1 Tree proximity affects soil respiration dynamics in a

2 coastal temperate deciduous forest

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17

18 **Abstract**

19 Soil respiration (R_s), the flow of CO_2 from the soil surface to the atmosphere, is one of the

20 largest carbon fluxes in the terrestrial biosphere. The spatial variability of R_s is both large and

21 poorly understood, limiting our ability to robustly scale it in time and space. One factor in R_s

22 spatial variability is the autotrophic contribution from plant roots, but it is uncertain how the

23 proximity of plants affects the magnitude and temperature sensitivity of R_s. This study examined

24 the effect of tree proximity on R_s in the growing and dormant seasons, as well as during

25   moisture-limited times, in a temperate, coastal, deciduous forest in eastern Maryland, USA. In a

26   linear mixed-effects model, tree basal area within 5 m (BA_5) exerted a significant positive effect

27   on the temperature sensitivity of soil respiration. Soil moisture was the dominant control on R_S

28   during the dry portions of the year while soil moisture, temperature, and BA_5 all exerted

29   significant effects on R_S in wetter periods. Our results suggest that autotrophic respiration is

30   more sensitive to temperature than heterotrophic respiration at these sites, although we did not

31   measure these source fluxes directly, and that soil respiration is highly moisture-sensitive, even

32   in a record-rainfall year. The R_S flux magnitudes (0.3-16.6 µmol m^{-2} s^{-1}) and variability

33   (coefficient of variability 10%-22% across plots) observed in this study were comparable to

34   values observed over decades in similar forests. We estimate that four R_S observations were

35   required to be within 50% of the stand-level mean, and 311 to be within 5%, at 90% confidence.

36   A better understanding of the spatial interactions between plants and microbes that results in

37   measured R_S is necessary to link these processes with large scale soil-to-atmosphere C fluxes.

38

39   **Introduction**

40   Soil respiration (R_s), the flow of CO_2 from the soil to the atmosphere, is an important

41   carbon (C) flux at ecosystem (Granier et al., 2000) to global scales. R_s is among the largest C

42   fluxes in the terrestrial biosphere (Bond-Lamberty, 2018; Le Quéré et al., 2018), but poorly

43   constrained at large scales, and thus it is important to understand its variability and sensitivity to

44   processes such as land use and climate changes (Hursh et al., 2017; Schlesinger and Andrews,

45   2000). Unlike other large C fluxes such as net primary production, net ecosystem exchange,

46   and gross primary production, R_s cannot be measured, even indirectly, at scales larger than ~1

47   m^2 (Bond-Lamberty et al., 2016), limiting our ability to robustly scale it in time and space.

48   One obstacle to robust measurements is that the spatial variability of R_s is both large

49   and poorly understood. Controls on the spatial variability of R_s differ among sites and

50   ecosystems and include plant species, leaf habit, ecosystem productivity (Reichstein et al.,

51   2003), soil temperature, moisture, spatial variability of vegetation, management, and soil

52   compaction (Epron et al., 2004). This high variability has consequences for the sampling

53   strategy required to accurately measure R_s at the stand scale (Rodeghiero and Cescatti, 2008;

54   Saiz et al., 2006) and limits our ability to upscale R_s measurements to eddy covariance tower

55   scales (Barba et al., 2018).

56   At large scales, R_s differs between vegetation types and biomes (Raich et al., 2002;

57   Raich and Schlesinger, 1992), implying that the spatial distribution of vegetation might strongly

58   affect R_s via plant root respiration, which constitutes ~50% of R_s in many ecosystems (Subke et

59   al., 2006). At ecosystem scales, a number of studies have examined how the spatial distribution

60   of R_s is affected by vegetation. R_s is typically higher closer to tree stems (Epron et al., 2004;

61   Tang and Baldocchi, 2005), and with higher nearby stem density (Stegen et al., 2017).

62   Photosynthesis is also a driver of the rhizospheric component of soil respiration (Hopkins et al.,

63   2013), and influences seasonal trends in root contribution to total soil respiration (Brændholt et

64   al., 2018; Högberg et al., 2001). Any spatial influences of plants on R_s might be expected to be

65   particularly strong in temperate, deciduous forests, as such forests tend to be especially

66   productive (Gillman et al., 2015; Luyssaert et al., 2007).

67   This study examines the effect of tree proximity on measured R_s in a mid-Atlantic,

68   deciduous forest in the Chesapeake Bay, USA region. We hypothesized that:

69

70   (i) the amount of basal area close to R_s measurement locations would exert a significant and

71   positive effect on measured R_s after taking into account the effects of abiotic drivers;

72

73   (ii) this effect would occur in the growing (leaf on) season, but not in the dormant (leaf off)

74   season, because root respiration is much stronger during the growing season; and

75

76   (iii) this effect would be stronger during drier times of year, because trees might maintain access

77   to deep soil moisture (Burgess et al., 1998) and thus continue respiring even when the surface

78   soil is dry.

79

80   To test these hypotheses we performed a spatially explicit analysis of one year of frequent R_s

81   measurements in a temperate coastal deciduous forest in eastern Maryland, USA. To our

82   knowledge, no study has examined the influences of trees on spatial variation of R_s in the

83   Chesapeake Bay watershed, an area subject to rapid rates of sea level rise (Ezer and Corlett,

84   2012; Sallenger et al., 2012) that may exert significant effects on the carbon cycling of coastal

85   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_2 flux as the linear or exponential

108   regression of CO_2 accumulation in the closed chamber system over unit area and time; two

109   successive measurements were taken at each collar and averaged. Vegetation was removed

110   from inside the collar, and new vegetation was re-clipped as necessary, to remove any

111   aboveground autotrophic flux, so that the IRGA was measuring only soil-to-atmosphere CO_2.

112   Soil moisture and temperature (T_5) were also recorded at 5 cm depth, using auxiliary sensors

113   attached to the LI-8100A, at the same time as soil respiration measurements. Temperature at

114   20 cm depth (T_{20}) was also recorded using a hand-held thermometer at the time of

115   measurement.

116

117   *Tree proximity measurements*

118   We recorded distance from the soil collar, diameter at breast height (1.37 m), and

119   species of each tree within a 15 meter radius of each soil respiration measurement point

120   (**Figure 1b**). Dead trees were included in the dataset but only account for < 1% of total forest

121   basal area. Cumulative basal area was calculated at each 1 m radial distance from the collar,

122   summing the cross-sectional areas of all trees within each distance. Tree root extent can be

123   highly variable, but generally roots extend at least to the edge of the tree canopy (Stone and

124   Kalisz, 1991). Mature tree canopies at SERC are ~5 m in radius (S. Pennington, personal

125   observation), and we adopted this distance as an *a priori* assumption to test for the effect of

126   basal area at 5 meters (BA_5) on R_s.

127

128 *Statistical analysis*

129   Respiration data were checked visually for artifacts or unusual outliers, but we did not

130 exclude any data *a priori*. Data were then combined with the proximity measurements described

131 above based on collar number. We used a linear mixed-effects model to test for the influence of

132 BA_5 on R_s, treating temperature, soil moisture, BA_5 as fixed effects, and site as a random effect.

133 To ensure homoschedasticity of model residuals, the dependent variable R_s was transformed by

134 taking its natural logarithm. We used restricted maximum likelihood estimation using the *lme4*

135 package (Bates et al., 2015) in R version 3.5.3 (R Development Core Team, 2019). All models

136 were examined for influential outliers and deviations from normality. Non-significant terms were

137 then eliminated using a forward-and-back stepwise algorithm (using the R package *MASS*

138 version 7.3-47) based on the Akaike Information Criterion. Residuals from all fitted models were

139 plotted and checked for trends or heteroschedasticity.

140   Our secondary hypotheses, that effect of BA_5 varies with growing season and soil

141 moisture, were tested by subsetting the R_s data. We treated April 15-October 14 as the growing

142 season, based on 2018 leaf-out and senescence, and October 15-April 14 as the dormant

143 season. Soil moisture data were split up into equal thirds (low, <0.188 m^3 m^{-3}; medium, 0.188-

144 0.368 m^3 m^{-3}; and high, >0.368 m^3 m^{-3}; all values volumetric). We then applied the statistical

145 model described above to each subset of the data.

146   We used the spatial variability between collars within individual plots to estimate the

147 number of samples required for a robust estimate of the R_s 'population mean', i.e., a spatially-

148 representative mean. Specifically, we used a Student's t-test to calculate this based on the

149 standard deviation of hourly R_s, the desired power of the test, and the allowable delta

150 (difference from the true mean value), following Davidson et al. (2002).

151   All code and data necessary to reproduce our results are available in our online GitHub

152 repository (https://github.com/PNNL-PREMIS/PREMIS-ghg) and permanently archived at

153 Figshare (DOI if accepted).

154

Results

156   We measured R_s, soil temperature, and soil moisture on 31 different days across the

157   one-year period (Figure 2). Soil temperatures ranged from 0.1 to 27.7 ℃ (at 5 cm) and 1.7 to

158   24.4 ℃ (at 20 cm); volumetric soil moisture values were 0.01-0.56. R_s fluxes ranged from 0.17

159   µmol m^{-2} s^{-1} (in March 2019) to 16.55 µmol m^{-2} s^{-1} (in July 2018). The coefficient of variability

160   (CV) between collars within plots, a measure of spatial variability, ranged from 10% to 22%.

161   This implied that a large number of samples was required to estimate soil respiration accurately

162   (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 20 trees (with respective nearby basal areas of 0.0002 m^2, 0.24 m^2, and 0.91

166   m^2). Within our maximum radius of measurement, 15 m, there were on average 42 trees and 1.7

167   m^2 of cumulative basal area, ranging from a minimum of 0.55 m^2 to a maximum of 3.55 m^2. The

168   forest was thus highly spatially variable in its distribution of trees relative to the R_s measurement

169   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 almost half of the R_s variability (conditional R^2 = 0.40). BA$_5$ was not

174   significant by itself in a Type III ANOVA using this model (χ^2 = 0.495, P = 0.482), 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 ≤

180   0.001) and soil moisture (P = 0.0009) were significant terms. In addition, the dormant season

181   model explained more of the R_s variability (AIC = 258.75, marginal R^2 = 0.52). In summary,

182   collars with higher basal area within 5 m had significantly higher temperature sensitivity of soil

183   respiration after controlling for temperature and moisture effects, while basal area within 5 m of

184   sampling points was not correlated with R_s during the dormant season.

185   Our third hypothesis was that any basal area effect on R_s would be strongest in the

186   driest times of the year, when microbial respiration at the surface soil declines as the soil dries,

187   but (we speculated) trees would maintain access to deeper soil moisture. There were in fact

188   strong differences between the driest and wettest thirds of the data, but our hypothesis was not

189   supported. In the driest third of the data, neither BA_5 nor its interaction with T_5 was significant (P

190   = 0.1775 and 0.1078 respectively); T_{20} was never significant; and the dominant control was

191   instead soil moisture (χ^2 = 20.93, P < 0.001). In contrast, the wettest-third model resembled the

192   full-year model, with BA_5 interacting with temperature, and soil moisture also significant.

193

194   *Sensitivity test*

195   Our *a priori* choice of 5 m for the basal area test was one of many possible choices, and

196   could potentially bias the results, as the actual extent of tree roots at these sites is unknown.

197   Re-running the main statistical test across a wide range of distances, however, showed that

198   basal area by itself was almost never significant, while its interactions with T_5 and T_{20} were

199   almost always significant (**Figure 5**). Generally the BA effects were not significant at short (< 3

200   m) distances; this is expected, given that few collars were that close to trees. Interestingly, the

201   BA effects remained significant all the way to our maximum measured distance of 15 m. In

202   summary, our analytical choice of a 5 m radius did not appear to bias our results.

203

204 **Discussion**

205

206 *Results and implications of R_s values*

207   The R_s fluxes observed in this study, 0.3-16.6 µmol m^{-2} s^{-1}, were comparable to values in

208 similar forests (Giasson et al., 2013) and from the Soil Respiration Database (Bond-Lamberty

209 and Thomson, 2010), a synthesis of annual R_s studies (0 to 14.7 µmol m^{-2} s^{-1}, n = 1281

210 temperate deciduous studies). We observed a collar-to-collar R_s CV of 10.5-21.5%, a value also

211 comparable to previous studies. In a study of R_s in conifer forests and grasslands, Rodeghiero

212 (2008) reported 28.9-41.5% variability, Davidson et al. (2000) about 30% in forest ecosystems,

213 and a much broader range (0.11-84.5%) for temperature, deciduous forests from the SRDB.

214   Sample size requirements to estimate annual R_s were high at SERC compared to

215 previous studies. For example, to be within 10% of the mean R_s flux at 95% confidence required

216 from 41 (Davidson et al., 2002) in Harvard Forest, to 72 (Adachi et al., 2005) in a secondary

217 forest, to 133 sample points in this study. This high variability between studies likely arises

218 because controls on the spatial variability of R_s differ among sites and ecosystems. Within forest

219 biomes, topography and stand structure (Søe and Buchmann, 2005) can also be dominant

220 controls that likely contribute to the high variability seen in this study.

221

222 *Interactions between basal area and temperature sensitivity on R_s*

223   Many studies have examined whether autotrophic respiration (R_a) or heterotrophic

224 respiration (R_h) is more temperature-sensitive, and reached varying conclusions (Aguilos et al.,

225 2011; Boone et al., 1998; Wang et al., 2010). In this study, however, collars with higher basal

226 area within 5 m had significantly higher temperature sensitivity of soil respiration after controlling

227 for temperature and moisture effects. This suggests that R_a is more sensitive to temperature

228 than R_h at these sites, even though we did not directly measure the autotrophic and

229 heterotrophic source fluxes contributing to the overall R_s flux.

230   Mechanistically, these findings could be explained by a number of processes. For

231   example, when substrate supply from root exudates is ample, R_s tends to be more sensitive to

232   temperature (Luo and Zhou, 2006), presumably because R_s can be tightly coupled with

233   photosynthesis and thus roots, which access the photosynthate before microbes, respond more

234   strongly to temperature changes. There is also abundant evidence that soil moisture influences

235   temperature sensitivity: Suseela et al. (2012), for example, found that R_s is less sensitive to

236   temperature during water-limited times. If trees' roots have access to water consistently, their

237   respiratory flux R_a measured at the soil surface as part of R_s will be more temperature-sensitive

238   on average, because R_a will be limited by soil moisture less frequently (Misson et al., 2006). It is

239   important to note that these various mechanisms are not mutually exclusive.

240

241   *Soil moisture controls on BA significance*

242   We hypothesized that BA_5 effect would be particularly strong during the driest third of the

243   year, but found that only soil moisture controlled R_s during these periods, while neither

244   temperature nor tree proximity (BA_5) was significant. This demonstrates that R_s is highly

245   moisture-sensitive at these sites, but does not support our hypothesis that trees might have

246   access to deeper or different water sources than surface soil microbes. Soil moisture is

247   considered to be a primary R_s control in Mediterranean and desert ecosystems (Cable et al.,

248   2010), but interestingly even this deciduous forest, in a year with record rainfall (National

249   Weather Service, 2019), experienced significant moisture restrictions on R_s. Spatial variation in

250   soil moisture (CV 2.5%-18.7% between plots) was probably due to the topographic variability of

251   our study site, which allowed some measurement points to drain more quickly than others,

252   producing a wide range of soil moisture conditions.

253

254   *Dormant season R_s controls*

255   Tree basal area within 5 m of our R_s sampling points was not significant in the dormant

256   season model, supporting our hypothesis that total R_a contribution is often lower during the

257   dormant reason than the growing season (Hanson et al., 2000), which suggests that R_a

258   contributes less to R_s during the dormant season. This is expected, given the physiological link

259   between photosynthesis and root respiration (Sprugel et al., 1995). Interestingly, T_5 was not

260   significant in the dormant season model, but rather T_{20} was the dominant control. The study site

261   is in a mid-Atlantic, temperate location with cold air temperatures during the winter. Deeper soils

262   are more insulated from cold air temperatures, allowing more favorable conditions for R_s and

263   potentially making T_{20} a dominant control during these times.

264

265   *Limitations of this study*

266   A number of limitations should be noted in our study design and execution. First, this

267   was not a fully spatially-explicit analysis; we did not map the collars relative to each other, nor

268   construct a full spatial map of the forest stands (Atkins et al., 2018). Such mapping can be

269   useful to examine the R_s spatial structure in more detail, as for example in Stegen et al. (2017),

270   but our approach to mapping relative distances to trees provides an alternative spatial study

271   construct. In a similar vein, Tang and Baldocchi (2005) measured R_s within a transect of two oak

272   trees to draw inferences on the spatially variable contribution of R_h and R_a. This study design

273   still provides useful spatial information, however: the 15 m max distance in **Figure 5** implies that

274   the range of a semivariogram, i.e. the distance of maximum autocorrelation, would be at least

275   this far. This means that BA remained significant all the way to our maximum measured

276   distance of 15 m, implying that the spatial influence of large trees persisted at least this far

277   (Högberg et al., 2001).

278

279   This study tested the effect of basal area on R_s, based on the assumption that BA is

280   proportional to fine root biomass, the respiration of which is driven (with some time lag) by

281   photosynthesis and this in turn drives root respiration dynamics (Vose and Ryan, 2002). Stems

282   with a diameter below 2 cm and understory were not inventoried or, as a result, included in the

283   hypothesis-testing statistical models. If root respiration is instead correlated with number of

284   stems, which are disproportionately small due to forest demographics, this would bias our

285   results. There are not many understory/saplings at these sites (**Table 1**), however.

286

287   **Conclusion**

288   Autotrophic respiration was found to be more sensitive to temperature than heterotrophic

289   respiration, and collars with higher basal area within 5 m had significantly higher temperature

290   sensitivity. R_s is also highly moisture-sensitive at these sites, with large differences among R_s

291   controls in low- versus high-moisture times. These findings, in conjunction with large sample

292   size requirements, suggest soil respiration at this site to be highly dynamic and variable. This

293   could have implications for measurement requirements in sites with particular stand structures.

294   A better understanding of the spatial interactions between plants and microbes that results in

295   measured R_s is necessary to link these processes with collar- and ecosystem-scale soil-to-

296   atmosphere C fluxes.

297

298   **Acknowledgments**

305

306   **Author contributions**

307　This study was designed by B.B.-L. and S.C.P. All fieldwork and data analysis was performed

308　by S.C.P., except for the statistical analysis, which was written by B.B.-L. N.M., J.P.M., and

309　J.C.S. provided feedback on the study design, analysis, and interpretation of results. S.C.P.

310　wrote the manuscript in close collaboration with all authors.

311

312　**References**

313　Adachi, M., Bekku, Y. S., Konuma, A., Kadir, W. R., Okuda, T. and Koizumi, H.: Required

314　sample size for estimating soil respiration rates in large areas of two tropical forests and of two

315　types of plantation in Malaysia, For. Ecol. Manage., 210(1), 455–459, 2005.

316　Aguilos, M., Takagi, K., Liang, N., Watanabe, Y., Goto, S., Takahashi, Y., Mukai, H. and Sasa,

317　K.: Soil warming in a cool-temperate mixed forest with peat soil enhanced heterotrophic and

318　basal respiration rates but Q10 remained unchanged, Biogeosciences, 2011.

319　Atkins, J. W., Bohrer, G., Fahey, R. T., Hardiman, B. S., Morin, T. H., Stovall, A. E. L.,

320　Zimmerman, N. and Gough, C. M.: Quantifying vegetation and canopy structural complexity

321　from terrestrial LiDAR data using the forestr r package, edited by S. Goslee, Methods Ecol.

322　Evol., 9(10), 2057–2066, 2018.

323　Barba, J., Cueva, A., Bahn, M., Barron-Gafford, G. A., Bond-Lamberty, B., Hanson, P. J.,

324　Jaimes, A., Kulmala, L., Pumpanen, J., Scott, R. L., Wohlfahrt, G. and Vargas, R.: Comparing

325　ecosystem and soil respiration: Review and key challenges of tower-based and soil

326　measurements, Agric. For. Meteorol., 249(Supplement C), 434–443, 2018.

327　Bates, D., Mächler, M., Bolker, B. and Walker, S.: Fitting Linear Mixed-Effects Models Using

328　lme4, Journal of Statistical Software, Articles, 67(1), 1–48, 2015.

329　Bond-Lamberty, B.: New techniques and data for understanding the global soil respiration flux,

330   Earth's Future, doi:10.1029/2018EF000866, 2018.

331   Bond-Lamberty, B. and Thomson, A. M.: A global database of soil respiration data,

332   Biogeosciences, 7, 1915–1926, 2010.

333   Bond-Lamberty, B., Epron, D., Harden, J. W., Harmon, M. E., Hoffman, F. M., Kumar, J.,

334   McGuire, A. D. and Vargas, R.: Estimating heterotrophic respiration at large scales: challenges,

335   approaches, and next steps, Ecosphere, 7(6), d01380, 2016.

336   Boone, R. D., Nadelhoffer, K. J., Canary, J. D. and Kaye, J. P.: Roots exert a strong influence

337   on the temperature sensitivity of soil respiration, Nature, 396(6711), 570–572, 1998.

338   Brændholt, A., Ibrom, A., Larsen, K. S. and Pilegaard, K.: Partitioning of ecosystem respiration

339   in a beech forest, Agric. For. Meteorol., 252, 88–98, 2018.

340   Burgess, S. S. O., Adams, M. A., Turner, N. C. and Ong, C. K.: The redistribution of soil water

341   by tree root systems, Oecologia, 115(3), 306–311, 1998.

342   Cable, J. M., Ogle, K., Lucas, R. W., Huxman, T. E., Loik, M. E., Smith, S. D., Tissue, D. T.,

343   Ewers, B. E., Pendall, E. G., Welker, J. M., Charlet, T. N., Cleary, M., Griffith, A., Nowak, R. S.,

344   Rogers, M., Steltzer, H., Sullivan, P. F. and van Gestel, N. C.: The temperature responses of

345   soil respiration in deserts: a seven desert synthesis, Biogeochemistry, 103(1-3), 71–90, 2010.

346   Davidson, E. A., Verchot, L. V., Cattânio, J. H., Ackerman, I. L. and Carvalho, J. E. M.: Effects

347   of soil water content on soil respiration in forests and cattle pastures of eastern Amazonia,

348   Biogeochemistry, 48(1), 53–69, 2000.

349   Davidson, E. A., Savage, K. E., Verchot, L. V. and Navarro, R.: Minimizing artifacts and biases

350   in chamber-based measurements of soil respiration, Agric. For. Meteorol., 113, 21–37, 2002.

351   Epron, D., Nouvellon, Y., Roupsard, O., Mouvondy, W., Mabiala, A., Saint-André, L., Joffre, R.,

352 Jourdan, C., Bonnefond, J.-M., Berbigier, P. and Hamel, O.: Spatial and temporal variations of

353 soil respiration in a Eucalyptus plantation in Congo, For. Ecol. Manage., 202(1), 149–160, 2004.

354 Ezer, T. and Corlett, W. B.: Is sea level rise accelerating in the Chesapeake Bay? A

355 demonstration of a novel new approach for analyzing sea level data, Geophys. Res. Lett.,

356 39(19), doi:10.1029/2012GL053435, 2012.

357 Giasson, M.-A., Ellison, A. M., Bowden, R. D., Crill, P. M., Davidson, E. A., Drake, J. E., Frey, S.

358 D., Hadley, J. L., Lavine, M., Melillo, J. M., Munger, J. W., Nadelhoffer, K. J., Nicoll, L., Ollinger,

359 S. V., Savage, K. E., Steudler, P. A., Tang, J., Varner, R. K., Wofsy, S. C., Foster, D. R. and

360 Finzi, A. C.: Soil respiration in a northeastern US temperate forest: a 22-year synthesis,

361 Ecosphere, 4, art. 140, 2013.

362 Gillman, L. N., Wright, S. D., Cusens, J., McBride, P. D., Malhi, Y. and Whittaker, R. J.: Latitude,

363 productivity and species richness: Latitude and productivity, Glob. Ecol. Biogeogr., 24(1), 107–

364 117, 2015.

365 Granier, A., Biron, P. and Lemoine, D.: Water balance, transpiration and canopy conductance in

366 two beech stands, Agric. For. Meteorol., 100(4), 291–308, 2000.

367 Hanson, P. J., Edwards, N. T., Garten, C. T. and Andrews, J. A.: Separating root and soil

368 microbial contributions to soil respiration: A review of methods and observations,

369 Biogeochemistry, 48(1), 115–146, 2000.

370 Högberg, P., Nordgren, A., Buchmann, N., Taylor, A. F. S., Ekblad, A., Högberg, M. N., Nyberg,

371 G., Ottosson-Löfvenius, M. and Read, D. J.: Large-scale forest girdling shows that current

372 photosynthesis drives soil respiration, Nature, 411(6839), 789–792, 2001.

373 Hopkins, F. M., Gonzalez-Meler, M. A., Flower, C. E., Lynch, D. J., Czimczik, C. I., Tang, J. and

374 Subke, J.-A.: Ecosystem-level controls on root-rhizosphere respiration, New Phytol., 199(2),

375   339–351, 2013.

376   Hursh, A., Ballantyne, A., Cooper, L., Maneta, M., Kimball, J. and Watts, J.: The sensitivity of

377   soil respiration to soil temperature, moisture, and carbon supply at the global scale, Glob.

378   Chang. Biol., 23(5), 2090–2103, 2017.

379   Le Quéré, C., Andrew, R. M., Friedlingstein, P., Sitch, S., Pongratz, J., Manning, A. C.,

380   Korsbakken, J. I., Peters, G. P., Canadell, J. G., Jackson, R. B., Boden, T. A., Tans, P. P.,

381   Andrews, O. D., Arora, V. K., Bakker, D. C. E., Barbero, L., Becker, M., Betts, R. A., Bopp, L.,

382   Chevallier, F., Chini, L. P., Ciais, P., Cosca, C. E., Cross, J., Currie, K., Gasser, T., Harris, I.,

383   Hauck, J., Haverd, V., Houghton, R. A., Hunt, C. W., Hurtt, G., Ilyina, T., Jain, A. K., Kato, E.,

384   Kautz, M., Keeling, R. F., Klein Goldewijk, K., Körtzinger, A., Landschützer, P., Lefèvre, N.,

385   Lenton, A., Lienert, S., Lima, I., Lombardozzi, D., Metzl, N., Millero, F., Monteiro, P. M. S.,

386   Munro, D. R., Nabel, J. E. M. S., Nakaoka, S.-I., Nojiri, Y., Padin, X. A., Peregon, A., Pfeil, B.,

387   Pierrot, D., Poulter, B., Rehder, G., Reimer, J., Rödenbeck, C., Schwinger, J., Séférian, R.,

388   Skjelvan, I., Stocker, B. D., Tian, H., Tilbrook, B., Tubiello, F. N., Laan-Luijkx, I. T. van der,

389   Werf, G. R. van der, van Heuven, S., Viovy, N., Vuichard, N., Walker, A. P., Watson, A. J.,

390   Wiltshire, A. J., Zaehle, S. and Zhu, D.: Global Carbon Budget 2017, Earth System Science

391   Data, 10(1), 405–448, 2018.

392   Luo, Y. and Zhou, X.: Soil Respiration and the Environment, Elsevier/Academic Press,

393   Amsterdam., 2006.

394   Luyssaert, S., Inglima, I., Jung, M., Richardson, A. D., Reichstein, M., Papale, D., Piao, S.,

395   Schulze, E.-D., Wingate, L., Matteucci, G., Aragão, L. E. O. C., Aubinet, M., Beer, C., Bernhofer,

396   C., Black, K. G., Bonal, D., Bonnefond, J.-M., Chambers, J. L., Ciais, P., Cook, B. D., Davis, K.

397   J., Dolman, A. J., Gielen, B., Goulden, M. L., Grace, J., Granier, A., Grelle, A., Griffis, T. J.,

398   Grünwald, T., Guidolotti, G., Hanson, P. J., Harding, R. B., Hollinger, D. Y., Hutyra, L. R., Kolari,

399   P., Kruijt, B., Kutsch, W. L., Lagergren, F., Laurila, T., Law, B. E., Le Maire, G., Lindroth, A.,

400   Loustau, D., Malhi, Y., Mateus, J., Migliavacca, M., Misson, L., Montagnani, L., Moncrieff, J. B.,

401   Moors, E. J., Munger, J. W., Nikinmaa, E., Ollinger, S. V., Pita, G., Rebmann, C., Roupsard, O.,

402   Saigusa, N., Sanz, M. J., Seufert, G., Sierra, C. A., Smith, M.-L., Tang, J., Valentini, R., Vesala,

403   T. and Janssens, I. A.: CO2 balance of boreal, temperate, and tropical forests derived from a

404   global database, Glob. Chang. Biol., 13(12), 2509–2537, 2007.

405   Misson, L., Gershenson, A., Tang, J., McKay, M., Cheng, W. and Goldstein, A. H.: Influences of

406   canopy photosynthesis and summer rain pulses on root dynamics and soil respiration in a

407   young ponderosa pine forest, Tree Physiol., 26(7), 833–844, 2006.

408   National Weather Service: Record Rain and Flooding of 2018, [online] Available from:

409   https://www.weather.gov/lwx/2018floods (Accessed 30 May 2019), 2019.

410   Pitz, S. and Megonigal, J. P.: Temperate forest methane sink diminished by tree emissions,

411   New Phytol., 214(4), 1432–1439, 2017.

412   Raich, J. W. and Schlesinger, W. H.: The global carbon dioxide flux in soil respiration and its

413   relationship to vegetation and climate, Tellus B Chem. Phys. Meteorol., 44(2), 81–99, 1992.

414   Raich, J. W., Potter, C. S. and Bhagawati, D.: Interannual variability in global soil respiration,

415   1980-94, Glob. Chang. Biol., 8, 800–812, 2002.

416   R Development Core Team: R: A language and environment for statistical computing. Version

417   3.5.3. [online] Available from: http://www.R-project.org/, 2019.

418   Reichstein, M., Rey, A., Freibauer, A., Tenhunen, J. D., Valentini, R., Banza, J., Casals, P.,

419   Cheng, Y., Grünzweig, J. M., Irvine, J., Joffre, R., Law, B. E., Loustau, D., Miglietta, F., Oechel,

420   W. C., Ourcival, J.-M., Pereira, J., Peressotti, A., Ponti, F., Qi, Y., Rambal, S., Rayment, M. B.,

421   Romanya, J., Rossi, F., Tedeschi, V., Tirone, G., Xu, M. and Yakir, D.: Modeling temporal and

422   large-scale spatial variability of soil respiration from soil water availability, temperature and

423   vegetation productivity indices, Global Biochemical Cycles, 17(4), art. no. 1104 (15 p.), 2003.

424   Rodeghiero, M. and Cescatti, A.: Spatial variability and optimal sampling strategy of soil

425   respiration, For. Ecol. Manage., 255, 106–112, 2008.

426   Rogers, K., Kelleway, J. J., Saintilan, N., Megonigal, J. P., Adams, J. B., Holmquist, J. R., Lu,

427   M., Schile-Beers, L., Zawadzki, A., Mazumder, D. and Woodroffe, C. D.: Wetland carbon

428   storage controlled by millennial-scale variation in relative sea-level rise, Nature, 567(7746), 91–

429   95, 2019.

430   Saiz, G., Green, C., Butterbach-Bahl, K., Kiese, R., Avitabile, V. and Farrell, E. P.: Seasonal

431   and spatial variability of soil respiration in four Sitka spruce stands, Plant Soil, 287(1-2), 161–

432   176, 2006.

433   Sallenger, A. H., Jr, Doran, K. S. and Howd, P. A.: Hotspot of accelerated sea-level rise on the

434   Atlantic coast of North America, Nat. Clim. Chang., 2, 884, 2012.

435   Schlesinger, W. H. and Andrews, J. A.: Soil respiration and the global carbon cycle,

436   Biogeochemistry, 48(1), 7–20, 2000.

437   Søe, A. R. B. and Buchmann, N.: Spatial and temporal variations in soil respiration in relation to

438   stand structure and soil parameters in an unmanaged beech forest, Tree Physiol., 25, 1427–

439   1436, 2005.

440   Sprugel, D. G., Ryan, M. G., Brooks, J. R., Vogt, K. A. and Martin, T. A.: Respiration from the

441   organ level to the stand, in Resource Physiology of Conifers, edited by W. K. Smith and T. M.

442   Hinckley, pp. 255–299, Academic Press, San Diego., 1995.

443   Stegen, J. C., Anderson, C. G., Bond-Lamberty, B., Crump, A. R., Chen, X. and Hess, N.: Soil

444   respiration across a permafrost transition zone: spatial structure and environmental correlates,

445   Biogeosciences, 14(18), 4341–4354, 2017.

446   Stone, E. L. and Kalisz, P. J.: On the maximum extent of tree roots, For. Ecol. Manage., 46(1),

447   59–102, 1991.

448   Subke, J.-A., Inglima, I. and Cotrufo, M. F.: Trends and methodological impacts in soil CO2

449   efflux partitioning: A metaanalytical review, Glob. Chang. Biol., 12(2), 921–943, 2006.

450   Suseela, V., Conant, R. T., Wallenstein, M. D. and Dukes, J. S.: Effects of soil moisture on the

451   temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate

452   change experiment, Glob. Chang. Biol., 18(1), 336–348, 2012.

453   Tang, J. and Baldocchi, D. D.: Spatial-temporal variation in soil respiration in an oak-grass

454   savanna ecosystem in California and its partitioning into autotrophic and heterotrophic

455   components, Biogeochemistry, 73(1), 183–207, 2005.

456   Vose, J. M. and Ryan, M. G.: Seasonal respiration of foliage, fine roots, and woody tissues in

457   relation to growth, tissue N, and photosynthesis, Glob. Chang. Biol., 8, 182–193, 2002.

458   Wang, W., Chen, W. and Wang, S.: Forest soil respiration and its heterotrophic and autotrophic

459   components: Global patterns and responses to temperature and precipitation, Soil Biol.

460   Biochem., 42(8), 1236–1244, 2010.

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464 **Table 1** | Study site characteristics of each site along Muddy Creek, including trees per hectare,

465 cumulative basal area, main soil types, and dominant tree species by percent of basal area.

466 Values are mean ± standard deviation of N=3, 800 m^2 plots.

467

Site	Trees (ha^{-1})	BA (m^2 ha^{-1})	Dominant Soil Type	Dominant Tree Species (by BA %)
GCReW (38.876 °N, 76.553 °W)	637.5 ± 57.3	44.6 ± 4	Collington-Wist complex; Collington and Annapolis soils	28% *Liriodendron tulipifera* 11% *Quercus spp.* 11% *Fagus grandifolia*
Canoe Shed (38.884 °N, 76.557 °W)	529.2 ± 93.8	40.4 ± 6	Annapolis fine sandy loam	26% *Quercus spp.*, 23% *L. tulipifera* 20% *F. grandifolia*
North Branch (38.887 °N, 76.563 °W)	806.9 ± 180.7	34.5 ± 7.8	Collington and Annapolis soils; Collington, Wist, and Westphalia soils	42% *F. grandifolia* 26% *Quercus spp.* 12% *Liquidambar styraciflua*

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

	Power (1 - β)					
Delta	**0.5**	**0.6**	**0.7**	**0.8**	**0.9**	**0.95**
0.05	63 ± 21	97 ± 33	147 ± 50	226 ± 76	373 ± 124	532 ± 175
0.10	16 ± 6	25 ± 9	37 ± 13	57 ± 19	94 ± 31	133 ± 44
0.25	3 ± 1	4 ± 2	6 ± 2	10 ± 4	15 ± 5	22 ± 7
0.50	1 ± 1	1 ± 1	2 ± 1	3 ± 1	4 ± 2	6 ± 2

Biogeosciences
Discussions

479 **Table 3.** Summary of linear mixed-effects model testing main hypothesis of the effect of nearby

480 tree basal area on soil respiration (the dependent variable). Terms tested include soil

481 temperature at 5 and 20 cm (T_5 and T_{20} respectively), basal area (BA), and soil moisture (SM).

482 Model AIC = 662.7, marginal R^2 = 0.72.

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|	Value	Std.Error	DF	t-value	p-value
(Intercept)	-0.7824	0.1215	884	-6.4418	0.0000
T_5	0.0146	0.0080	884	1.8327	0.0672
BA	-0.1162	0.1659	884	-0.7006	0.4837
T_{20}	0.0873	0.0093	884	9.3562	0.0000
SM	3.3107	0.5627	884	5.8834	0.0000
SM^2	-5.4007	0.8867	884	-6.0913	0.0000
T_5:BA	0.1165	0.0297	884	3.9144	0.0001
BA:T_{20}	-0.1018	0.0332	884	-3.0667	0.0022

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486   **Figure 1** | a) Tree proximity measurement schematic. Distance to each tree was recorded within

487   a 15 meter radius of each soil respiration measurement point, along with DBH and species. b)

488   Map of the Smithsonian Environmental Research Center with the three sites labeled in black.
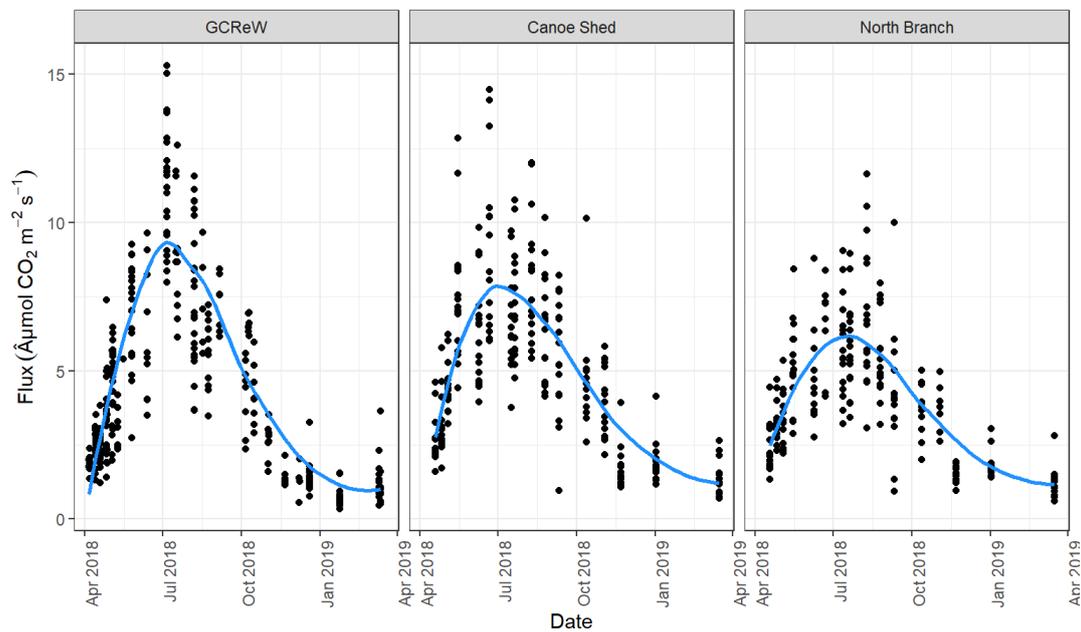
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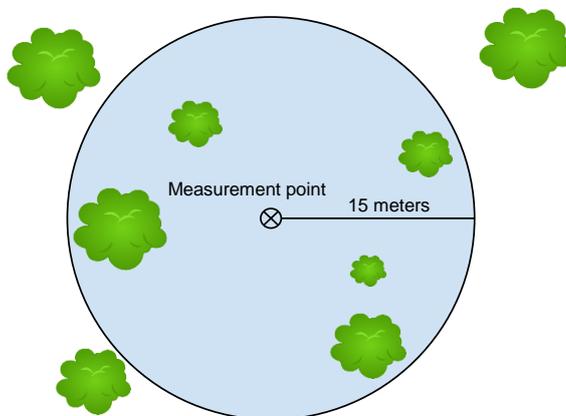
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508 **Figure 2** | Mean flux over time from April 2018 to April 2019 for 36 measurement points across

509 three sites; blue line shows the seasonal trend using a loess smoother.
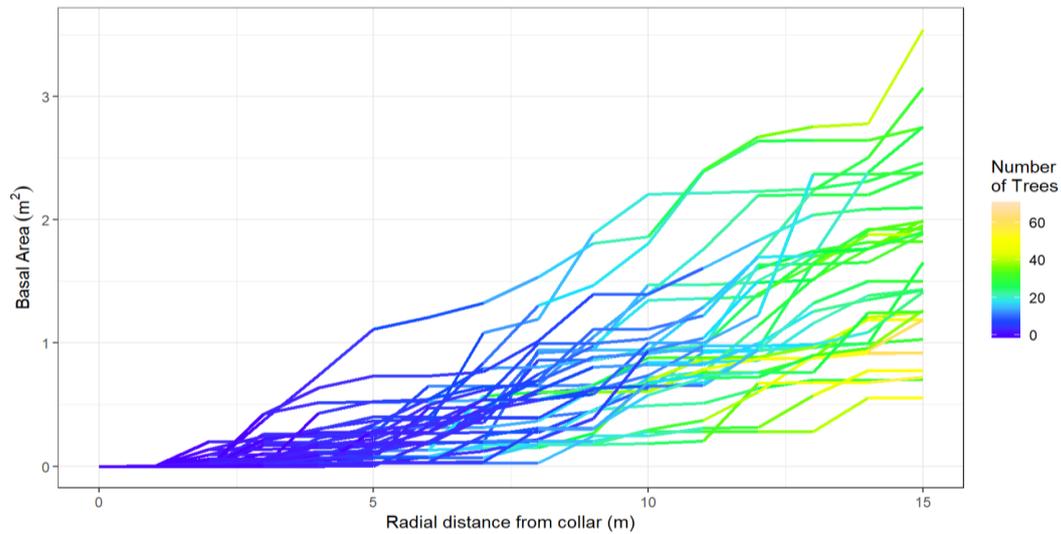

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512 **Figure 3** | Cumulative basal area for each collar (N = 36) up to 15 meters; color indicates
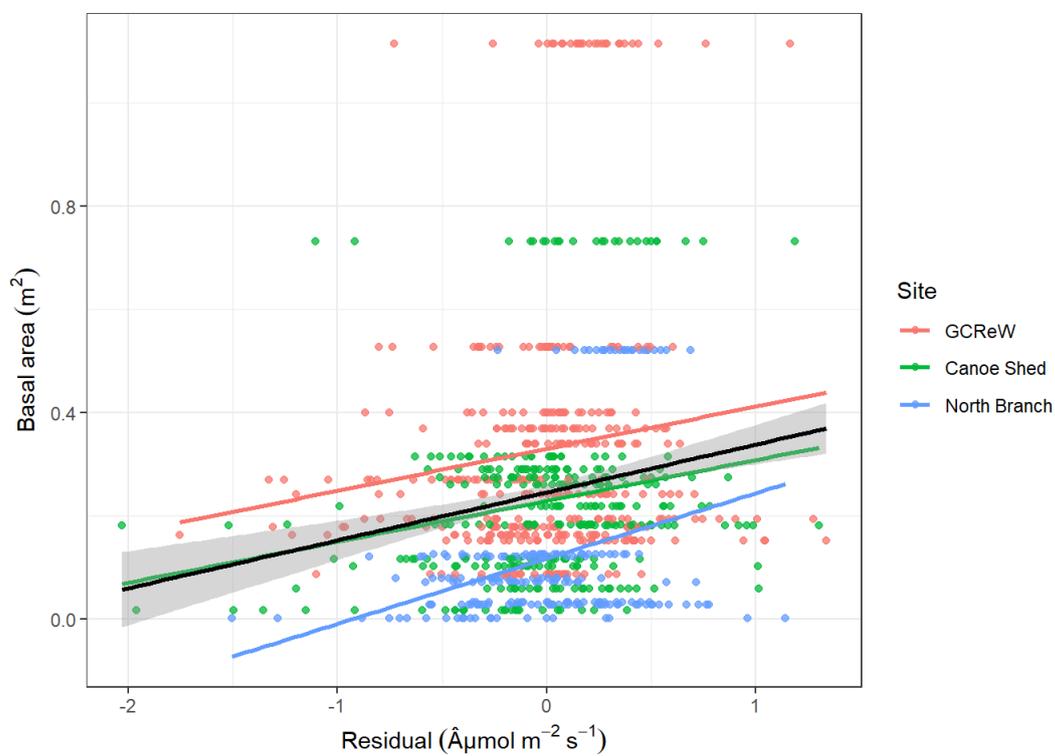
513 number of trees at each distance.

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516 **Figure 4.** Residuals of a soil respiration model, incorporating temperature and soil moisture as

517 independent variables, versus cumulative tree basal area within 5 m, by site. Each point is an

518 individual observation (cf. Figure 2). Regression lines are shown for each site; black line is the
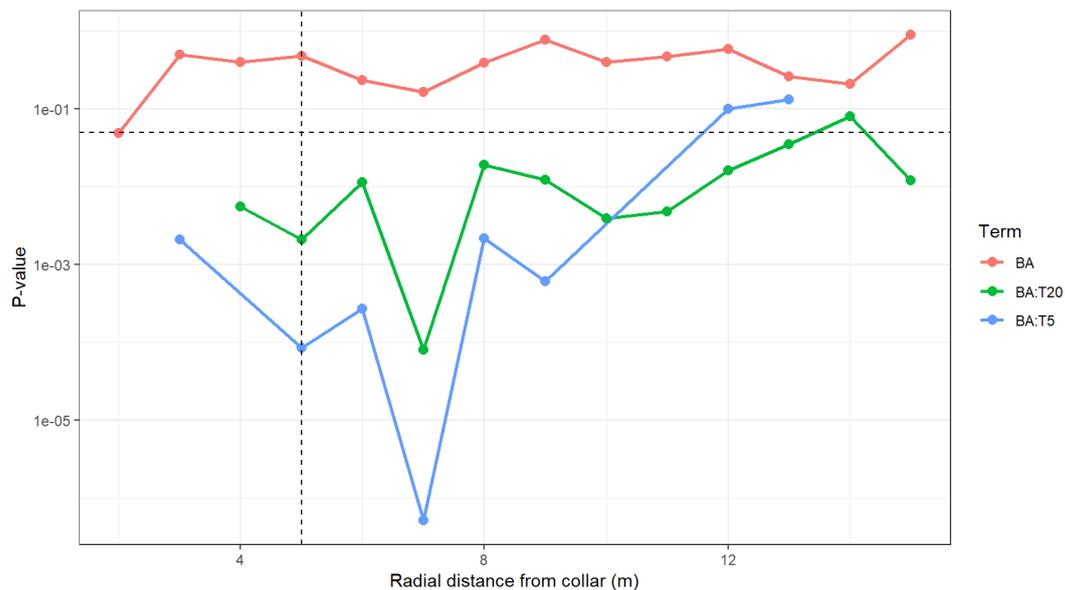
519 overall trend.

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522 **Figure 5.** Test of robustness of results, run at various distances from measurement collars (x

523 axis). Figures shows the significance (chi square p-value from Type III ANOVA of the linear

524 mixed effects model, y axis; note logarithmic scale) of basal area (BA), as well as the interaction

525 of BA and temperatures at 5 and 20 cm (T_5 and T_{20} respectively). Horizontal dashed line shows

526 the standard 0.05 significance cutoff; vertical dashed line the 5 m radius used in **Table 3** and

527 **Figure 4** results. Note that 'missing' green and blue dots at distances < 5 m mean that the

528 terms were dropped from the model and are thus not significant.

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