1 Localized basal area affects soil respiration temperature sensitivity in a

2 coastal deciduous forest

3 Biogeosciences

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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$_5$) exerted a significant positive effect on the temperature sensitivity of soil respiration. Soil

27   moisture was the dominant control on R$_S$ during the dry portions of the year while soil moisture,

28   temperature, and BA$_5$ all exerted significant effects on R$_S$ 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$_S$ flux magnitudes (0.35-15.3 µmol

32   m^{-2} s^{-1}) and variability (coefficient of variability 10%-23% across plots) observed in this study

33   were comparable to values observed in similar forests. Six R$_S$ 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$_s$), the flow of CO_2 from the soil to the atmosphere, is an important

42   carbon (C) flux at ecosystem (Granier et al., 2000) to global scales. R$_s$ 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$_s$ 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$_s$ is both large

50   and poorly understood. Controls on the spatial variability of R$_s$ 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; Luyssaert 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_2 flux as the exponential regression of

108   CO_2 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_2. Soil moisture

112   and temperature (T_5) 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_{20})

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_5) on R_s.

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_5 on R_s, treating temperature, soil moisture (SM), and BA_5 as fixed effects, and site as a

132   random effect. To ensure homoscedasticity of model residuals, the dependent variable R_s was

133   transformed by taking its natural logarithm, and thus the full linear model was specified as:

134         $\log(R_s) \sim T_5 * BA_5 + T_{20} * BA_5 + SM + SM^2$ (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_5 varies with growing season and soil

142   moisture, were tested by subsetting the R_s 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^3 m^{-3}; medium, 0.188-

145   0.368 m^3 m^{-3}; and high, >0.368 m^3 m^{-3}; all values volumetric). We then applied the statistical

146   model described above to each subset of the data to test for BA_5 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^2.

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_s '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   μmol m^{-2} s^{-1} (in January 2019) to 15.3 μmol m^{-2} 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 m^2, 0.24 m^2, and 0.88

166   m^2). Within our maximum radius of measurement, 15 m, there were on average 43 trees and

167   1.64 m^2 of cumulative basal area, ranging from a minimum of 0.43 m^2 to a maximum of 3.55 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 (χ^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 ≤

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 affect 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 (χ^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, 0.35-15.3 µmol m^{-2} 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 µmol

208   m^{-2} 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 temperature, 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% ± 4.0 within plots) and thus Rs. 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 Rs

235 contributed by Ra, 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 reason 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 Rh and Ra 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

Acknowledgments

Author contributions

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

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

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

wrote the manuscript in close collaboration with all authors.

Competing Interests

There are no competing interests reported by the authors that might have influenced the work

described in this manuscript.

Code/Data Availability

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

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

Figshare (DOI if accepted).

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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 ± standard deviation of N=3, 800 m^2 plots.

Site	Trees (ha^{-1})	BA (m^2 ha^{-1})	Dominant Soil Type	Dominant Tree Species (by BA %)	Altitude (m)
GCReW (38.876 °N, 76.553 °W)	637.5 ± 57.3	45.2 ± 7.344.6 ± 4	Collington-Wist complex; Collington and Annapolis soils	28% *Liriodendron tulipifera* 11% *Quercus spp.* 11% *Fagus grandifolia*	3-10
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*	7-10
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*	8-20

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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

	Power (1 - β)					
delta	0.5	0.6	0.7	0.8	0.9	0.95
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)

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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
(Intercept)	-0.767 ± 0.148	440	-5.199	0.000
T_5	0.010 ± 0.009	440	1.055	0.292
BA_5	0.022 ± 0.219	440	0.098	0.922
T_{20}	0.095 ± 0.011	440	8.397	0.000
SM	2.505 ± 0.699	440	3.581	0.004
I(SM^2)	-3.542 ± 1.144	440	-3.095	0.002
T_5:BA_5	0.079 ± 0.036	440	2.181	0.030
BA_5:T_{20}	-0.069 ± 0.041	440	-1.689	0.092

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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. b)

520   Map of the Smithsonian Environmental Research Center with the three sites labeled in black.

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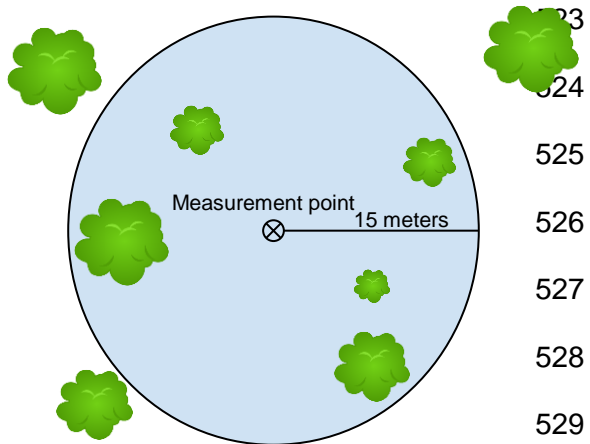
522   a)   b)
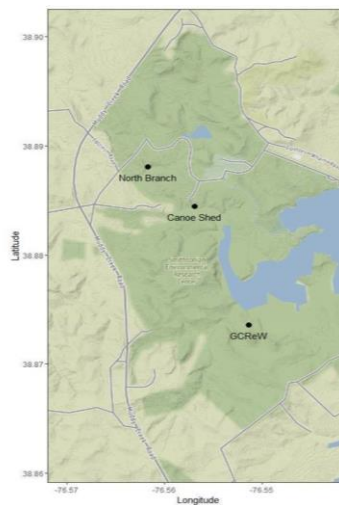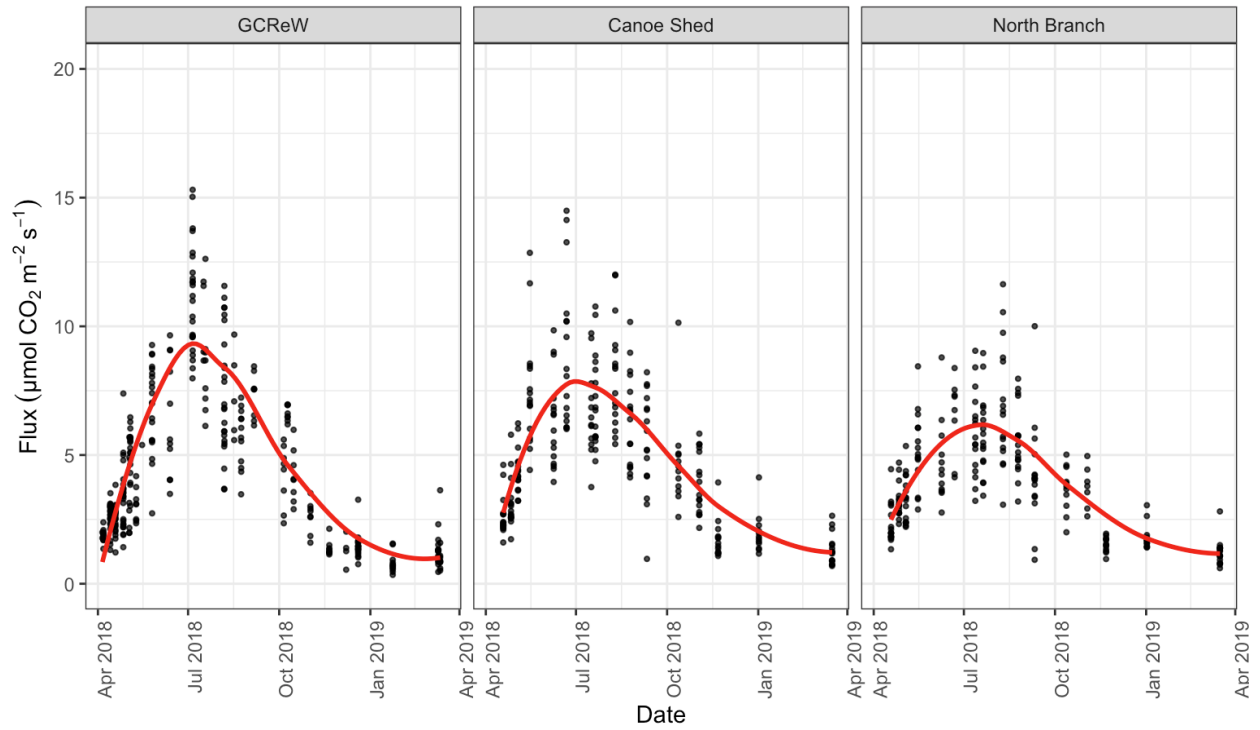

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540 **Figure 2** | CO_2 flux over time from April 2018 to April 2019 for 36 measurement points across

541 three sites; red line shows the seasonal trend using a loess smoother.

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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.
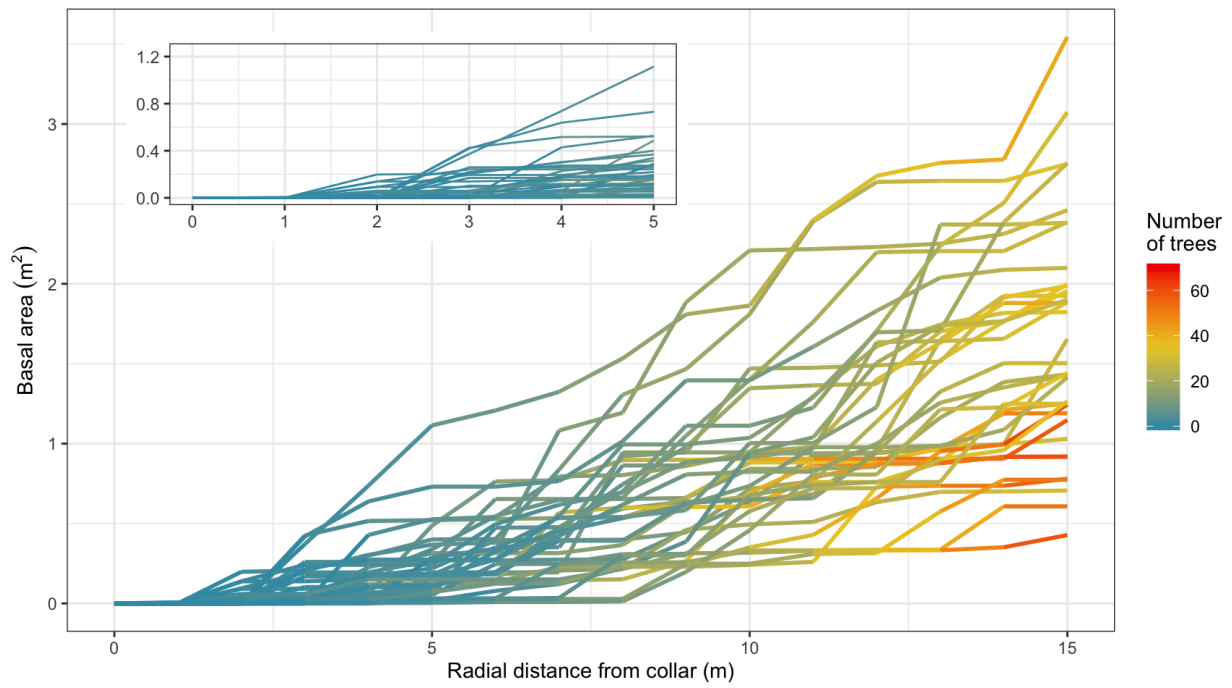

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548 **Figure 4.** Residuals of a soil respiration model, incorporating temperature and soil moisture as

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.
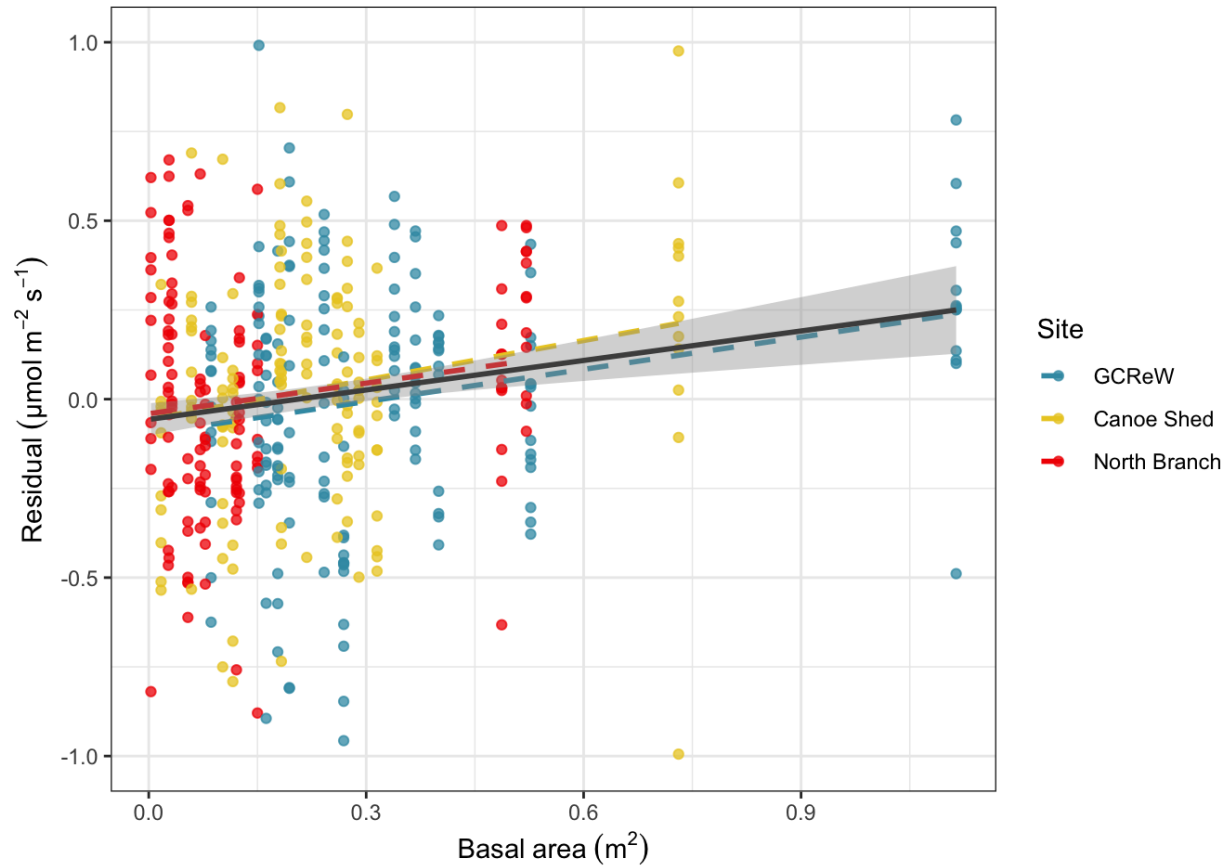
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555   **Figure 5.** Test of robustness of results, run at various distances from soil respiration

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.
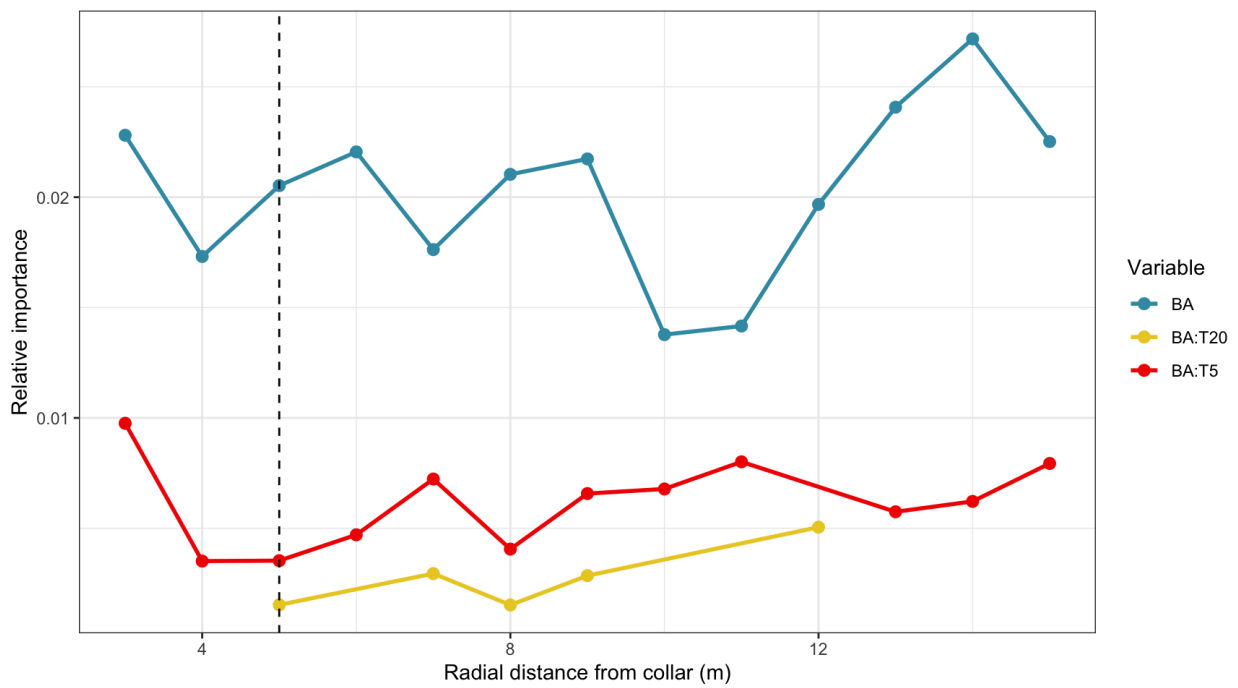
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