

1 Localized basal area affects soil respiration temperature sensitivity in a  
2 coastal deciduous forest

3 Biogeosciences

4

5 Stephanie C. Pennington\*<sup>1</sup>, Nate G. McDowell<sup>2</sup>, J. Patrick Megonigal<sup>3</sup>, James C. Stegen<sup>2</sup>, and  
6 Ben Bond-Lamberty<sup>1</sup>

7

8 \*Corresponding author, [stephanie.pennington@pnl.gov](mailto:stephanie.pennington@pnl.gov)

9

10 1. Joint Global Change Research Institute, Pacific Northwest National Laboratory, 5825  
11 University Research Ct. #3500, College Park, MD 20740 USA

12 2. Pacific Northwest National Laboratory, Biological Sciences Division, Richland, WA, USA

13 3. Smithsonian Environmental Research Center, Edgewater, MD, USA

14

15 Keywords: *spatial variability, soil respiration, temperate forest, carbon cycling*

16

17 **Abstract**

18 Soil respiration ( $R_s$ ), the flow of  $CO_2$  from the soil surface to the atmosphere, is one of the  
19 largest carbon fluxes in the terrestrial biosphere. The spatial variability of  $R_s$  is both large and  
20 poorly understood, limiting our ability to robustly scale it in space. One factor in  $R_s$  spatial  
21 variability is the autotrophic contribution from plant roots, but it is uncertain how the presence of  
22 plants affects the magnitude and temperature sensitivity of  $R_s$ . This study used one year of  $R_s$   
23 measurements to examine the effect of localized basal area on  $R_s$  in the growing and dormant  
24 seasons, as well as during moisture-limited times, in a temperate, coastal, deciduous forest in  
25 eastern Maryland, USA. In a linear mixed-effects model, tree basal area within a 5 m radius

26 (BA<sub>5</sub>) exerted a significant positive effect on the temperature sensitivity of soil respiration. Soil  
27 moisture was the dominant control on R<sub>S</sub> during the dry portions of the year while soil moisture,  
28 temperature, and BA<sub>5</sub> all exerted significant effects on R<sub>S</sub> in wetter periods. Our results suggest  
29 that autotrophic respiration is more sensitive to temperature than heterotrophic respiration at  
30 these sites, although we did not measure these source fluxes directly, and that soil respiration is  
31 highly moisture-sensitive, even in a record-rainfall year. The R<sub>S</sub> flux magnitudes (0.35-15.3 μmol  
32 m<sup>-2</sup> s<sup>-1</sup>) and variability (coefficient of variability 10%-23% across plots) observed in this study  
33 were comparable to values observed in similar forests. Six R<sub>S</sub> observations would be required in  
34 order to estimate the mean across all study sites to within 50%, and 516 would be required in  
35 order to estimate it to within 5%, with 90% confidence. A better understanding of the spatial  
36 interactions between plants and microbes, as well as the strength and speed of above- and  
37 belowground coupling, is necessary to link these processes with large scale soil-to-atmosphere  
38 C fluxes.

39

## 40 **Introduction**

41 Soil respiration (R<sub>S</sub>), the flow of CO<sub>2</sub> from the soil to the atmosphere, is an important  
42 carbon (C) flux at ecosystem (Granier et al., 2000) to global scales. R<sub>S</sub> is among the largest C  
43 fluxes in the terrestrial biosphere (Bond-Lamberty, 2018; Le Quéré et al., 2018), but poorly  
44 constrained at large scales, and thus it is important to understand its variability and sensitivity to  
45 processes such as land use and climate changes (Hursh et al., 2017; Schlesinger and Andrews,  
46 2000). Unlike other large C fluxes such as net primary production, net ecosystem exchange,  
47 and gross primary production, R<sub>S</sub> cannot be measured, even indirectly, at scales larger than a  
48 few square meters (Bond-Lamberty et al., 2016), limiting our ability to robustly scale it in space.

49 One obstacle to robust measurements is that the spatial variability of R<sub>S</sub> is both large  
50 and poorly understood. Controls on the spatial variability of R<sub>S</sub> differ among sites and  
51 ecosystems and include plant species, ecosystem productivity (Reichstein et al., 2003), soil

52 temperature (Fang et al. 1998), moisture, spatial variability of vegetation, management, and soil  
53 compaction (Epron et al., 2004). This high variability has consequences for the sampling  
54 strategy required to accurately measure  $R_s$  at the stand scale (Rodeghiero and Cescatti, 2008;  
55 Saiz et al., 2006) and limits our ability to upscale  $R_s$  measurements to eddy covariance tower  
56 scales (Barba et al., 2018).

57 At large scales,  $R_s$  differs between vegetation types and biomes (Raich et al., 2002;  
58 Raich and Schlesinger, 1992), implying that the spatial distribution of vegetation might strongly  
59 affect  $R_s$  via plant root respiration, which constitutes ~50% of  $R_s$  in many ecosystems (Subke et  
60 al., 2006). At ecosystem scales, a number of studies have examined how the spatial distribution  
61 of  $R_s$  is affected by vegetation.  $R_s$  is typically higher closer to tree stems (Epron et al., 2004;  
62 Tang and Baldocchi, 2005), and with higher nearby stem density (Schwendenmann and  
63 Macinnis-Ng, 2016; Stegen et al., 2017). Photosynthesis is also a driver of the rhizospheric  
64 component of soil respiration (Hopkins et al., 2013), and influences seasonal trends in root  
65 contribution to total soil respiration (Brændholt et al., 2018; Högberg et al., 2001). Any spatial  
66 influences of plants on  $R_s$  might be expected to be strong in temperate, deciduous forests, as  
67 such forests tend to be highly productive (Gillman et al., 2015; Luysaert et al., 2007).

68 This study examines the effect of tree proximity on measured  $R_s$  in a mid-Atlantic,  
69 deciduous forest in the Chesapeake Bay, USA region. We hypothesized that:

70

71 (i) the amount of basal area close to  $R_s$  measurement locations would exert a significant and  
72 positive effect on measured  $R_s$  after taking into account the effects of abiotic drivers;

73

74 (ii) this effect would occur in the growing (leaf on) season, but not in the dormant (leaf off)  
75 season, because root respiration is much higher during the growing season; and

76

77 (iii) this effect would be stronger during drier times of year, because trees might maintain access  
78 to deep soil moisture (Burgess et al., 1998) and thus continue respiring even when the surface  
79 soil is dry.

80  
81 To test these hypotheses we performed a spatially explicit analysis of one year of frequent  $R_s$   
82 measurements in a temperate coastal deciduous forest in eastern Maryland, USA. Our study  
83 was conducted in the Chesapeake Bay watershed, an area subject to rapid rates of sea level  
84 rise (Ezer and Corlett, 2012; Sallenger et al., 2012) that may exert significant effects on the  
85 carbon cycling of coastal ecosystems (Rogers et al., 2019).

86

## 87 **Methods**

88

### 89 *Site characteristics*

90 This study was conducted in a mid-Atlantic, temperate, deciduous forest at the  
91 Smithsonian Environmental Research Center (SERC) in Edgewater, MD, USA. Three sites were  
92 chosen along Muddy Creek, a stream draining into an arm of Chesapeake Bay. Each site was  
93 separated by ~1 km (**Figure 1a**). These sites were comprised of both lowland and upland forest  
94 with a mean annual precipitation of 1001 mm and mean annual temperature of 12.9°C (Pitz and  
95 Megonigal, 2017). Dominant tree species include *Liriodendron tulipifera*, *Fagus grandifolia*, and  
96 *Quercus spp.*; soil types vary between Collington, Wist, and Annapolis soil. (**Table 1**). At each  
97 site, three 20 m x 40 m plots were installed, separated by ~25 m and oriented perpendicular to  
98 the creek. The total elevation change between plots at each site was ~2 m. Within each plot, we  
99 installed 4, 20-cm diameter PVC collars, randomly separated from each other by 2–15 m, for a  
100 total of 36 measurement collars. Collars were installed ~1 week prior to the first sampling and  
101 left in place for the duration of the study.

102

103 *Soil respiration measurements*

104           Soil respiration measurements were taken using an infrared gas analyzer (LI-8100A, LI-  
105 COR Inc., Lincoln, NE) with a 20 cm diameter soil chamber attached. Measurements were  
106 taken every 10-14 days from April 2018 to April 2019. The IRGA measures concentrations every  
107 second over a one minute period and calculates the CO<sub>2</sub> flux as the exponential regression of  
108 CO<sub>2</sub> accumulation in the closed chamber system over unit area and time; two successive  
109 measurements were taken at each collar and averaged. Vegetation was removed from inside  
110 the collar, and new vegetation was re-clipped as necessary, to remove any aboveground  
111 autotrophic flux, so that the IRGA was measuring only soil-to-atmosphere CO<sub>2</sub>. Soil moisture  
112 and temperature (T<sub>5</sub>) were also recorded at 5 cm depth, using auxiliary sensors attached to the  
113 LI-8100A, at the same time as soil respiration measurements. Temperature at 20 cm depth (T<sub>20</sub>)  
114 was also recorded using a hand-held thermometer at the time of measurement.

115

116 *Tree proximity measurements*

117           We recorded distance from the soil collar, diameter at breast height (1.37 m), and  
118 species of each tree within a 15 meter radius of each soil respiration measurement point  
119 (**Figure 1b**). Dead trees were included in the dataset but only account for < 1% of total forest  
120 basal area. Cumulative basal area was calculated at each 1 m radial distance from the collar,  
121 summing the cross-sectional areas of all trees within each distance. Tree root extent can be  
122 highly variable, but generally roots extend at least to the edge of the tree canopy (Stone and  
123 Kalisz, 1991). Mature tree canopies at SERC are ~5 m in radius (S. Pennington, personal  
124 observation), and we adopted this distance as an *a priori* assumption to test for the effect of  
125 basal area at 5 meters (BA<sub>5</sub>) on R<sub>s</sub>.

126

127 *Statistical analysis*

128           Respiration data were checked visually for artifacts or unusual outliers, but we did not  
129 exclude any data *a priori*. Data were then combined with the proximity measurements described  
130 above based on collar number. We used a linear mixed-effects model to test for the influence of  
131 BA<sub>5</sub> on R<sub>s</sub>, treating temperature, soil moisture (SM), and BA<sub>5</sub> as fixed effects, and site as a  
132 random effect. To ensure homoscedasticity of model residuals, the dependent variable R<sub>s</sub> was  
133 transformed by taking its natural logarithm, and thus the full linear model was specified as:

$$134 \quad \log(R_s) \sim T_5 * BA_5 + T_{20} * BA_5 + SM + SM^2 \quad (\text{Equation 1})$$

135 We used restricted maximum likelihood estimation using the *lme4* package (Bates et al., 2015)  
136 in R version 3.5.3 (R Development Core Team, 2019). All models were examined for influential  
137 outliers and deviations from normality. Non-significant terms were then eliminated using a  
138 forward-and-back stepwise algorithm (using the R package *MASS* version 7.3-47) based on the  
139 Akaike Information Criterion. Residuals from all fitted models were plotted and checked for  
140 trends or heteroscedasticity.

141           Our secondary hypotheses, that effect of BA<sub>5</sub> varies with growing season and soil  
142 moisture, were tested by subsetting the R<sub>s</sub> data. We treated April 15-October 14 as the growing  
143 season, based on 2018 leaf-out and senescence, and October 15-April 14 as the dormant  
144 season. Soil moisture data were split up into equal thirds (low, <0.188 m<sup>3</sup> m<sup>-3</sup>; medium, 0.188-  
145 0.368 m<sup>3</sup> m<sup>-3</sup>; and high, >0.368 m<sup>3</sup> m<sup>-3</sup>; all values volumetric). We then applied the statistical  
146 model described above to each subset of the data to test for BA<sub>5</sub> significance in the model. The  
147 ‘relaimpo’ package version 2.2-3 was used to calculate relative importance metrics for all terms  
148 in each model, in particular its ‘lmg’ metric that averages sequential sums of squares over all  
149 orders of regressors (Lindeman et al. 1980), providing a robust decomposition of model R<sup>2</sup>.

150           We used the spatial variability between collars within individual plots to estimate the  
151 number of samples required for a robust estimate of the R<sub>s</sub> ‘population mean’, i.e., a spatially-  
152 representative mean. Specifically, we used a Student’s t-test to calculate this based on the

153 standard deviation of hourly  $R_s$ , the desired power of the test, and the allowable delta  
154 (difference from the true mean value), following Davidson et al. (2002).

155

## 156 **Results**

157 We measured  $R_s$ , soil temperature, and soil moisture on 31 different days across the  
158 one-year period (Figure 2). Soil temperatures ranged from 0.1 to 27.5 °C (at 5 cm) and 1.7 to  
159 24.4 °C (at 20 cm); volumetric soil moisture values were 0.01-0.56.  $R_s$  fluxes ranged from 0.35  
160  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (in January 2019) to 15.3  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (in July 2018). The coefficient of variability  
161 (CV) between collars within plots, a measure of spatial variability, was  $16.7\% \pm 4.0$ . This implied  
162 that a large number of samples was required to estimate soil respiration accurately (Table 2).

163 There was large variability in the basal area and number of trees close to the  
164 measurement collars (Figure 3). The mean number of trees within 1 m, 5 m, and 10 m distance  
165 were one, six, and 21 trees (with respective nearby basal areas of 0.0002  $\text{m}^2$ , 0.24  $\text{m}^2$ , and 0.88  
166  $\text{m}^2$ ). Within our maximum radius of measurement, 15 m, there were on average 43 trees and  
167 1.64  $\text{m}^2$  of cumulative basal area, ranging from a minimum of 0.43  $\text{m}^2$  to a maximum of 3.55  $\text{m}^2$ .  
168 The forest was thus highly spatially variable in its distribution of trees relative to the  $R_s$   
169 measurement collars.

170

### 171 *Effect of BA on $R_s$*

172 The linear mixed-effects model using temperature, soil moisture, and basal area within  
173 five meters ( $BA_5$ ) predicted 37% of the  $R_s$  variability (conditional  $R^2 = 0.37$ ).  $BA_5$  was not  
174 significant by itself in a Type III ANOVA using this model ( $\chi^2 = 0.081$ ,  $P = 0.776$ ), but exhibited  
175 strong and significant interactions with  $T_5$  and  $T_{20}$  (**Table 3**). In addition, the residuals of a model  
176 fit without  $BA_5$  had a significant trend with  $BA_5$  (**Figure 4**). Separating the data into growing- and  
177 dormant-season subsets provided contrasting results. In the growing season, model outputs  
178 were similar to those of the full year model, with  $BA_5$  having significant interactions with  $T_5$  and

179  $T_{20}$  (data not shown). The dormant season model, however, was quite different: only  $T_{20}$  ( $P \leq$   
180 0.000) and soil moisture ( $P = 0.0377$ ) were significant terms. In addition, the dormant season  
181 model explained more of the  $R_s$  variability (AIC = 119.80, marginal  $R^2 = 0.48$ ). In summary,  
182 collars with higher basal area within 5 m had significantly higher temperature sensitivity of soil  
183 respiration, while basal area within 5 m of sampling points was not correlated with  $R_s$  during the  
184 dormant season.

185         There were strong differences between the driest and wettest thirds of the data, but our  
186 hypothesis that any basal area effect would be strongest in the driest time of year was not  
187 supported. In the driest third of the data, neither  $BA_5$  nor its interaction with  $T_5$  was significant ( $P$   
188 = 0.096 and 0.054 respectively);  $T_{20}$  was never significant; and the dominant control was instead  
189 soil moisture ( $\chi^2 = 15.23$ ,  $P < 0.001$ ). In contrast, the wettest-third model resembled the full-year  
190 model, with  $BA_5$  interacting with temperature, and soil moisture also significant.

191

## 192 *Sensitivity test*

193         Our *a priori* choice of 5 m for the basal area test was one of many possible choices, and  
194 could potentially bias the results, as the actual extent of tree roots at these sites is unknown.  
195 Re-fitting the main statistical model and calculating variable importance metrics across a wide  
196 range of distances, however, showed that basal area and its interactions with  $T_5$  and  $T_{20}$  were  
197 almost always statistically significant (**Figure 5**). Generally the BA effects were not significant at  
198 short (< 3 m) distances; this is expected, given that few collars were that close to trees.  
199 Interestingly, the BA effects remained significant all the way to our maximum measured distance  
200 of 15 m. In summary, our *a priori* analytical choice of a 5 m radius did not appear to bias our  
201 results.

202

## 203 **Discussion**



204

205           The  $R_s$  fluxes observed in this study,  $0.35\text{-}15.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ , were comparable to values  
206 in similar forests (Giasson et al., 2013) as well as those from the Soil Respiration Database  
207 (SRDB; Bond-Lamberty and Thomson, 2010), a synthesis of annual  $R_s$  studies (0 to  $14.7 \mu\text{mol}$   
208  $\text{m}^{-2} \text{s}^{-1}$ ,  $n = 1281$  temperate deciduous studies). We observed a  $R_s$  CV of 10-22% between plots,  
209 a value also comparable to previous studies. In a study of  $R_s$  in conifer forests and grasslands,  
210 Rodeghiero (2008) reported 28.9-41.5% variability, Davidson et al. (2000) about 30% in forest  
211 ecosystems, and a much broader range (0.11-84.5%) for temperate, deciduous forests from  
212 the SRDB.

213           Sample size requirements to estimate annual  $R_s$  were high at SERC compared to  
214 previous studies. For example, to be within 10% of the mean  $R_s$  flux at 95% confidence required  
215 from 41 (Davidson et al., 2002) in Harvard Forest, to 72 (Adachi et al., 2005) in a secondary  
216 forest, to 129 sample points in this study. Within forest biomes, topography and stand structure  
217 (Søe and Buchmann, 2005) can be dominant controls. Significant spatial variation in stand  
218 structure and topography across the study domain may have resulted in high variability seen in  
219 this study. In particular, the measurement points at our study sites ranged from 3-15 meters in  
220 elevation (Table 1), as at all sites the land rises quickly away from Muddy Creek. These  
221 elevation gradients mean that some measurement points drain more quickly than others,  
222 creating strong differences in soil water content (CV  $16.7\% \pm 4.0$  within plots) and thus  $R_s$ . This  
223 is consistent with the idea that topographic complexity can be an important and complex factor  
224 in  $R_s$  variation across sites (Riveros-Iregui et al. 2012) .

225

#### 226 *Interactions between basal area and temperature sensitivity on $R_s$*

227           Many studies have examined whether autotrophic respiration ( $R_a$ ) or heterotrophic  
228 respiration ( $R_h$ ) is more temperature-sensitive, and reached varying conclusions (Aguilos et al.,  
229 2011; Boone et al., 1998; Wei et al., 2010). In this study, the Type III SS interaction between

230 BA5 and temperature was highly significant, meaning that collars with higher basal area within 5  
231 m exhibited significantly higher temperature sensitivity of soil respiration. This suggests that  $R_a$   
232 might be more sensitive to temperature than  $R_h$  at these sites. However, it is important to note  
233 that we did not directly measure the autotrophic and heterotrophic source fluxes contributing to  
234 the overall  $R_s$  flux. Instead, we assume that collars closer to trees have a larger fraction of  $R_s$   
235 contributed by  $R_a$ , an assumption also made in previous studies such as Tang and Baldocchi  
236 (2005).

237 Mechanistically, these findings could be explained by a number of processes. When  
238 substrate supply from root exudates is higher during the growing season,  $R_s$  tends to be more  
239 sensitive to temperature (Luo and Zhou, 2006), presumably because under these conditions  $R_s$   
240 is tightly coupled with photosynthesis (Ekblad and Högberg, 2001), as roots access  
241 photosynthate before microbes, and thus can respond more strongly to temperature changes.  
242 Leaf phenology likely also plays a role in a deciduous forest such as the one studied here,  
243 where the growth of photosynthetically active foliage in the spring can promote carbon allocation  
244 belowground and hence  $R_a$ . Input of leaf material in the fall may also stimulate  $R_h$  (Curiel Yuste  
245 et al., 2004; Epron et al., 2001; Ruehr et al., 2010) and is dependent on tree size and  
246 distribution (Bréchet et al., 2011).

247 There is also abundant evidence that soil moisture influences temperature sensitivity:  
248 Suseela et al. (2012), for example, found that  $R_s$  is less sensitive to temperature during water-  
249 limited times. If trees' roots have access to water consistently, their respiratory flux  $R_a$  measured  
250 at the soil surface as part of  $R_s$  will be more temperature-sensitive on average, because  $R_a$  will  
251 be limited by soil moisture less frequently (Misson et al., 2006). It is important to note that these  
252 various mechanisms are not mutually exclusive.

253

254 *Soil moisture controls on BA significance*

255 We hypothesized that any  $BA_5$  effect would be particularly strong during the driest third  
256 of the year, but instead found that only soil moisture controlled  $R_s$  during these periods, while  
257 neither temperature nor tree proximity ( $BA_5$ ) was significant. This demonstrates that  $R_s$  is highly  
258 moisture-sensitive at these sites, but does not support our idea that trees might have access to  
259 deeper or different water sources than surface soil microbes. Soil moisture is considered to be a  
260 primary  $R_s$  control in Mediterranean and desert ecosystems (Cable et al., 2010), but  
261 interestingly even this deciduous forest, in a year with record rainfall (National Weather Service,  
262 2019), experienced significant moisture restrictions on  $R_s$ .

263

#### 264 *Dormant season $R_s$ controls*

265 Tree basal area within 5 m of our  $R_s$  sampling points was not significant in the dormant  
266 season model, supporting our hypothesis that total  $R_a$  contribution is often lower during the  
267 dormant season than the growing season (Hanson et al., 2000), which suggests that  $R_a$   
268 contributes less to  $R_s$  during the dormant season. This is expected, given the physiological link  
269 between photosynthesis and root respiration (Sprugel et al., 1995). Interestingly,  $T_5$  was not  
270 significant in the dormant season model, but rather  $T_{20}$  was the dominant control. The study site  
271 is in a mid-Atlantic, temperate location with cold air temperatures during the winter. Deeper soils  
272 are more insulated from cold air temperatures, allowing more favorable conditions for respiration  
273 and thus making  $T_{20}$  a dominant control on  $R_s$  during these times.

274

#### 275 *Limitations of this study*

276 A number of limitations should be noted in our study design and execution. First, this  
277 was not a fully spatially-explicit analysis; we did not map the collars relative to each other, nor  
278 construct a full spatial map of the forest stands (Atkins et al., 2018). Such mapping can be  
279 useful to examine the  $R_s$  spatial structure in more detail, as for example in Stegen et al. (2017),  
280 but our approach to mapping relative distances to trees provides an alternative spatial study

281 construct. In a similar vein, Tang and Baldocchi (2005) measured  $R_s$  within a transect of two oak  
282 trees to draw inferences on the spatially variable contribution of  $R_h$  and  $R_a$ . Our study design still  
283 provides useful spatial information, however: the 15 m max distance in **Figure 5** implies that the  
284 range of a semivariogram, i.e. the distance of maximum autocorrelation, would be at least this  
285 far. This means that BA remained significant all the way to our maximum measured distance of  
286 15 m, implying that the spatial influence of large trees persisted at least this far (Högberg et al.,  
287 2001).

288

289         Second, this study tested the effect of basal area on  $R_s$ , based on the assumption that  
290 BA is proportional to fine root biomass, the respiration of which is driven (with some time lag) by  
291 photosynthesis and this in turn drives root respiration dynamics (Vose and Ryan, 2002). Stems  
292 with a diameter below 2 cm and understory were not inventoried or, as a result, included in the  
293 hypothesis-testing statistical models. If root respiration is instead correlated with number of  
294 stems, which are disproportionately small due to forest demographics, this would bias our  
295 results. There are not many understory/saplings at these sites (**Table 1**), however.

296

## 297 **Conclusion**

298         We found that measurement collars with higher basal area within 5 m had significantly  
299 higher temperature sensitivity.  $R_s$  was also highly moisture-sensitive at these sites, with large  
300 differences among  $R_s$  in low- versus high-moisture times. These findings, in conjunction with  
301 large sample size requirements, suggest soil respiration at this site to be highly dynamic and  
302 variable. This could have implications for measurement requirements in sites with particular  
303 stand structures. A better understanding of the spatial interactions between plants and microbes  
304 through  $R_h$  and  $R_a$  partitioning, as well as the speed and coupling between above- and  
305 belowground processes, is necessary to link these processes with collar- and ecosystem-scale  
306 soil-to-atmosphere C fluxes.

307

## 308 **Acknowledgments**

309 This research is part of the PREMIS Initiative at Pacific Northwest National Laboratory (PNNL).  
310 It was conducted under the Laboratory Directed Research and Development Program at PNNL,  
311 a multi-program national laboratory operated by Battelle for the U.S. Department of Energy  
312 under Contract DE-AC05-76RL01830. This research was supported by the Smithsonian  
313 Environmental Research Center. We thank Alexey Shiklomanov for pointing out a crucial  
314 mistake in our statistical code.

315

## 316 **Author contributions**

317 This study was designed by B.B.-L. and S.C.P. All fieldwork and data analysis was performed  
318 by S.C.P., except for the statistical analysis, which was written by B.B.-L. N.M., J.P.M., and  
319 J.C.S. provided feedback on the study design, analysis, and interpretation of results. S.C.P.  
320 wrote the manuscript in close collaboration with all authors.

321

## 322 **Competing Interests**

323 There are no competing interests reported by the authors that might have influenced the work  
324 described in this manuscript.

325

## 326 **Code/Data Availability**

327 All code and data necessary to reproduce our results are available in our online GitHub  
328 repository (<https://github.com/PNNL-PREMIS/PREMIS-ghg>) and permanently archived at  
329 Figshare (DOI if accepted).

330

## 331 **References**

332 Adachi, M., Bekku, Y. S., Konuma, A., Kadir, W. R., Okuda, T. and Koizumi, H.: Required  
333 sample size for estimating soil respiration rates in large areas of two tropical forests and of two  
334 types of plantation in Malaysia, *For. Ecol. Manage.*, 210(1), 455–459, 2005.

335 Aguilos, M., Takagi, K., Liang, N., Watanabe, Y., Goto, S., Takahashi, Y., Mukai, H. and Sasa,  
336 K.: Soil warming in a cool-temperate mixed forest with peat soil enhanced heterotrophic and  
337 basal respiration rates but Q10 remained unchanged, *Biogeosciences*, 2011.

338 Atkins, J. W., Bohrer, G., Fahey, R. T., Hardiman, B. S., Morin, T. H., Stovall, A. E. L.,  
339 Zimmerman, N. and Gough, C. M.: Quantifying vegetation and canopy structural complexity  
340 from terrestrial LiDAR data using the *forestr* package, edited by S. Goslee, *Methods Ecol.*  
341 *Evol.*, 9(10), 2057–2066, 2018.

342 Barba, J., Cueva, A., Bahn, M., Barron-Gafford, G. A., Bond-Lamberty, B., Hanson, P. J.,  
343 Jaimes, A., Kulmala, L., Pumpanen, J., Scott, R. L., Wohlfahrt, G. and Vargas, R.: Comparing  
344 ecosystem and soil respiration: Review and key challenges of tower-based and soil  
345 measurements, *Agric. For. Meteorol.*, 249(Supplement C), 434–443, 2018.

346 Bates, D., Mächler, M., Bolker, B. and Walker, S.: Fitting Linear Mixed-Effects Models Using  
347 *lme4*, *Journal of Statistical Software, Articles*, 67(1), 1–48, 2015.

348 Bond-Lamberty, B.: New techniques and data for understanding the global soil respiration flux,  
349 *Earth's Future*, doi:10.1029/2018EF000866, 2018.

350 Bond-Lamberty, B. and Thomson, A. M.: A global database of soil respiration data,  
351 *Biogeosciences*, 7, 1915–1926, 2010.

352 Bond-Lamberty, B., Epron, D., Harden, J. W., Harmon, M. E., Hoffman, F. M., Kumar, J.,  
353 McGuire, A. D. and Vargas, R.: Estimating heterotrophic respiration at large scales: challenges,  
354 approaches, and next steps, *Ecosphere*, 7(6), d01380, 2016.

355 Boone, R. D., Nadelhoffer, K. J., Canary, J. D. and Kaye, J. P.: Roots exert a strong influence  
356 on the temperature sensitivity of soil respiration, *Nature*, 396(6711), 570–572, 1998.

357 Brændholt, A., Ibrom, A., Larsen, K. S. and Pilegaard, K.: Partitioning of ecosystem respiration  
358 in a beech forest, *Agric. For. Meteorol.*, 252, 88–98, 2018.

359 Bréchet, L., Ponton, S., Alméras, T., Bonal, D. and Epron, D.: Does spatial distribution of tree  
360 size account for spatial variation in soil respiration in a tropical forest?, *Plant Soil*, 347(1), 293,  
361 2011.

362 Burgess, S. S. O., Adams, M. A., Turner, N. C. and Ong, C. K.: The redistribution of soil water  
363 by tree root systems, *Oecologia*, 115(3), 306–311, 1998.

364 Cable, J. M., Ogle, K., Lucas, R. W., Huxman, T. E., Loik, M. E., Smith, S. D., Tissue, D. T.,  
365 Ewers, B. E., Pendall, E. G., Welker, J. M., Charlet, T. N., Cleary, M., Griffith, A., Nowak, R. S.,  
366 Rogers, M., Steltzer, H., Sullivan, P. F. and van Gestel, N. C.: The temperature responses of  
367 soil respiration in deserts: a seven desert synthesis, *Biogeochemistry*, 103(1-3), 71–90, 2010.

368 Curiel Yuste, J., Janssens, I. A., Carrara, A. and Ceulemans, R.: Annual Q10 of soil respiration  
369 reflects plant phenological patterns as well as temperature sensitivity, *Glob. Chang. Biol.*, 10(2),  
370 161–169, 2004.

- 371 Davidson, E. A., Verchot, L. V., Cattânio, J. H., Ackerman, I. L. and Carvalho, J. E. M.: Effects  
372 of soil water content on soil respiration in forests and cattle pastures of eastern Amazonia,  
373 *Biogeochemistry*, 48(1), 53–69, 2000.
- 374 Davidson, E. A., Savage, K. E., Verchot, L. V. and Navarro, R.: Minimizing artifacts and biases  
375 in chamber-based measurements of soil respiration, *Agric. For. Meteorol.*, 113, 21–37, 2002.
- 376 Ekblad, A. and Högberg, P.: Natural abundance of <sup>13</sup>C in CO<sub>2</sub> respired from forest soils reveals  
377 speed of link between tree photosynthesis and root respiration, *Oecologia*, 127, 305–308, 2001.
- 378 Epron, D., Le Dantec, V., Dufrene, E. and Granier, A.: Seasonal dynamics of soil carbon dioxide  
379 efflux and simulated rhizosphere respiration in a beech forest, *Tree Physiol.*, 21(2/3), 145–152,  
380 2001.
- 381 Epron, D., Nouvellon, Y., Roupsard, O., Mouvondy, W., Mabilia, A., Saint-André, L., Joffre, R.,  
382 Jourdan, C., Bonnefond, J.-M., Berbigier, P. and Hamel, O.: Spatial and temporal variations of  
383 soil respiration in a Eucalyptus plantation in Congo, *For. Ecol. Manage.*, 202(1), 149–160, 2004.
- 384 Ezer, T. and Corlett, W. B.: Is sea level rise accelerating in the Chesapeake Bay? A  
385 demonstration of a novel new approach for analyzing sea level data, *Geophys. Res. Lett.*,  
386 39(19), doi:10.1029/2012GL053435, 2012.
- 387 Giasson, M.-A., Ellison, A. M., Bowden, R. D., Crill, P. M., Davidson, E. A., Drake, J. E., Frey, S.  
388 D., Hadley, J. L., Lavine, M., Melillo, J. M., Munger, J. W., Nadelhoffer, K. J., Nicoll, L., Ollinger,  
389 S. V., Savage, K. E., Steudler, P. A., Tang, J., Varner, R. K., Wofsy, S. C., Foster, D. R. and  
390 Finzi, A. C.: Soil respiration in a northeastern US temperate forest: a 22-year synthesis,  
391 *Ecosphere*, 4, art. 140, 2013.
- 392 Gillman, L. N., Wright, S. D., Cusens, J., McBride, P. D., Malhi, Y. and Whittaker, R. J.: Latitude,  
393 productivity and species richness: Latitude and productivity, *Glob. Ecol. Biogeogr.*, 24(1), 107–  
394 117, 2015.
- 395 Granier, A., Biron, P. and Lemoine, D.: Water balance, transpiration and canopy conductance in  
396 two beech stands, *Agric. For. Meteorol.*, 100(4), 291–308, 2000.
- 397 Hanson, P. J., Edwards, N. T., Garten, C. T. and Andrews, J. A.: Separating root and soil  
398 microbial contributions to soil respiration: A review of methods and observations,  
399 *Biogeochemistry*, 48(1), 115–146, 2000.
- 400 Högberg, P., Nordgren, A., Buchmann, N., Taylor, A. F. S., Ekblad, A., Högberg, M. N., Nyberg,  
401 G., Ottosson-Löfvenius, M. and Read, D. J.: Large-scale forest girdling shows that current  
402 photosynthesis drives soil respiration, *Nature*, 411(6839), 789–792, 2001.
- 403 Hopkins, F. M., Gonzalez-Meler, M. A., Flower, C. E., Lynch, D. J., Czimczik, C. I., Tang, J. and  
404 Subke, J.-A.: Ecosystem-level controls on root-rhizosphere respiration, *New Phytol.*, 199(2),  
405 339–351, 2013.
- 406 Hursh, A., Ballantyne, A., Cooper, L., Maneta, M., Kimball, J. and Watts, J.: The sensitivity of  
407 soil respiration to soil temperature, moisture, and carbon supply at the global scale, *Glob.  
408 Chang. Biol.*, 23(5), 2090–2103, 2017.
- 409 Le Quéré, C., Andrew, R. M., Friedlingstein, P., Sitch, S., Pongratz, J., Manning, A. C.,

410 Korsbakken, J. I., Peters, G. P., Canadell, J. G., Jackson, R. B., Boden, T. A., Tans, P. P.,  
411 Andrews, O. D., Arora, V. K., Bakker, D. C. E., Barbero, L., Becker, M., Betts, R. A., Bopp, L.,  
412 Chevallier, F., Chini, L. P., Ciais, P., Cosca, C. E., Cross, J., Currie, K., Gasser, T., Harris, I.,  
413 Hauck, J., Haverd, V., Houghton, R. A., Hunt, C. W., Hurtt, G., Ilyina, T., Jain, A. K., Kato, E.,  
414 Kautz, M., Keeling, R. F., Klein Goldewijk, K., Körtzinger, A., Landschützer, P., Lefèvre, N.,  
415 Lenton, A., Lienert, S., Lima, I., Lombardozzi, D., Metzl, N., Millero, F., Monteiro, P. M. S.,  
416 Munro, D. R., Nabel, J. E. M. S., Nakaoka, S.-I., Nojiri, Y., Padin, X. A., Peregón, A., Pfeil, B.,  
417 Pierrot, D., Poulter, B., Rehder, G., Reimer, J., Rödenbeck, C., Schwinger, J., Séférian, R.,  
418 Skjelvan, I., Stocker, B. D., Tian, H., Tilbrook, B., Tubiello, F. N., Laan-Luijckx, I. T. van der,  
419 Werf, G. R. van der, van Heuven, S., Viovy, N., Vuichard, N., Walker, A. P., Watson, A. J.,  
420 Wiltshire, A. J., Zaehle, S. and Zhu, D.: Global Carbon Budget 2017, *Earth System Science*  
421 *Data*, 10(1), 405–448, 2018.

422 Luo, Y. and Zhou, X.: *Soil Respiration and the Environment*, Elsevier/Academic Press,  
423 Amsterdam., 2006.

424 Luysaert, S., Inglisma, I., Jung, M., Richardson, A. D., Reichstein, M., Papale, D., Piao, S.,  
425 Schulze, E.-D., Wingate, L., Matteucci, G., Aragão, L. E. O. C., Aubinet, M., Beer, C., Bernhofer,  
426 C., Black, K. G., Bonal, D., Bonnefond, J.-M., Chambers, J. L., Ciais, P., Cook, B. D., Davis, K.  
427 J., Dolman, A. J., Gielen, B., Goulden, M. L., Grace, J., Granier, A., Grelle, A., Griffis, T. J.,  
428 Grünwald, T., Guidolotti, G., Hanson, P. J., Harding, R. B., Hollinger, D. Y., Hutyyra, L. R., Kolari,  
429 P., Kruijt, B., Kutsch, W. L., Lagergren, F., Laurila, T., Law, B. E., Le Maire, G., Lindroth, A.,  
430 Loustau, D., Malhi, Y., Mateus, J., Migliavacca, M., Misson, L., Montagnani, L., Moncrieff, J. B.,  
431 Moors, E. J., Munger, J. W., Nikinmaa, E., Ollinger, S. V., Pita, G., Rebmann, C., Roupsard, O.,  
432 Saigusa, N., Sanz, M. J., Seufert, G., Sierra, C. A., Smith, M.-L., Tang, J., Valentini, R., Vesala,  
433 T. and Janssens, I. A.: CO<sub>2</sub> balance of boreal, temperate, and tropical forests derived from a  
434 global database, *Glob. Chang. Biol.*, 13(12), 2509–2537, 2007.

435 Misson, L., Gershenson, A., Tang, J., McKay, M., Cheng, W. and Goldstein, A. H.: Influences of  
436 canopy photosynthesis and summer rain pulses on root dynamics and soil respiration in a  
437 young ponderosa pine forest, *Tree Physiol.*, 26(7), 833–844, 2006.

438 National Weather Service: Record Rain and Flooding of 2018, [online] Available from:  
439 <https://www.weather.gov/lwx/2018floods> (Accessed 30 May 2019), 2019.

440 Pitz, S. and Megonigal, J. P.: Temperate forest methane sink diminished by tree emissions,  
441 *New Phytol.*, 214(4), 1432–1439, 2017.

442 Raich, J. W. and Schlesinger, W. H.: The global carbon dioxide flux in soil respiration and its  
443 relationship to vegetation and climate, *Tellus B Chem. Phys. Meteorol.*, 44(2), 81–99, 1992.

444 Raich, J. W., Potter, C. S. and Bhagawati, D.: Interannual variability in global soil respiration,  
445 1980-94, *Glob. Chang. Biol.*, 8, 800–812, 2002.

446 R Development Core Team: R: A language and environment for statistical computing. Version  
447 3.5.3. [online] Available from: <http://www.R-project.org/>, 2019.

448 Reichstein, M., Rey, A., Freibauer, A., Tenhunen, J. D., Valentini, R., Banza, J., Casals, P.,  
449 Cheng, Y., Grünzweig, J. M., Irvine, J., Joffre, R., Law, B. E., Loustau, D., Miglietta, F., Oechel,  
450 W. C., Ourcival, J.-M., Pereira, J., Peressotti, A., Ponti, F., Qi, Y., Rambal, S., Rayment, M. B.,  
451 Romanya, J., Rossi, F., Tedeschi, V., Tirone, G., Xu, M. and Yakir, D.: Modeling temporal and  
452 large-scale spatial variability of soil respiration from soil water availability, temperature and



- 453 vegetation productivity indices, *Global Biochemical Cycles*, 17(4), art. no. 1104 (15 p.), 2003.
- 454 Rodeghiero, M. and Cescatti, A.: Spatial variability and optimal sampling strategy of soil  
455 respiration, *For. Ecol. Manage.*, 255, 106–112, 2008.
- 456 Rogers, K., Kelleway, J. J., Saintilan, N., Megonigal, J. P., Adams, J. B., Holmquist, J. R., Lu,  
457 M., Schile-Beers, L., Zawadzki, A., Mazumder, D. and Woodroffe, C. D.: Wetland carbon  
458 storage controlled by millennial-scale variation in relative sea-level rise, *Nature*, 567(7746), 91–  
459 95, 2019.
- 460 Ruehr, N. K., Knohl, A. and Buchmann, N.: Environmental variables controlling soil respiration  
461 on diurnal, seasonal and annual time-scales in a mixed mountain forest in Switzerland,  
462 *Biogeochemistry*, 98(1), 153–170, 2010.
- 463 Saiz, G., Green, C., Butterbach-Bahl, K., Kiese, R., Avitabile, V. and Farrell, E. P.: Seasonal  
464 and spatial variability of soil respiration in four Sitka spruce stands, *Plant Soil*, 287(1-2), 161–  
465 176, 2006.
- 466 Sallenger, A. H., Jr, Doran, K. S. and Howd, P. A.: Hotspot of accelerated sea-level rise on the  
467 Atlantic coast of North America, *Nat. Clim. Chang.*, 2, 884, 2012.
- 468 Schlesinger, W. H. and Andrews, J. A.: Soil respiration and the global carbon cycle,  
469 *Biogeochemistry*, 48(1), 7–20, 2000.
- 470 Schwendenmann, L. and Macinnis-Ng, C.: Soil CO<sub>2</sub> efflux in an old-growth southern conifer  
471 forest ( *Agathis australis* ) – magnitude, components and controls, , doi:10.5194/soil-2-403-  
472 2016, 2016.
- 473 Sørensen, A. R. B. and Buchmann, N.: Spatial and temporal variations in soil respiration in relation to  
474 stand structure and soil parameters in an unmanaged beech forest, *Tree Physiol.*, 25, 1427–  
475 1436, 2005.
- 476 Sprugel, D. G., Ryan, M. G., Brooks, J. R., Vogt, K. A. and Martin, T. A.: Respiration from the  
477 organ level to the stand, in *Resource Physiology of Conifers*, edited by W. K. Smith and T. M.  
478 Hinckley, pp. 255–299, Academic Press, San Diego., 1995.
- 479 Stegen, J. C., Anderson, C. G., Bond-Lamberty, B., Crump, A. R., Chen, X. and Hess, N.: Soil  
480 respiration across a permafrost transition zone: spatial structure and environmental correlates,  
481 *Biogeosciences*, 14(18), 4341–4354, 2017.
- 482 Stone, E. L. and Kalisz, P. J.: On the maximum extent of tree roots, *For. Ecol. Manage.*, 46(1),  
483 59–102, 1991.
- 484 Subke, J.-A., Inglima, I. and Cotrufo, M. F.: Trends and methodological impacts in soil CO<sub>2</sub>  
485 efflux partitioning: A metaanalytical review, *Glob. Chang. Biol.*, 12(2), 921–943, 2006.
- 486 Suseela, V., Conant, R. T., Wallenstein, M. D. and Dukes, J. S.: Effects of soil moisture on the  
487 temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate  
488 change experiment, *Glob. Chang. Biol.*, 18(1), 336–348, 2012.
- 489 Tang, J. and Baldocchi, D. D.: Spatial-temporal variation in soil respiration in an oak-grass  
490 savanna ecosystem in California and its partitioning into autotrophic and heterotrophic  
491 components, *Biogeochemistry*, 73(1), 183–207, 2005.

492 Vose, J. M. and Ryan, M. G.: Seasonal respiration of foliage, fine roots, and woody tissues in  
493 relation to growth, tissue N, and photosynthesis, *Glob. Chang. Biol.*, 8, 182–193, 2002.

494 Wei, W., Weile, C. and Shaopeng, W.: Forest soil respiration and its heterotrophic and  
495 autotrophic components: Global patterns and responses to temperature and precipitation, *Soil*  
496 *Biol. Biochem.*, 42(8), 1236–1244, 2010.

497

498

499

500 **Table 1** | Study site characteristics of each site along Muddy Creek, including trees per hectare,  
 501 cumulative basal area, main soil types, and dominant tree species by percent of basal area.  
 502 Values are mean  $\pm$  standard deviation of N=3, 800 m<sup>2</sup> plots.

Site	Trees (ha <sup>-1</sup> )	BA (m <sup>2</sup> ha <sup>-1</sup> )	Dominant Soil Type	Dominant Tree Species (by BA %)	Altitude (m)
GCRew  (38.876 °N, 76.553 °W)	637.5 $\pm$ 57.3	45.2 $\pm$ 7.344.6 $\pm$ 4	Collington-Wist complex; Collington and Annapolis soils	28% <i>Liriodendron tulipifera</i> 11% <i>Quercus spp.</i> 11% <i>Fagus grandifolia</i>	3-10
Canoe Shed  (38.884 °N, 76.557 °W)	529.2 $\pm$ 93.8	40.4 $\pm$ 6	Annapolis fine sandy loam	26% <i>Quercus spp.</i> , 23% <i>L. tulipifera</i> 20% <i>F. grandifolia</i>	7-10
North Branch  (38.887 °N, 76.563 °W)	806.9 $\pm$ 180.7	34.5 $\pm$ 7.8	Collington and Annapolis soils; Collington, Wist, and Westphalia soils	42% <i>F. grandifolia</i> 26% <i>Quercus spp.</i> 12% <i>Liquidambar styraciflua</i>	8-20

503

504

505 **Table 2.** Sample size required to estimate soil respiration with a particular error (delta, left  
 506 column, fraction of mean flux), for different statistical power values. Values are mean (standard  
 507 deviation) between plots. “Power” is the probability that the test rejects the null hypothesis when  
 508 a specific alternative hypothesis is true, and informally connotes the degree of confidence that  
 509 the measurement within some delta value of the true mean.

510

	<b>Power (1 - <math>\beta</math>)</b>					
<b>delta</b>	<b>0.5</b>	<b>0.6</b>	<b>0.7</b>	<b>0.8</b>	<b>0.9</b>	<b>0.95</b>
0.05	61 (24)	95 (37)	143 (55)	219 (84)	362 (138)	516 (196)
0.10	16 (6)	24 (10)	36 (14)	55 (21)	91 (35)	129 (49)
0.25	3 (1)	4 (2)	6 (3)	9 (4)	15 (6)	21 (8)
0.50	1 (1)	1 (1)	2 (1)	3 (1)	4 (2)	6 (2)

511

512

513 **Table 3.** Summary of linear mixed-effects model testing main hypothesis of the effect of nearby  
 514 tree basal area on soil respiration (the dependent variable). Terms tested include soil  
 515 temperature at 5 and 20 cm ( $T_5$  and  $T_{20}$  respectively), basal area (BA), and soil moisture (SM).  
 516 Model AIC = 381.6, marginal  $R^2 = 0.36$ .

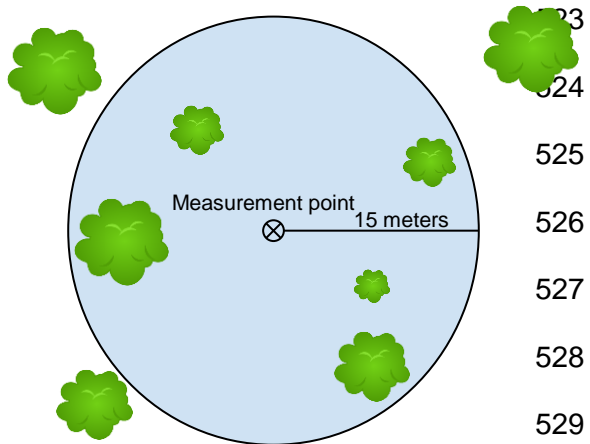
	value	degrees of freedom	t-value	p-value
<b>(Intercept)</b>	-0.767 ± 0.148	440	-5.199	0.000
<b>T<sub>5</sub></b>	0.010 ± 0.009	440	1.055	0.292
<b>BA<sub>5</sub></b>	0.022 ± 0.219	440	0.098	0.922
<b>T<sub>20</sub></b>	0.095 ± 0.011	440	8.397	0.000
<b>SM</b>	2.505 ± 0.699	440	3.581	0.004
<b>I(SM<sup>2</sup>)</b>	-3.542 ± 1.144	440	-3.095	0.002
<b>T<sub>5</sub>:BA<sub>5</sub></b>	0.079 ± 0.036	440	2.181	0.030
<b>BA<sub>5</sub>:T<sub>20</sub></b>	-0.069 ± 0.041	440	-1.689	0.092

517

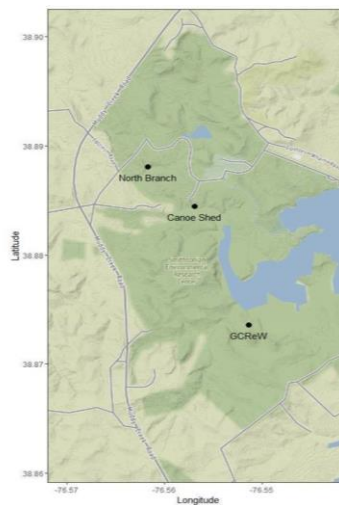
518 **Figure 1** | a) Tree proximity measurement schematic. Distance to each tree was recorded within  
519 a 15 meter radius of each soil respiration measurement point, along with DBH and species.  
520 Map of the Smithsonian Environmental Research Center with the three sites labeled in black.

521

522 a)



b)



530

531

532

533

534

535

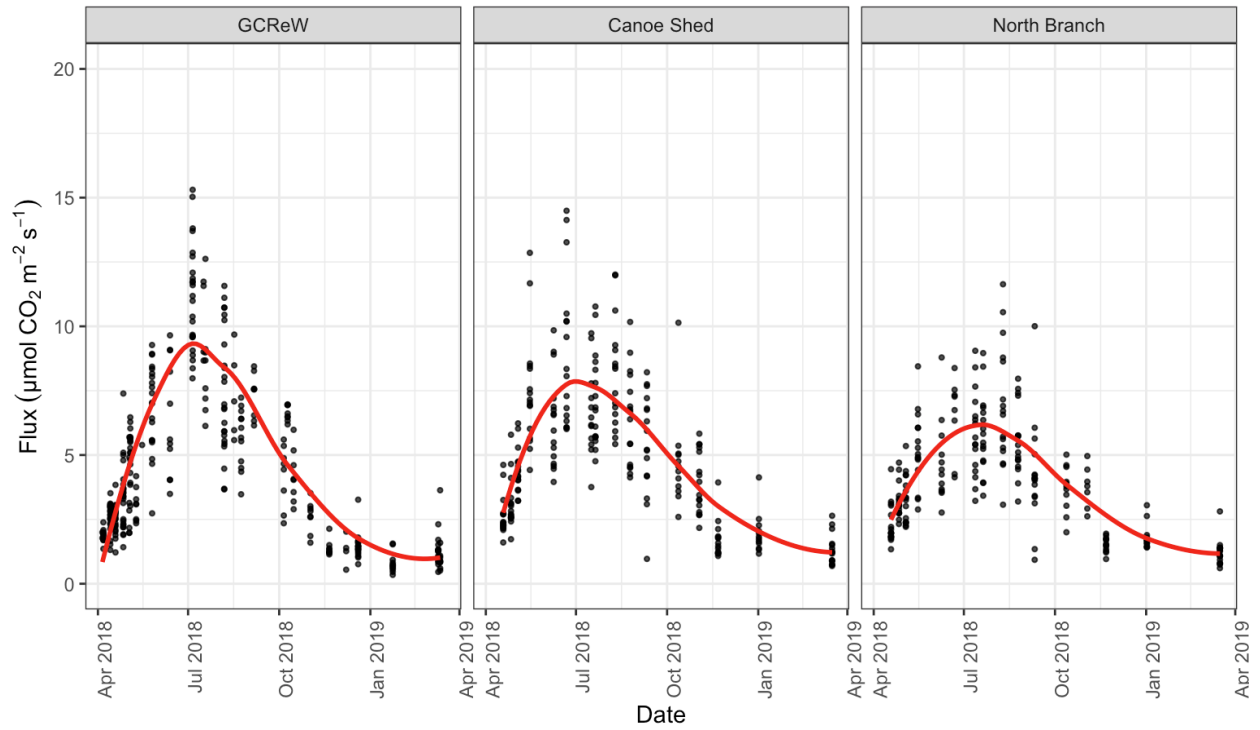
536

537

538

539

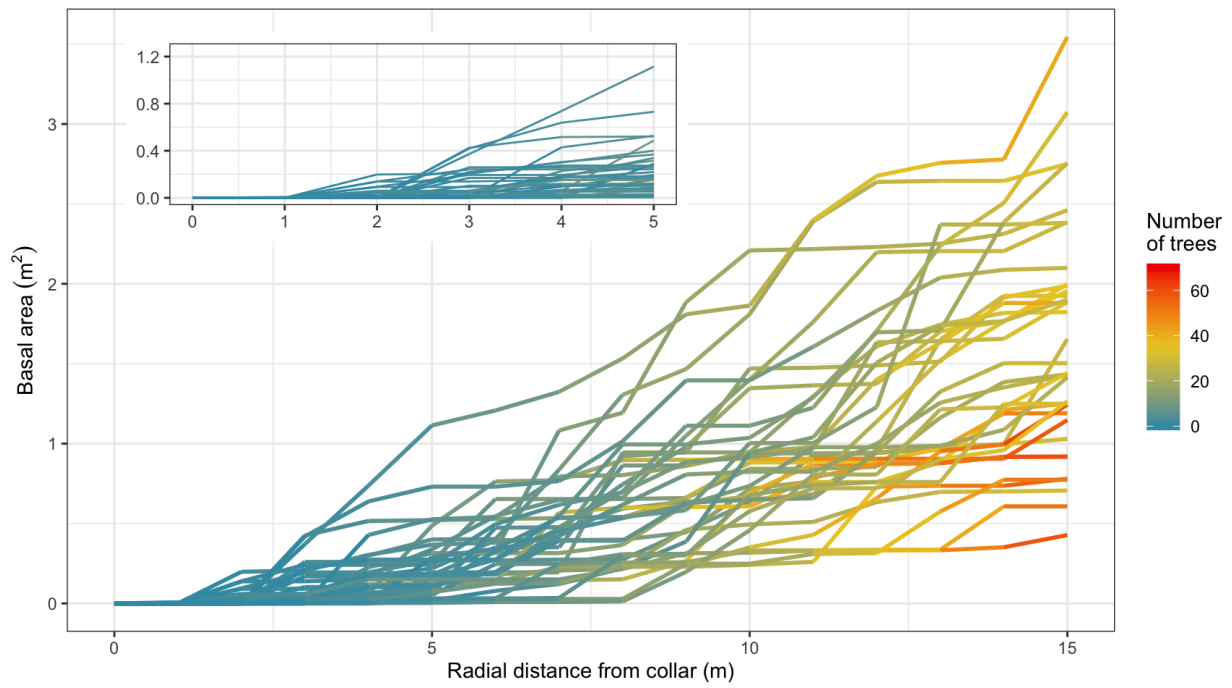
540 **Figure 2** | CO<sub>2</sub> flux over time from April 2018 to April 2019 for 36 measurement points across  
541 three sites; red line shows the seasonal trend using a loess smoother.



542

543

544 **Figure 3** | Cumulative basal area for each collar (N = 36) up to 15 meters; color indicates  
545 number of trees at each distance. Inset graph shows a close up of 0 to 5 meters for more detail.

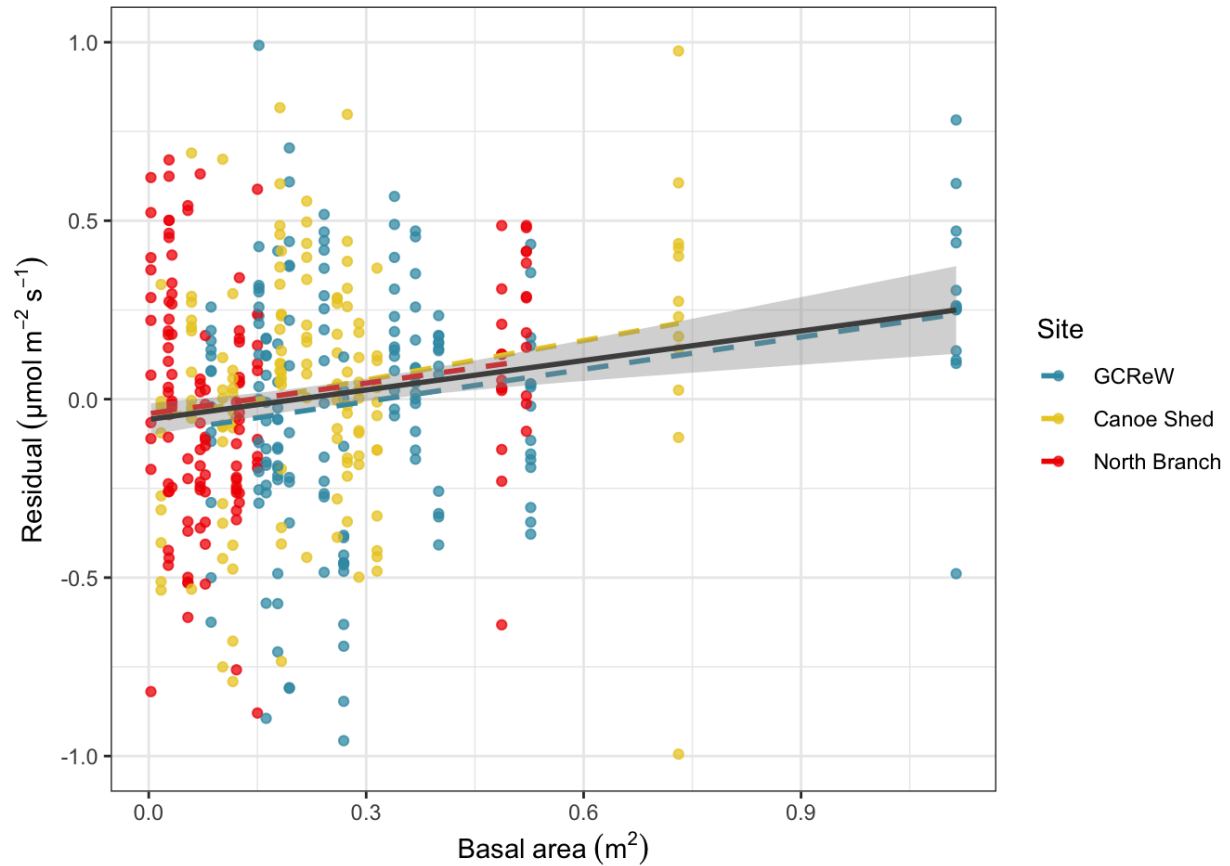


546

547



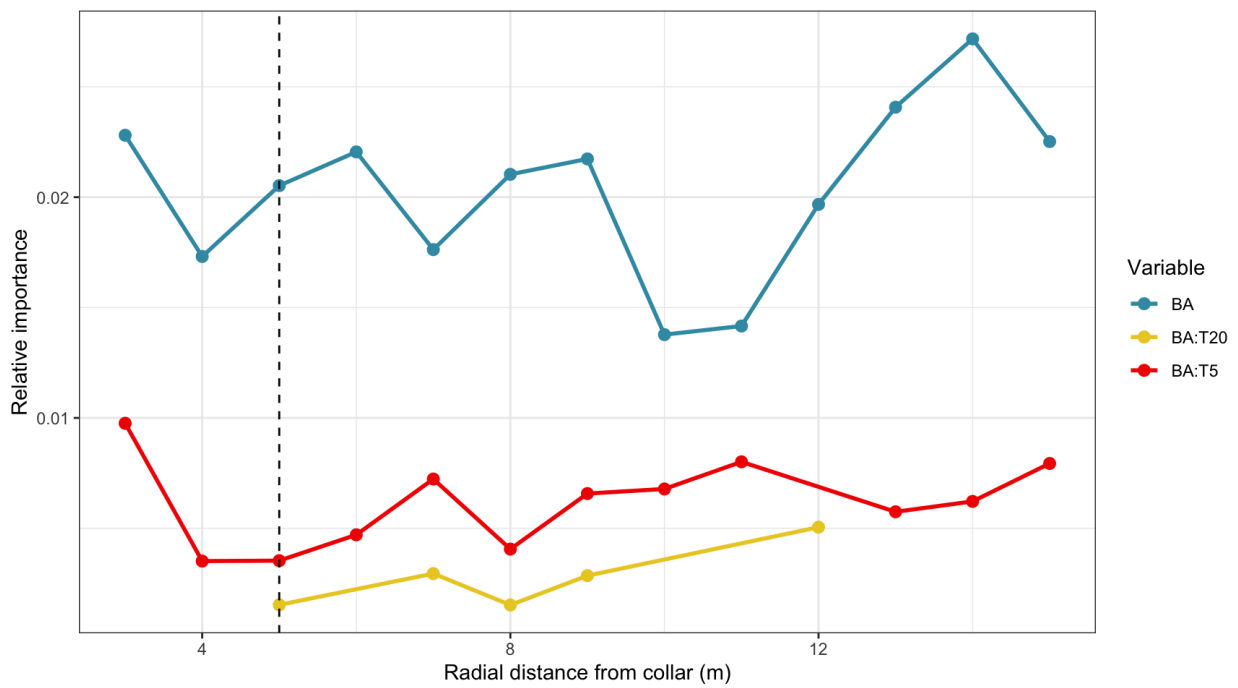
548 **Figure 4.** Residuals of a soil respiration model, incorporating temperature and soil moisture as  
549 independent variables, versus cumulative tree basal area within 5 m, by site. Each point is an  
550 individual observation (cf. **Figure 2**). Regression lines are shown for each site; black line is the  
551 overall trend. Note that 5 extreme points are out of the plot but are accounted for in the  
552 regression lines.



553

554

555 **Figure 5.** Test of robustness of results, run at various distances from soil respiration  
 556 measurement collars (x axis). Lines show the variable importance (calculated as  $R^2$  partitioned  
 557 by averaging over orders; see Methods) of basal area (BA), as well as the interaction of BA and  
 558 temperatures at 5 and 20 cm ( $T_5$  and  $T_{20}$  respectively). Vertical dashed line shows the 5 m  
 559 radius used in **Table 3** and **Figure 4** results. Note that 'missing' BA:T20 (in yellow) dots at  
 560 distances  $< 5$  m and  $> 12$  m mean that the terms were dropped from the model and are thus not  
 561 significant.



562

563

564

565

566

567 --- END OF MANUSCRIPT ---

568

569