak, P., Bieganski, A., and Osborne, B.: How Can Litter
815 Modify the Fluxes of CO₂ and CH₄ from Forest Soils? A Mini-Review, *Forests*, 12, 1276,
816 <https://doi.org/10.3390/f12091276>, 2021.

817 Wang, Y., Wang, H., Ma, Z., Dai, X., Wen, X., Liu, Y., and Wang, Z.-L.: The litter layer acts
818 as a moisture-induced bidirectional buffer for atmospheric methane uptake by soil of a
819 subtropical pine plantation, *Soil Biol Biochem*, 66, 45–50,
820 <https://doi.org/10.1016/j.soilbio.2013.06.018>, 2013.

821 Warner, D. L., Vargas, R., Seyfferth, A., and Inamdar, S.: Transitional slopes act as hotspots
822 of both soil CO₂ emission and CH₄ uptake in a temperate forest landscape, *Biogeochemistry*,
823 138, 121–135, <https://doi.org/10.1007/s10533-018-0435-0>, 2018.

824 Webster, K. L., Creed, I. F., Bourbonnière, R. A., and Beall, F. D.: Controls on the
825 heterogeneity of soil respiration in a tolerant hardwood forest, *J Geophys Res*, 113, G03018,
826 <https://doi.org/10.1029/2008JG000706>, 2008.

827 Wrage, N., Lauf, J., del Prado, A., Pinto, M., Pietrzak, S., Yamulki, S., Oenema, O., and
828 Gebauer, G.: Distinguishing sources of N₂O in European grasslands by stable isotope
829 analysis, *Rapid Communications in Mass Spectrometry*, 18, 1201–1207,
830 <https://doi.org/10.1002/rcm.1461>, 2004.

831 Yu, K., Faulkner, S. P., and Baldwin, M. J.: Effect of hydrological conditions on nitrous
832 oxide, methane, and carbon dioxide dynamics in a bottomland hardwood forest and its
833 implication for soil carbon sequestration, *Glob Chang Biol*, 14, 798–812,
834 <https://doi.org/10.1111/j.1365-2486.2008.01545.x>, 2008.

835 Yu, L., Zhu, J., Ji, H., Bai, X., Lin, Y., Zhang, Y., Sha, L., Liu, Y., Song, Q., Dörsch, P.,
836 Mulder, J., and Zhou, W.: Topography-related controls on N₂O emission and CH₄ uptake in a
837 tropical rainforest catchment, *Science of The Total Environment*, 775, 145616,
838 <https://doi.org/10.1016/j.scitotenv.2021.145616>, 2021.

839 Zechmeister-Boltenstern, S., Díaz-Pinés, E., Spann, C., Hofmann, K., Schneckner, J., and
840 Reinsch, S.: Soil—The Hidden Part of Climate, in: *Soil and Climate*, CRC Press, Boca Raton,
841 FL : CRC Press, Taylor & Francis Group, 2018. | Series: *Advances in soil science*, 11–60,
842 <https://doi.org/10.1201/b21225-2>, 2018.

843 Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A., and Smith, G. M.: *Mixed effects models*
844 *and extensions in ecology with R*, Springer New York, New York, NY,
845 <https://doi.org/10.1007/978-0-387-87458-6>, 2009.

846