

Referee Comments and Responses

Anonymous Referee #1

Received and published: 24 July 2019

The manuscript entitled “Tree proximity affects soil respiration dynamics in a coastal temperate deciduous forest” is in fact addressing three different questions: (1) tree proximity and soil respiration, (2) temperature sensitivity, and (3) required sampling effort. Only the first one is clearly reflected in the title.

This is a great point, also pointed out by Reviewer #2. We will change the title to something that reflects the overall R_s variability in the context of localized basal area affect/vegetation. For example, Reviewer #2 suggested “localized basal area affects soil respiration dynamics in a coastal temperate deciduous forest”, which we agree would work better than the current title.

These three questions are relevant and within the scope of BG, but they are not novel and there is no novel concept, idea or tool that emerged for this study. This is an additional set of data (a case study). (1) The approach of linearly connecting the basal area of trees to a fixed distance (5 m) and ground respiration is simplistic. The distance at which an individual tree influenced soil respiration is probably dependent on the size of this tree. In other words, biggest trees are expected to have a stronger influence than smaller trees.

While aspects of the relationship between R_s and basal area have been previously studied, the issue is hardly closed; there is little consensus on the strength and spatial patterns of this effect, for example. We believe that the novelty of this study lies in its examination of how basal area affects the spatial variability of R_s in different phenological seasons and soil moisture conditions. We will explain this more clearly in the revised manuscript.

There are several (many papers) relating addressing the effect of tree size and proximity on soil respiration that are not cited in this manuscript. Among them: Fang C, Moncrieff JB, Gholz HL, Clark KL (1998) Soil CO₂ efflux and its spatial variation in a Florida slash pine plantation. *Plant Soil* 205:135–146. doi:10.1023/A:1004304309827 Metcalfe DB, Meir P, Aragão LEOC, Malhi Y, da Costa ACL, Braga A, Gonçalves PHL, de Athaydes J, de Almeida SS, Williams M (2007) Factors controlling spatio-temporal variation in carbon dioxide efflux from surface litter, roots, and soil organic matter at four rain forest sites in the eastern Amazon: PARTITIONING AMAZON SOIL RESPIRATION. *J Geophys Res* 112. doi:10.1029/2007JG000443 Katayama A, Kume T, Komatsu H, Ohashi M, Nakagawa M, Yamashita M, Otsuki K, Suzuki M, Kumagai T (2009) Effect of forest structure on the spatial variation in soil respiration in a Bornean tropical rainforest. *Agric For Meteorol* 149:1666–1673. doi :10.1016/j.agrformet.2009.05.007 Bréchet L, Ponton S, Alméras T, Bonal D, Epron D (2011) Does spatial distribution of tree size account for spatial variation in soil respiration in a tropical forest? *Plant and Soil* 347:293–303. doi: 10.1007/s11104-011-0848-1 Schwendenmann L, Macinnis-Ng C (2016) Soil CO₂ efflux in an

old-growth southern conifer forest (*Agathis australis*) – magnitude, components and controls. SOIL 2:403–419. doi: 10.5194/soil-2-403-2016 Reading these papers (but the list is not limitative) would have given way to analyze more finely the results, especially the last two.

We appreciate these suggestions, and agree that additional citation of the literature would strengthen the discussion.

(2) The observation that autotrophic respiration is more sensitive to temperature than heterotrophic respiration is also confirmative of many studies. Note that the paper Aguilos et al 2011 that is cited when discussing this point has not been accepted for publication in Biogeoscience, so the citation is wrong. Note that the citation Wei et al is incorrect: should be Wei et al (doi: 10.1016/j.soilbio.2010.04.013).

Thank you for catching these mistakes, which will be fixed.

The discussion of this fact is rather poor and miss one of the most important drivers of the apparent temperature sensitivity of RA: phenology. This may be important in the present study since soil respiration was measured over a full year and species are deciduous. Among many other sources, this has been discussed in: Epron D, Le Dantec V, Dufrêne E, Granier A (2001) Seasonal dynamics of soil carbon dioxide efflux and simulated rhizosphere respiration in a beech forest. *Tree Physiology* 21:145–152. doi: 10.1093/treephys/21.2-3.145 Ruehr NK, Buchmann N (2010) Soil respiration fluxes in a temperate mixed forest: seasonality and temperature sensitivities differ among microbial and root-rhizosphere respiration. *Tree Physiol* 30:165–176.

We agree, a discussion of phenological influence will help to explain the high spatial variability at this site and temperature sensitivity found.

(3) The third point deals with estimate the number of samples required for a robust estimate of the R_s . This has also been done plenty of time so there are two options: use it as a description of the site in the materials and methods section or do not only compare with other estimates but discuss more the reason why the number of samples required is higher in this study than in many others, thus why spatial variability is higher. Four lines is not enough. The discussion now is poor.

Thank you for pointing this out. While we agree the sample requirement section should be better addressed, we propose to leave this in the discussion for three reasons. The spatial variability could be a product of 1) the topographic variability at the study site led some collars to be better drained than others, 2) the record rainfall year in 2018, and 3) species diversity. All which could contribute to the high variability and thus high number of samples required. We will expand beyond the original four lines of text to better cover sampling challenges and solutions.

In conclusion, while the manuscript is based on an interesting data set obtained with valid methods, the discussion is not strong enough to reach substantial conclusions. A little more time would have been needed, maybe. One may expect the last sentence of the abstract to be the core of the discussion. The state of the art in the introduction should also be reinforced by looking more in detail in the huge relevant literature. The argument that no study has examined the influences of trees on spatial variation of R_s in the Chesapeake Bay watershed can be used for millions of watersheds in the world. This sentence should be removed.

We agree, and will remove this sentence.

OVERALL RESPONSE TO R1:

Thank you for your review. Overall, we agree that (1) the title should be reconsidered to include the entire scope of the study (also pointed out by Review 2), (2) better acknowledgement of current literature will give the study motivation more context and (3) a more in-depth consideration of phenology will strengthen the discussion. However, while the relationship between R_s and basal area has been previously cited, we believe the novelty of this study lies in the examination of how vegetation influences the spatial variability in forest ecosystems.

Specific comments:

Line 21 (and 47): remove “in time” there is no evidence that a better knowledge of spatial variation will improve scaling soil respiration “in time”

We agree and have removed “in time” where necessary, lines 20 and 48.

Line 35: need a clear definition of what is stand. In the description, there are 3 sites and 3 plots within site, but no stand.

Here a “stand” can be considered equivalent to a “site”. We have clarified this point in the text (line 34).

Lines 64-66: This sentence is very speculative, probably wrong and not needed. At similar age, tropical forests are at least as productive as temperate forest, and evergreen forests in a given climate are at least as productive as deciduous forests on an annual basis.

We have revised this sentence in lines 65-67 to note merely that these are productive, mid-latitude deciduous forests and thus autotrophic effects on R_s might be particularly strong.

Line 107: linear or exponential regression. . . which one is reported?

Good catch; yes, the IRGA reports both. For this analysis, we used the exponential regression values. The manuscript has been updated in line 107 to reflect this.

Line 122: why not try to consider the size of the tree when increasing the radial distance. I mean include only big trees when far from the collar and all trees when close to the collar.

This would have been an interesting approach, balancing sampling efficiency with including very local effects of small trees, and similar in spirit to that employed by Bréchet et al. (2011). We appreciate the suggestion and will consider it for our next study.

Why not testing all distances from 1 to 15 m and use the one that give the best correlation with soil respiration?

This would definitely have been possible. We preferred to start with a biologically-driven hypothesis of 5 m (effect radius) and test that, before proceeding to test all possible differences (i.e. in Figure 5). Both approaches have their strengths but in this case we think a hypothesis-driven framework is the right choice, providing a clear test and straightforward interpretation.

Lines 125-139: provide the model. According to Table 3, soil moisture has a specific equation. Which non-significant terms were eliminated using the forward-and-back stepwise algorithm. This is not so clear that terms have been removed when looking at Table 3

We now provide the full model specification in the methods, line 134. This provides a useful reference against the model results given in Table 3.

Lines 140-145: it will be better to add the type of season as an additional factor in your model rather than running the model on a split dataset. Same comment for the dryness splitting.

This would have been a good technique—thank you. Here, however, following Reviewer 2’s advice, we have elected to keep the separate model approach paired with a robust measurement of variable importance using R’s ‘relaimpo’ package.

Line 173: 40% is not almost half. But maybe it is 49%, not 40 (table 3)

Thank you for the comment, the model predicted 37% of the variability, so we changed the phrase “almost half” to reflect this in line 173.

Lines 185-187: not need to recall hypothesis in the result section.

We have removed the first sentence of this paragraph for clarity and concision (lines 185-190).

Lines 195-201: the analysis will be greatly improved by considering not only the distance but also the size of the neighbour trees that interact with the distance (bigger trees have influence on longer distance)

Please see our response to the line 122 comment above.

Lines 293: the data does not support the idea that the high spatial variation is related to stand structure. First, only BA is considered for characterising stand structure, which probably is not enough. And second, this BA does not explain so much the variation.

*We respectfully disagree. We are not saying that BA controls *all* spatial Rs variation, just that it is indisputably linked to it.*

Table 1: add the altitude of the three sites so that the risk of submersion can be evaluated by the readers

Thank you for the comment, Table 1 now has a column for altitude ranges at our three sites, see line 502.

Table 2: do not use +/- for SD, this is statistically incorrect (OK with SE or CI only). Instead use parentheses.

We have replaced +/- with parentheses, line 510.

Table 3: Improve the presentation (less digit, SE in the same column than value with +/-). Check df values, there is a problem. And show, in addition to the global model, the all the sub models you use (dormant versus growing). And the three dryness thirds as well. But see previous comments on the model.

Thank you for your comment. We have removed a digit and put SE in the same column with value as you suggested (line 516).

Figure 1 is not very informative (not useful)

In explaining our study design at numerous meetings and conferences, we have found that people frequently get confused about whether our measurements were conducted with respect to individual trees or individual Rs measurement points. For this reason, and because studies of tree proximity and RS more typically measure from trees or in a transect (Tang, J. and Baldocchi, 2005), we prefer to keep Figure 1.

Figure 2: why mean flux? It is called individual observation in Fig 4 which seems better

At each measurement point, the IRGA took two consecutive measurements. By “mean flux” we meant that the two consecutive measurements were averaged. This is stated in the methods section (lines 106-109) and has been clarified in the caption of Figure 2 (line 540).

Figure 3: hard to see what happens at short distance, especially at 5 m that is the selected distance. Can a log scale improve readability?

A log scale did not improve readability enough, however we have decreased the line size and added a subplot of 0-5 (line 545).

Figure 4: check x-axis labelled

Thank you. We have corrected this in line 552.

Anonymous Referee #2

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This paper addresses a current knowledge gap with forest soil respiration research: how important is the presence of vegetation for helping to explain some of the variability in soil respiration over space? We often treat forests as homogeneous when designing field studies. However, there is an accumulation of research that suggests that the spatial arrangement, size and density of trees can affect soil respiration measured in a particular spot. It's important to be able to characterize this effect for many reasons, which the authors point out - designing the spatial arrangement of measurements, interpreting relationships of soil respiration with environmental variables and seasonality, to name a few. I appreciate the authors' study design, especially their decision to sample sub-monthly and not just focusing on the growing season but also reporting results from the dormant season. The paper has some weaknesses that dilute the impact of the study, I believe, that can be improved. There are also some omissions that should be included, and some of the statistical approach should be re-considered. The paper is generally well-written but (like most papers) could use some further clarification in places.

Thanks for the thoughtful comments and assessment.

I have concerns with the title of the paper that affects some of the text in the paper and the way the problem is framed and studied. 'Tree proximity' implies that the research is focused on understanding how the degree of closeness of trees to soil respiration measurement influences respiration. This is not what the study is doing. Rather, I think a more accurate title would be something like "localized basal area affects soil respiration dynamics in a coastal temperate deciduous forest". This is because the only variable included in the models that involves trees is basal area within a 5 m radius, and the focus of the statistical modeling was on determining if localized basal area had an effect in addition to temperature and moisture. Based on the title, I was expecting a different kind of analysis, such as kriging or a spatial regression. 'Tree

proximity' could be interpreted to mean different kinds of things. 'Localized basal area' is more specific to the actual variable that was examined.

This is a great point and also noted by Reviewer 1. Your title suggestion is a good one; we will change the title to something that reflects the overall R_s variability in the context of localized basal area affect/vegetation.

Parts of the discussion and conclusion involve making assumptions about autotrophic and heterotrophic respiration based on their findings. It is tempting to make these statements (I've been there before), but you have to be careful here. Trees do not just influence autotrophic respiration - they provide fresh substrate for heterotrophic respiration as well. I think it is okay to include some speculation of how tree presence/absence might influence respiration rates, but try to avoid the assumption that trees only affect the autotrophic side of things.

This is a fair point - upon revision, we will clarify that these are broad assumptions but may not reflect the complex real-world links between R_a and R_h . We also believe that (as pointed out by Review 1) a further discussion of phenology will allow us to acknowledge other processes that may influence R_s .

The statistical methods used to determine whether variables were stronger or weaker and to compare dormant season model fit to growing season model fit should be re-examined. Differences in R^2 and AIC between models that use different input data do not necessarily indicate that the fit is better or worse. You could look into using an effect size analysis or examining relative importance of regression parameters (package `relaimpo` in R). Overall, this is an interesting study that investigates the influence of localized basal area on soil respiration - with some improvements, this should be an impactful contribution to the literature. Keep up the good work.

This is absolutely correct; our initial approach here is vulnerable, as you note, to differences in dataset size and other factors. We appreciate the introduction to the 'relaimpo' package, and will use it, or an equivalent approach, to robustly examine the relative importance of model terms in our linear regression analyses.

OVERALL RESPONSE TO R2:

Thank you for the critique. To best address your suggestions, we will (1) create a new title that better reflects the purpose of the study, (2) clarify assumptions being made, especially in regards to R_h and R_a drivers and the links between them, and (3) change our statistical analysis to more robustly compare models of differing sample sizes, especially between our growing and dormant season models.

Line by line edits:

23: I would remove all mentions of 'proximity' (since you aren't measuring how close each tree is to the collars) and replace with something more descriptive. 'Presence' would work here.

Thank you and we agree, this wording does not reflect the entire scope of the study. We have replaced the mentions of 'proximity' in lines 21 and 23.

24: Again, I would replace 'tree proximity' with 'localized basal area'.

Please see our response to the line 23 comment above.

26: Needs to be more specific - within a 5m 'radius'

This is revised in line 25.

46: This statement is misleading - large whole-tree chambers, for example, are in effect measuring soil respiration at scales larger than 1 m. Re-write this sentence to better say what you mean.

*We have tweaked the sentence (lines 46-48); but feel obliged to note that 'whole tree chambers' measure plant respiration *in addition to* soil respiration, and it's not straightforward to separate the two. (Similarly, by this logic, eddy covariance towers 'measure' Rs too.) We believe it is accurate, however, to say that Rs can't be directly measured, all by itself, at scales larger than $\sim 1 \text{ m}^2$.*

74: 'Higher' would probably be better than 'stronger'

This is a good point and has been revised on line 75.

90-101: A description of the soils present at the sites should be included.

Thank you for the comment. We included the dominant soil types at each site in Table 1 (line 502).

99: Need more detail here - was the separation distance randomly selected, the direction from plot center, or...?

The collars were randomly placed within each plot (line 99).

132: I don't think you need the second 'h' in homoscedasticity. I could be wrong though.

Yes, you are correct. This has been revised in lines 132 and 140.

145: It would help the reader if you explicitly stated what you were looking for in your models (even though it should be obvious). For example: 'a higher parameter for BA5 in the dormant season model would support the hypothesis that. . .'

We have expanded the sentence in lines 145-146 to state that we are looking for significance in the BA5 parameter of our model. We hope this makes our methods more explicit.

227: This is confusing - how would you have a temperature effect after controlling for temperature effects?

Thank you for the comment. We have rephrased this finding for clarity in lines 229-231 and 298-299.

227: I disagree - you cannot attribute an effect of trees solely to autotrophic respiration. Tree presence is also correlated with substrate for microbes.

We agree with you. Because we did not directly measure Ra and Rh contributions, we cannot attribute the BA5 effect solely to Ra. We have changed the wording to reflect this statement as a hypothesis as well as added that trees (BA) also contributes to Rh. See lines 231-236.

246: This is another assumption that is not well-supported - that trees do not have shallow roots that contribute to respiration.

We don't suggest that trees don't have shallow respiring roots, but rather that they probably have access to deeper water sources. We respectfully suggest to leave the wording of our hypothesis as is.

248: I suggest searching the literature for more references on soil moisture restrictions on respiration from deciduous forests. Here are a couple to get you started: Contosta, A.R., Burakowski, E.A., Varner, R.K., Frey, S.D., 2016. Winter soil respiration in a humid temperate forest: the roles of moisture, temperature, and snowpack. *J. Geophys. Res. Biogeosci.* 2016JG003450. <https://doi.org/10.1002/2016JG003450> Jiang, H., Deng, Q., Zhou, G., Hui, D., Zhang, D., Liu, S., Chu, G., Li, J., 2013. Responses of soil respiration and its temperature/moisture sensitivity to precipitation in three subtropical forests in southern China. *Biogeosciences* 10, 3963–3982.

Thank you for these suggestions. We have added more referenced on soil restrictions, specifically for deciduous forests, to reinforce our results. (see lines 219-224 and lines 247-252).

288: Autotrophic and heterotrophic respiration were not partitioned in this study - please revise this sentence to better communicate the overall finding of your work.

We have removed the first part of this sentence since Rh and Ra were not partitioned (lines 298-299).

479: Column header abbreviations should be defined. 'DF' should be clarified as 'denominator degrees of freedom'.

We have defined 'DF' in the revised manuscript for clarity, which can be found in line 516.

Anonymous Referee #3

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Pennington et al report on a well designed study of the effect of nearby trees on soil respiration, which finds that nearby trees increase the temperature sensitivity (but not the rate) of soil respiration except during dry periods and during the dormant season. The topic is important and appropriate to the journal, and the article is very well written. It was a pleasure to read.

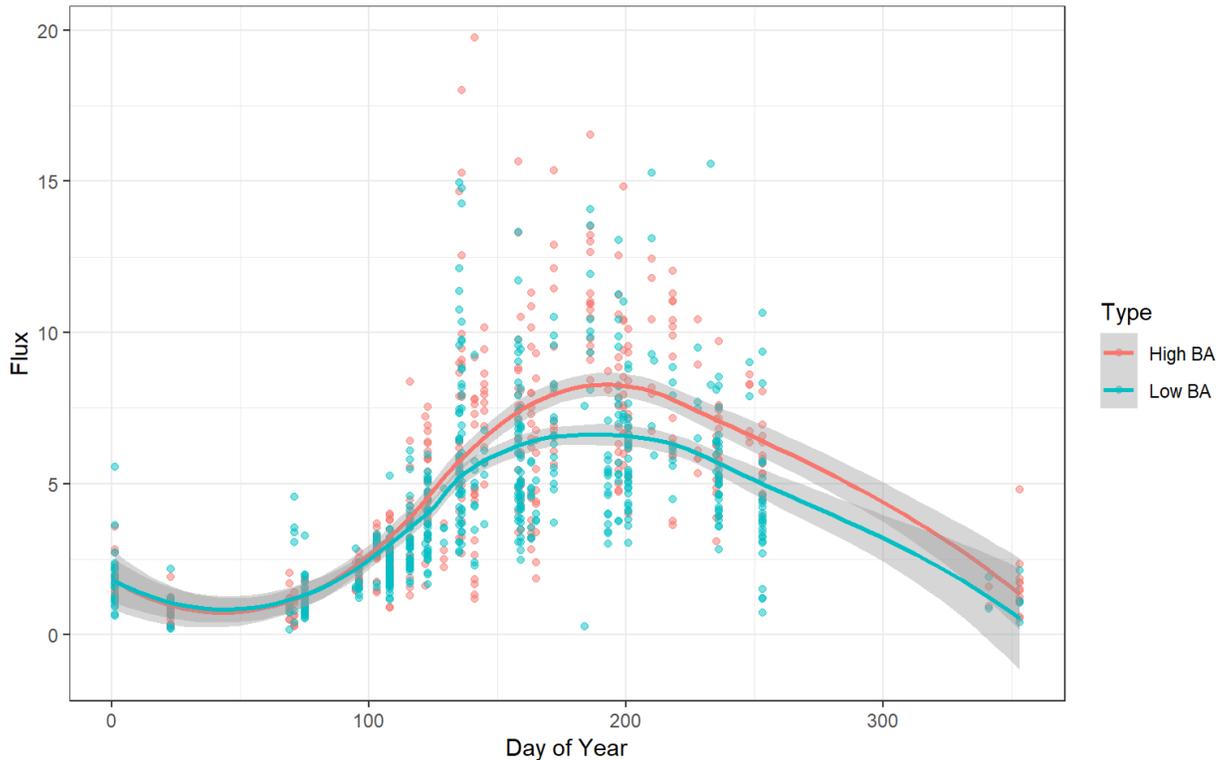
Thanks for the kind words, and thoughtful comments.

My general criticism is that the article does not discuss what for me is the 'elephant in the results'. The authors take the effect of BA5 on the T sensitivity of Rs to mean that Ra is more sensitive than Rh to T. The logic is that when there is more nearby basal area (and hence, by assumption, root biomass), Ra is a greater component Rs. However, BA5 was not found to be a significant driver of the spatial variability of Rs. It seems to me that the only way to reconcile those two ideas is to suppose that as root biomass increases, Ra increases but Rh decreases by the same amount in order to keep Rs the same, which as far as I know is not something that is believed to happen. If anything, the literature suggests that root exudates fuel soil respiration, rather than competing with it. I therefore think the discussion needs to acknowledge this paradox and tackle the question of how roots could plausibly impact the T sensitivity of Rs without impacting the magnitude of Rs. Could it be some kind of statistical artifact? The article doesn't necessarily have to have the answer, but it should at least lay out the key questions and suggest what kind of further work might be able to answer them.

OVERALL RESPONSE TO R3:

Thank you for pointing this out. This isn't an "artifact", but it is a consequence of the model we used, that was not well communicated. Localized basal area entered the model as a fixed effect (i.e., testing whether it raised RS by itself; this was not significant) and in an interaction with temperature (testing whether it changed temperature sensitivity; this was significant). Because, over the course of the day/month/year, temperature varies significantly in these forests, the result is that the changed temperature sensitivity results in a higher cumulative RS flux for collars in high-

*BA locations. This can be seen by plotting the raw respiration data and fitting a **spline** curve, separating the data into low- and high-BA colors:*



(Conversely, one could imagine a situation where these lines were perfectly parallel throughout the year. In this case the BA effect would be significant, but there would be no difference in the temperature sensitivity.)

We will clarify this point in the text, and think including a version of this figure in the revised manuscript will help readers understand the practical consequences of the statistical model.

Specific lines

34-5: “We estimate that four RS observations were required to be within 50% of the stand-level mean, and 311 to be within 5%, at 90% confidence.” After reading the article, the meaning of this sentence became clear, but when it is first encountered in the abstract, its grammatical ambiguity causes it to sound like nonsense (who required your observations to be close to the mean, and what does it mean to be within 50% of a mean?). I would rephrase it to something like: “Due to that variability, we determine that four RS observations would be required in order to estimate the stand level mean to within 50%, and 311 would be required in order to estimate it to within 5%, at 90% confidence.”

We agree and have revised the sentence for clarity based on your suggestion, thank you. Please see lines 33-35.

line 50: What is “leaf habit”? And does ecosystem-scale productivity really affect the sub-ecosystem-scale spatial variability, or do you mean to say something different?

“Leaf habit” denotes whether a tree or ecosystem is deciduous or evergreen. We have clarified this in the text (lines 50-53).

lines 133-4: It seems to me that taking the log shouldn't turn heteroschedasticity into homoschedasticity: if the variability in R_s varies with R_s , then the variability in $\log(R_s)$ will also vary with $\log(R_s)$, no?

Thank you for the comment, taking the log of the dependent variable is a standard approach to mitigate heteroscedasticity; see e.g. <https://en.wikipedia.org/wiki/Heteroscedasticity#Fixes>. However, you are correct that the variability growth is still present after transformation, but it's so slow that it's no longer causing problems for least squares.

line 213: I think “temperature” should be “temperate”.

Good catch! We have corrected this in line 211.

Figure 4: This figure's axes are swapped. Right now it is basal area vs residual (not residual vs basal area as the caption says). The residual is the independent variable that should be on the x axis. More importantly, it looks like the regression lines were calculated with this reversal of dependent and independent variables as well, so that all variability is attributed to the basal area measurement (which is actually quite precise I'm sure) rather than to the respiration (which is actually quite noisy). Also, there is a strange character in the x axis label.

We have fixed axes and label errors in Figure 4, see line 552. The regression lines were calculated as $R_s \sim BA$.

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

~~Tree proximity affects soil respiration dynamics in a coastal temperate deciduous forest~~

Biogeosciences

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

Abstract

Soil respiration (R_s), the flow of CO_2 from the soil surface to the atmosphere, is one of the largest carbon fluxes in the terrestrial biosphere. The spatial variability of R_s is both large and poorly understood, limiting our ability to robustly scale it in ~~time and~~ space. One factor in R_s spatial variability is the autotrophic contribution from plant roots, but it is uncertain how the ~~presence proximity~~ of plants affects the magnitude and temperature sensitivity of R_s . This study used one year of R_s measurements to examined the effect of localized basal area~~tree proximity~~ on R_s in the growing and dormant seasons, as well as during moisture-limited times, in a

temperate, coastal, deciduous forest in eastern Maryland, USA. In a linear mixed-effects model, tree basal area within a 5 m radius (BA₅) exerted a significant positive effect on the temperature sensitivity of soil respiration. Soil moisture was the dominant control on R_s during the dry portions of the year while soil moisture, temperature, and BA₅ all exerted significant effects on R_s in wetter periods. Our results suggest that autotrophic respiration is more sensitive to temperature than heterotrophic respiration at these sites, although we did not measure these source fluxes directly, and that soil respiration is highly moisture-sensitive, even in a record-rainfall year. The R_s flux magnitudes (0.35-~~15.3~~~~16.6~~ μmol m⁻² s⁻¹) and variability (coefficient of variability 10%-~~23~~~~2~~% across plots) observed in this study were comparable to values observed ~~over decades~~ in similar forests. ~~We determine that four R_s observations would be required in order to estimate the mean across all study sites to within 50%, and 129 would be required in order to estimate it to within 5%, with 90% confidence. We estimate that four R_s observations were required to be within 50% of the stand-level mean, and 311 to be within 5%, at 90% confidence.~~ A better understanding of the spatial interactions between plants and microbes, as well as the strength and speed of above- and belowground coupling, ~~that results in measured~~ R_s is necessary to link these processes with large scale soil-to-atmosphere C fluxes.

Introduction

Soil respiration (R_s), the flow of CO₂ from the soil to the atmosphere, is an important carbon (C) flux at ecosystem (Granier et al., 2000) to global scales. R_s is among the largest C fluxes in the terrestrial biosphere (Bond-Lamberty, 2018; Le Quéré et al., 2018), but poorly constrained at large scales, and thus it is important to understand its variability and sensitivity to processes such as land use and climate changes (Hursh et al., 2017; Schlesinger and Andrews, 2000). Unlike other large C fluxes such as net primary production, net ecosystem exchange, and gross primary production, R_s cannot be measured, even indirectly, at scales larger than a

~~few square meters~~ $\sim 1 \text{ m}^2$ (Bond-Lamberty et al., 2016), limiting our ability to robustly scale it in ~~time and~~ space.

One obstacle to robust measurements is that the spatial variability of R_s is both large and poorly understood. Controls on the spatial variability of R_s differ among sites and ecosystems and include plant species, ~~leaf habit~~, ecosystem productivity (Reichstein et al., 2003), soil temperature ([Fang et al. 1998](#)), moisture, spatial variability of vegetation, management, and soil compaction (Epron et al., 2004). This high variability has consequences for the sampling strategy required to accurately measure R_s at the stand scale (Rodeghiero and Cescatti, 2008; Saiz et al., 2006) and limits our ability to upscale R_s measurements to eddy covariance tower scales (Barba et al., 2018).

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

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

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

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

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

To test these hypotheses we performed a spatially explicit analysis of one year of frequent R_s measurements in a temperate coastal deciduous forest in eastern Maryland, USA. Our study was conducted in ~~To our knowledge, no study has examined the influences of trees on spatial variation of R_s in t~~he Chesapeake Bay watershed, an area subject to rapid rates of sea level rise (Ezer and Corlett, 2012; Sallenger et al., 2012) that may exert significant effects on the carbon cycling of coastal ecosystems (Rogers et al., 2019).

Methods

Site characteristics

This study was conducted in a mid-Atlantic, temperate, deciduous forest at the Smithsonian Environmental Research Center (SERC) in Edgewater, MD, USA. Three sites were chosen along Muddy Creek, a stream draining into an arm of Chesapeake Bay. Each site was separated by ~1 km (**Figure 1a**). These sites were comprised of both lowland and upland forest with a mean annual precipitation of 1001 mm and mean annual temperature of 12.9°C (Pitz and Megonigal, 2017). Dominant tree species include *Liriodendron tulipifera*, *Fagus grandifolia*, and

Quercus spp.; soil types vary between Collington, Wist, and Annapolis soil. (**Table 1**). At each site, three 20 m x 40 m plots were installed, separated by ~25 m and oriented perpendicular to the creek. The total elevation change between plots at each site was ~2 m. Within each plot, we installed 4, 20-cm diameter PVC collars, randomly separated from each other by 2–15 m, for a total of 36 measurement collars. Collars were installed ~1 week prior to the first sampling and left in place for the duration of the study.

Soil respiration measurements

Soil respiration measurements were taken using an infrared gas analyzer (LI-8100A, LI-COR Inc., Lincoln, NE) with a 20 cm diameter soil chamber attached. Measurements were taken every 10-14 days from April 2018 to April 2019. The IRGA measures concentrations every second over a one minute period and calculates the CO₂ flux as the ~~linear or~~ exponential regression of CO₂ accumulation in the closed chamber system over unit area and time; two successive measurements were taken at each collar and averaged. Vegetation was removed from inside the collar, and new vegetation was re-clipped as necessary, to remove any aboveground autotrophic flux, so that the IRGA was measuring only soil-to-atmosphere CO₂. Soil moisture and temperature (T₅) were also recorded at 5 cm depth, using auxiliary sensors attached to the LI-8100A, at the same time as soil respiration measurements. Temperature at 20 cm depth (T₂₀) was also recorded using a hand-held thermometer at the time of measurement.

Tree proximity measurements

We recorded distance from the soil collar, diameter at breast height (1.37 m), and species of each tree within a 15 meter radius of each soil respiration measurement point (**Figure 1b**). Dead trees were included in the dataset but only account for < 1% of total forest basal area. Cumulative basal area was calculated at each 1 m radial distance from the collar,

summing the cross-sectional areas of all trees within each distance. Tree root extent can be highly variable, but generally roots extend at least to the edge of the tree canopy (Stone and Kalisz, 1991). Mature tree canopies at SERC are ~5 m in radius (S. Pennington, personal observation), and we adopted this distance as an *a priori* assumption to test for the effect of basal area at 5 meters (BA₅) on R_s.

Statistical analysis

Respiration data were checked visually for artifacts or unusual outliers, but we did not exclude any data *a priori*. Data were then combined with the proximity measurements described above based on collar number. We used a linear mixed-effects model to test for the influence of BA₅ on R_s, treating temperature, soil moisture (SM), and BA₅ as fixed effects, and site as a random effect. To ensure homoscedasticity of model residuals, the dependent variable R_s was transformed by taking its natural logarithm, and thus the full linear model was specified as:

$$\log(R_s) \sim T5 * BA_5 + T20 * BA_5 + SM + SM2 \quad (\text{Equation 1})$$

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

Our secondary hypotheses, that effect of BA₅ varies with growing season and soil moisture, were tested by subsetting the R_s data. We treated April 15-October 14 as the growing season, based on 2018 leaf-out and senescence, and October 15-April 14 as the dormant season. Soil moisture data were split up into equal thirds (low, <0.188 m³ m⁻³; medium, 0.188-0.368 m³ m⁻³; and high, >0.368 m³ m⁻³; all values volumetric). We then applied the statistical model described above to each subset of the data to test for BA₅ significance in the model. The

'relaimpo' package version 2.2-3 was used to calculate relative importance metrics for all terms in each model, in particular its 'lmg' metric that averages sequential sums of squares over all orders of regressors (Lindeman et al. 1980), providing a robust decomposition of model R².

We used the spatial variability between collars within individual plots to estimate the number of samples required for a robust estimate of the R_s 'population mean', i.e., a spatially-representative mean. Specifically, we used a Student's t-test to calculate this based on the standard deviation of hourly R_s, the desired power of the test, and the allowable delta (difference from the true mean value), following Davidson et al. (2002).

~~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).~~

Results

We measured R_s, soil temperature, and soil moisture on 31 different days across the one-year period (Figure 2). Soil temperatures ranged from 0.1 to 27.57 °C (at 5 cm) and 1.7 to 24.4 °C (at 20 cm); volumetric soil moisture values were 0.01-0.56. R_s fluxes ranged from 0.3517 μmol m⁻² s⁻¹ (in ~~January~~March 2019) to 15.316.55 μmol m⁻² s⁻¹ (in July 2018). The coefficient of variability (CV) between collars within plots, a measure of spatial variability, was 16.7% ± 4.0~~ranged from 10% to 232%~~. This implied that a large number of samples was required to estimate soil respiration accurately (Table 2).

There was large variability in the basal area and number of trees close to the measurement collars (Figure 3). The mean number of trees within 1 m, 5 m, and 10 m distance were one, six, and 210 trees (with respective nearby basal areas of 0.0002 m², 0.24 m², and 0.8894 m²). Within our maximum radius of measurement, 15 m, there were on average 432 trees and 1.647 m² of cumulative basal area, ranging from a minimum of 0.4355 m² to a

maximum of 3.55 m². The forest was thus highly spatially variable in its distribution of trees relative to the R_s measurement collars.

Effect of BA on R_s

The linear mixed-effects model using temperature, soil moisture, and basal area within five meters (BA₅) predicted ~~37% almost half~~ of the R_s variability (conditional R² = 0.~~3740~~). BA₅ was not significant by itself in a Type III ANOVA using this model ($\chi^2 = 0.~~081495~~, P = 0.~~776482~~), but exhibited strong and significant interactions with T₅ and T₂₀ (**Table 3**). In addition, the residuals of a model fit without BA₅ had a significant trend with BA₅ (**Figure 4**). Separating the data into growing- and dormant-season subsets provided contrasting results. In the growing season, model outputs were similar to those of the full year model, with BA₅ having significant interactions with T₅ and T₂₀ (data not shown). The dormant season model, however, was quite different: only T₂₀ (P ≤ 0.00~~04~~) and soil moisture (P = 0.0~~377009~~) were significant terms. In addition, the dormant season model explained more of the R_s variability (AIC = ~~119.80258.75~~, marginal R² = 0.~~4852~~). In summary, ~~collars with higher basal area within 5 m had significantly higher temperature sensitivity of soil respiration~~~~collars with higher basal area within 5 m had significantly higher temperature sensitivity of soil respiration after controlling for temperature and moisture effects~~, while basal area within 5 m of sampling points was not correlated with R_s during the dormant season.$

~~Our third hypothesis was that any basal area effect on R_s would be strongest in the driest times of the year, when microbial respiration at the surface soil declines as the soil dries, but (we speculated) trees would maintain access to deeper soil moisture.~~ There were in fact strong differences between the driest and wettest thirds of the data, but our hypothesis that any basal area affect would be strongest in the driest time of year was not supported. In the driest third of the data, neither BA₅ nor its interaction with T₅ was significant (P = 0.~~0964775~~ and

0.~~0541078~~ respectively); T_{20} was never significant; and the dominant control was instead soil moisture ($\chi^2 =$ ~~15.2320.93~~, $P < 0.001$). In contrast, the wettest-third model resembled the full-year model, with BA_5 interacting with temperature, and soil moisture also significant.

Sensitivity test

Our *a priori* choice of 5 m for the basal area test was one of many possible choices, and could potentially bias the results, as the actual extent of tree roots at these sites is unknown.

~~Re-fitting the main statistical model and calculating variable importance metrics~~
~~Re-running the main statistical test~~ across a wide range of distances, however, showed that basal area ~~and~~ by itself was almost never significant, while its interactions with T_5 and T_{20} were almost always statistically significant (**Figure 5**). Generally the BA effects were not significant at short (< 3 m) distances; this is expected, given that few collars were that close to trees. Interestingly, the BA effects remained significant all the way to our maximum measured distance of 15 m. In summary, our a priori analytical choice of a 5 m radius did not appear to bias our results.

Discussion

Results and implications of R_s values

The R_s fluxes observed in this study, ~~0.35-15.316.6~~ $\mu\text{mol m}^{-2} \text{s}^{-1}$, were comparable to values in similar forests (Giasson et al., 2013) as well as those and from the Soil Respiration Database (SRDB; Bond-Lamberty and Thomson, 2010), a synthesis of annual R_s studies (0 to $14.7 \mu\text{mol m}^{-2} \text{s}^{-1}$, $n = 1281$ temperate deciduous studies). We observed a ~~collar-to-collar~~ R_s CV of ~~10.5-224.5%~~ between plots, a value also comparable to previous studies. In a study of R_s in conifer forests and grasslands, Rodeghiero (2008) reported 28.9-41.5% variability, Davidson et al. (2000) about 30% in forest ecosystems, and a much broader range (0.11-84.5%) for temperature, deciduous forests from the SRDB.

Sample size requirements to estimate annual R_s were high at SERC compared to previous studies. For example, to be within 10% of the mean R_s flux at 95% confidence required from 41 (Davidson et al., 2002) in Harvard Forest, to 72 (Adachi et al., 2005) in a secondary forest, to 129433 sample points in this study. ~~This high variability between studies likely arises because controls on the spatial variability of R_s differ among sites and ecosystems. Within forest biomes, topography and stand structure (Søe and Buchmann, 2005) can also be dominant controls. Significant spatial variation in stand structure and topography across the study domain may have resulted in high variability seen in this study. Within forest biomes, topography and stand structure (Søe and Buchmann, 2005) can also be dominant controls that likely contributed to the high variability seen in this study.~~ In particular, the measurement points at our study sites ranged from 3-15 meters in elevation (Table 1), as at all sites the land rises quickly away from Muddy Creek. These elevation gradients mean that some measurement points drain more quickly than others, which created strong differences in soil water content (CV 16.7% \pm 4.0 within plots) and thus R_s , leading some measurement points to drain more quickly than others. This is consistent with the idea there is evidence that topographic complexity can be an important and complex factor in R_s variation across sites (Riveros-Iregui et al. 2012).

Interactions between basal area and temperature sensitivity on R_s

Many studies have examined whether autotrophic respiration (R_a) or heterotrophic respiration (R_h) is more temperature-sensitive, and reached varying conclusions (Aguilos et al., 2011; Boone et al., 1998; Wei et al., 2010). In this study, however, the Type III SS interaction between BA5 and temperature was highly significant, meaning that collars with higher basal area within 5 m exhibited had significantly higher temperature sensitivity of soil respiration. ~~In this study, however, collars with higher basal area within 5 m had significantly higher temperature sensitivity of soil respiration after controlling for temperature and moisture effects.~~ This suggests that R_a might be more is more sensitive to temperature than R_h at these sites. However, it is

important to note that we even though we did not directly measure the autotrophic and heterotrophic source fluxes contributing to the overall R_s flux. Instead, we assume that collars closer to trees have a larger fraction of R_s contributed by R_a , an assumption also made in previous studies such as Tang and Baldocchi (2005).

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

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

Soil moisture controls on BA significance

We hypothesized that any BA_5 effect would be particularly strong during the driest third of the year, but instead found that only soil moisture controlled R_s during these periods, while neither temperature nor tree proximity (BA_5) was significant. This demonstrates that R_s is highly

moisture-sensitive at these sites, but does not support our ~~idea hypothesis~~ that trees might have access to deeper or different water sources than surface soil microbes. Soil moisture is considered to be a primary R_s control in Mediterranean and desert ecosystems (Cable et al., 2010), but interestingly even this deciduous forest, in a year with record rainfall (National Weather Service, 2019), experienced significant moisture restrictions on R_s . ~~Spatial variation in soil moisture (CV 2.5%–18.7% between plots) was probably due to the topographic variability of our study site, which allowed some measurement points to drain more quickly than others, producing a wide range of soil moisture conditions.~~

Dormant season R_s controls

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

Limitations of this study

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

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

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

Conclusion

We found that measurement c~~Autotrophic respiration was found to be more sensitive to temperature than heterotrophic respiration, and c~~ollars with higher basal area within 5 m had significantly higher temperature sensitivity. R_s wa~~s~~ also highly moisture-sensitive at these sites, with large differences among R_s ~~controls~~ in low- versus high-moisture times. These findings, in conjunction with large sample size requirements, suggest soil respiration at this site to be highly dynamic and variable. This could have implications for measurement requirements in sites with particular stand structures. A better understanding of the spatial interactions between plants and microbes through R_h and R_a partitioning, as well as the speed and coupling between above-

and belowground processes, that results in measured R_s is necessary to link these processes with collar- and ecosystem-scale soil-to-atmosphere C fluxes.

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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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Table 1 | Study site characteristics of each site along Muddy Creek, including trees per hectare, cumulative basal area, main soil types, and dominant tree species by percent of basal area.

Values are mean \pm standard deviation of N=3, 800 m² plots.

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 \pm 57.3	44.6 \pm 4	Collington-Wist complex; Collington and Annapolis soils	28% <i>Liriodendron tulipifera</i> 11% <i>Quercus spp.</i> 11% <i>Fagus grandifolia</i>
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>
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>

<u>Site</u>	<u>Trees (ha-1)</u>	<u>BA (m2 ha-1)</u>	<u>Dominant Soil Type</u>	<u>Dominant Tree Species (by BA %)</u>	<u>Altitude (m)</u>
<u>GCRew</u> <u>(38.876 °N,</u> <u>76.553 °W)</u>	<u>637.5 ± 57.3</u>	<u>45.2 ± 7.3</u> <u>44.6 ± 4</u>	<u>Collington-Wist complex; Collington and Annapolis soils</u>	<u>28% Liriodendron tulipifera</u> <u>11% Quercus spp.</u> <u>11% Fagus grandifolia</u>	<u>3-10</u>
<u>Canoe Shed</u> <u>(38.884 °N,</u> <u>76.557 °W)</u>	<u>529.2 ± 93.8</u>	<u>40.4 ± 6</u>	<u>Annapolis fine sandy loam</u>	<u>26% Quercus spp.,</u> <u>23% L. tulipifera</u> <u>20% F. grandifolia</u>	<u>7-10</u>
<u>North Branch</u> <u>(38.887 °N,</u> <u>76.563 °W)</u>	<u>806.9 ± 180.7</u>	<u>34.5 ± 7.8</u>	<u>Collington and Annapolis soils; Collington, Wist, and Westphalia soils</u>	<u>42% F. grandifolia</u> <u>26% Quercus spp.</u> <u>12% Liquidambar styraciflua</u>	<u>8-20</u>

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 (\pm 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 \pm 24	97 \pm 33	147 \pm 50	226 \pm 76	373 \pm 124	532 \pm 175
0.10	16 \pm 6	25 \pm 9	37 \pm 13	57 \pm 19	94 \pm 31	133 \pm 44
0.25	3 \pm 1	4 \pm 2	6 \pm 2	10 \pm 4	15 \pm 5	22 \pm 7
0.50	1 \pm 1	1 \pm 1	2 \pm 1	3 \pm 1	4 \pm 2	6 \pm 2

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

<u>0.50</u>	<u>1 (1)</u>	<u>1 (1)</u>	<u>2 (1)</u>	<u>3 (1)</u>	<u>4 (2)</u>	<u>6 (2)</u>
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Table 3. Summary of linear mixed-effects model testing main hypothesis of the effect of nearby tree basal area on soil respiration (the dependent variable). Terms tested include soil temperature at 5 and 20 cm (T_5 and T_{20} respectively), basal area (BA), and soil moisture (SM).

Model AIC = 381.6662-7, marginal $R^2 = 0.3672$.

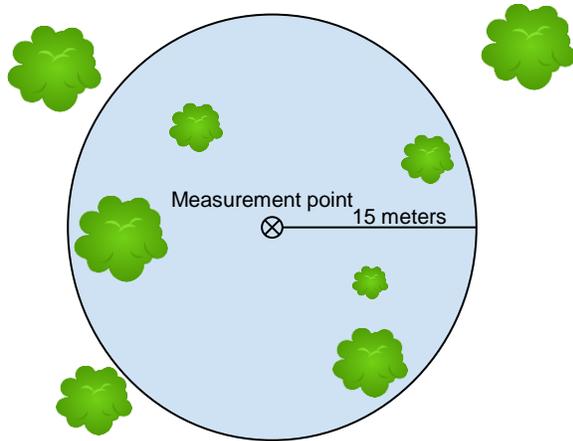
	Value	Std.Error	DF	t-value	p-value
(Intercept)	-0.7824	0.1215	884	-6.4418	0.0000
T₅	0.0146	0.0080	884	1.8327	0.0672
BA	-0.1162	0.1659	884	-0.7006	0.4837
T₂₀	0.0873	0.0093	884	9.3562	0.0000
SM	3.3107	0.5627	884	5.8834	0.0000
SM²	-5.4007	0.8867	884	-6.0913	0.0000
T₅:BA	0.1165	0.0297	884	3.9144	0.0001
BA:T₂₀	-0.1018	0.0332	884	-3.0667	0.0022

	<u>value</u>	<u>degrees of freedom</u>	<u>t-value</u>	<u>p-value</u>
<u>(Intercept)</u>	<u>-0.767 ± 0.148</u>	<u>440</u>	<u>-5.199</u>	<u>0.000</u>
<u>T₅</u>	<u>0.010 ± 0.009</u>	<u>440</u>	<u>1.055</u>	<u>0.292</u>
<u>BA₅</u>	<u>0.022 ± 0.219</u>	<u>440</u>	<u>0.098</u>	<u>0.922</u>
<u>T₂₀</u>	<u>0.095 ± 0.011</u>	<u>440</u>	<u>8.397</u>	<u>0.000</u>
<u>SM</u>	<u>2.505 ± 0.699</u>	<u>440</u>	<u>3.581</u>	<u>0.004</u>
<u>I(SM²)</u>	<u>-3.542 ± 1.144</u>	<u>440</u>	<u>-3.095</u>	<u>0.002</u>

<u>T5:BA5</u>	<u>0.079 ± 0.036</u>	<u>440</u>	<u>2.181</u>	<u>0.030</u>
<u>BA5:T20</u>	<u>-0.069 ± 0.041</u>	<u>440</u>	<u>-1.689</u>	<u>0.092</u>

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

a) _____ b)



b)

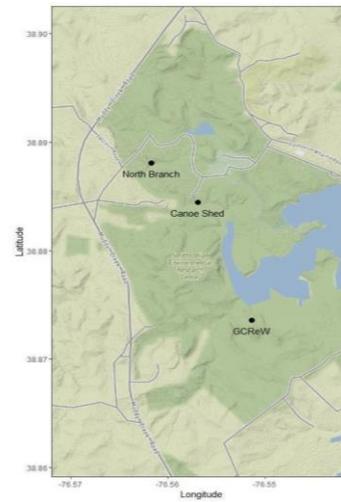


Figure 2 | CO₂ flux ~~Mean flux~~ over time from April 2018 to April 2019 for 36 measurement points across three sites; red ~~blue~~ line shows the seasonal trend using a loess smoother.

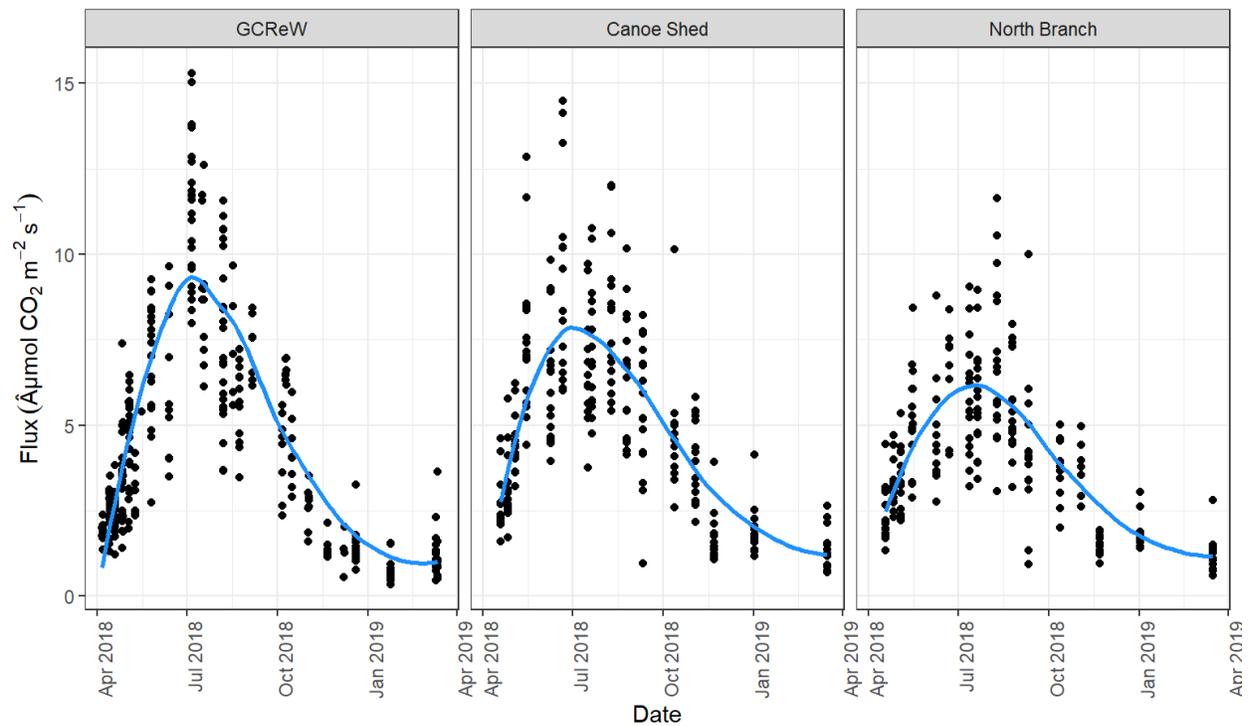
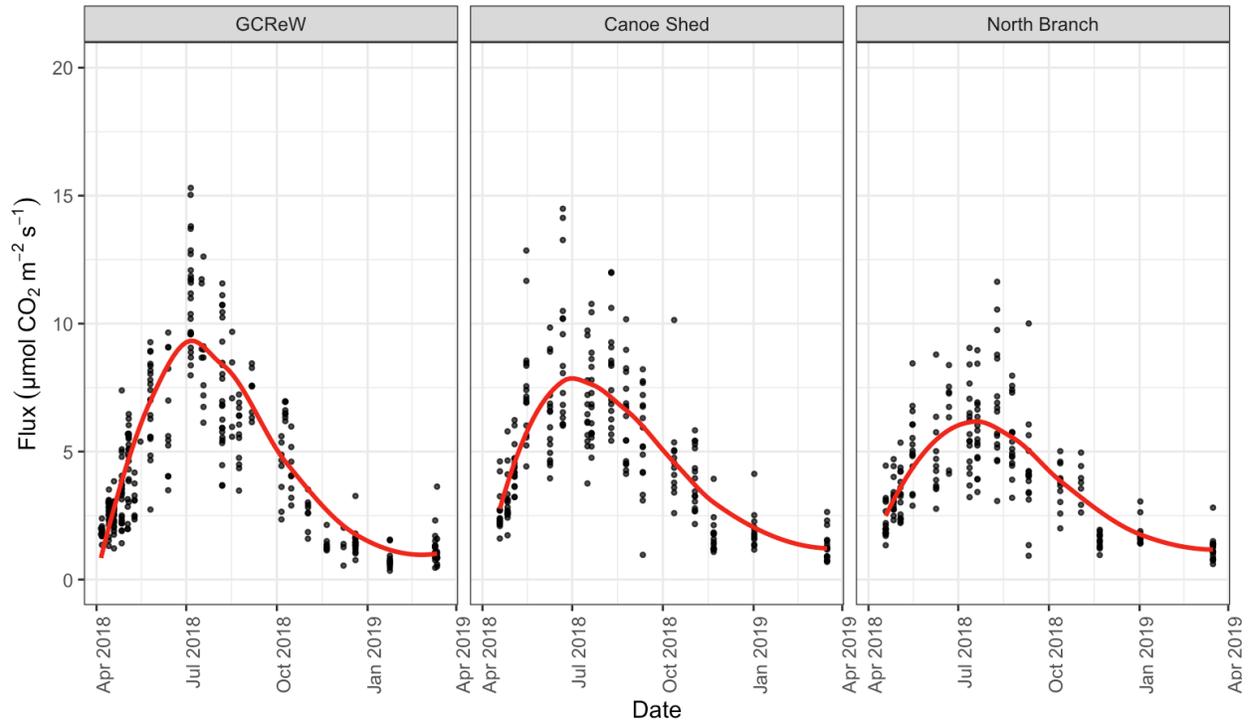


Figure 3 | Cumulative basal area for each collar (N = 36) up to 15 meters; color indicates number of trees at each distance. [Inset graph shows a close up of 0 to 5 meters for more detail.](#)

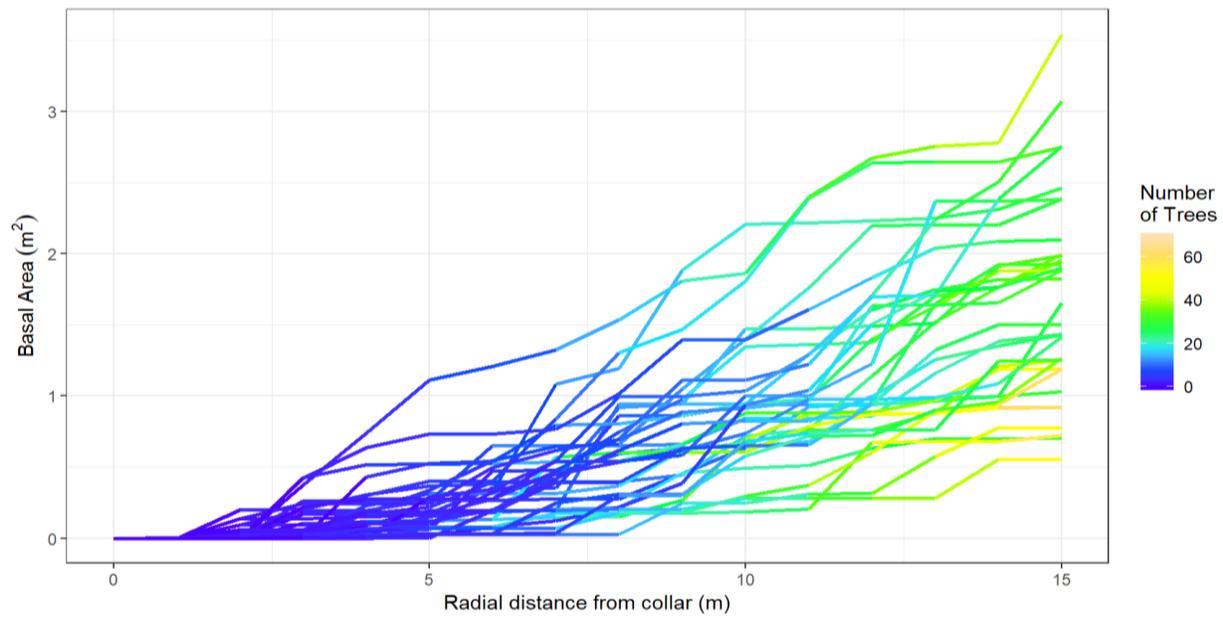
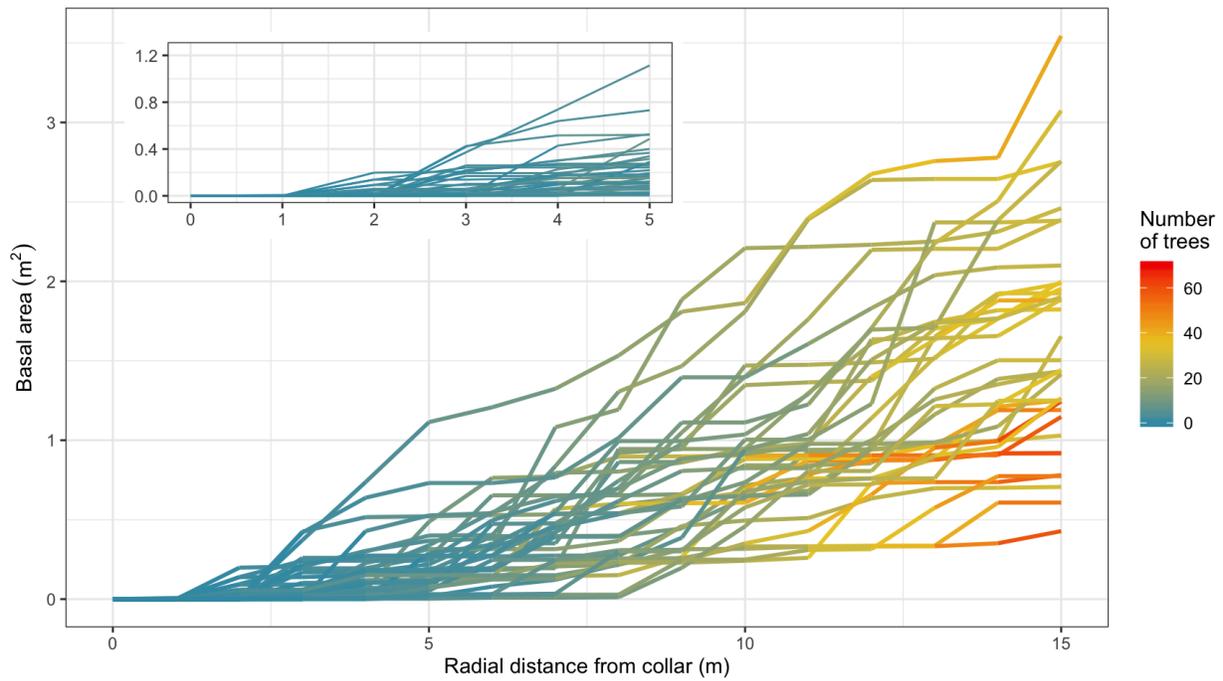
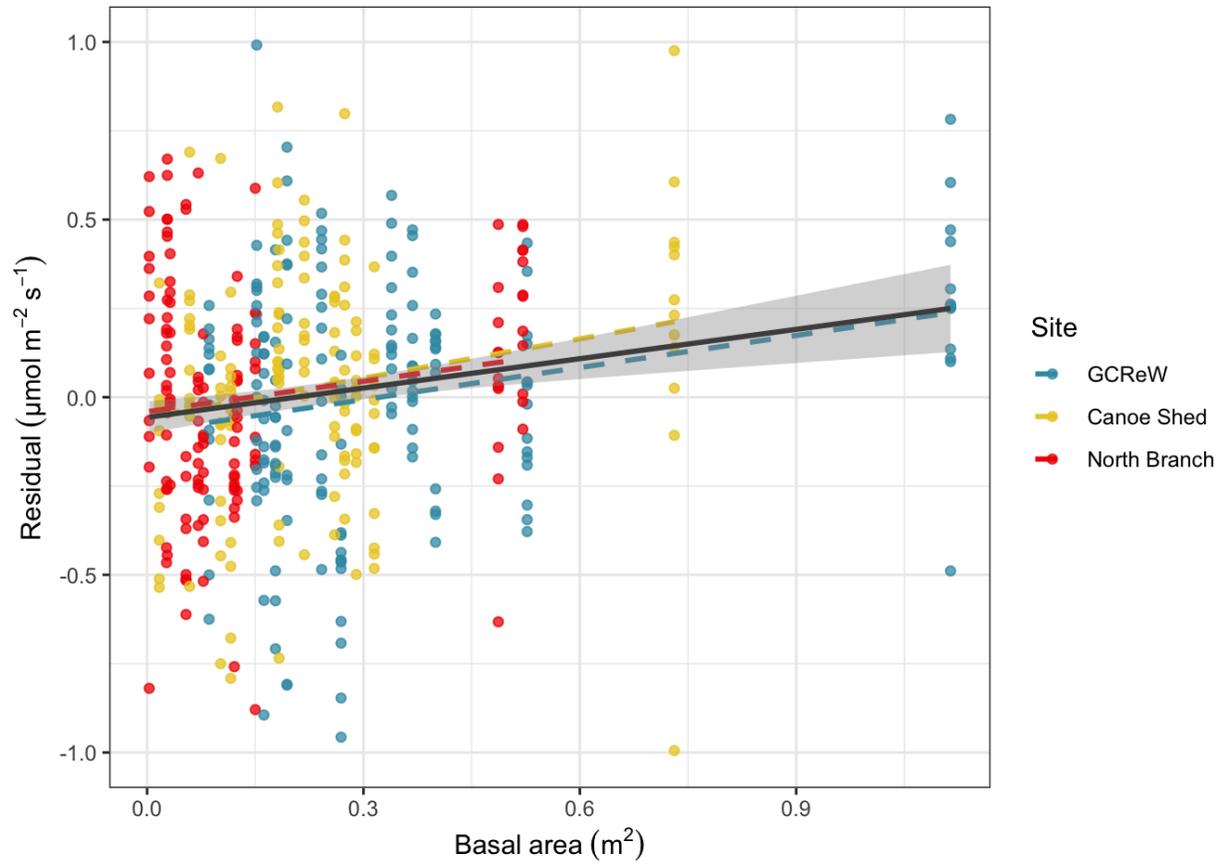


Figure 4. Residuals of a soil respiration model, incorporating temperature and soil moisture as independent variables, versus cumulative tree basal area within 5 m, by site. Each point is an individual observation (cf. **Figure 2**). Regression lines are shown for each site; black line is the overall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



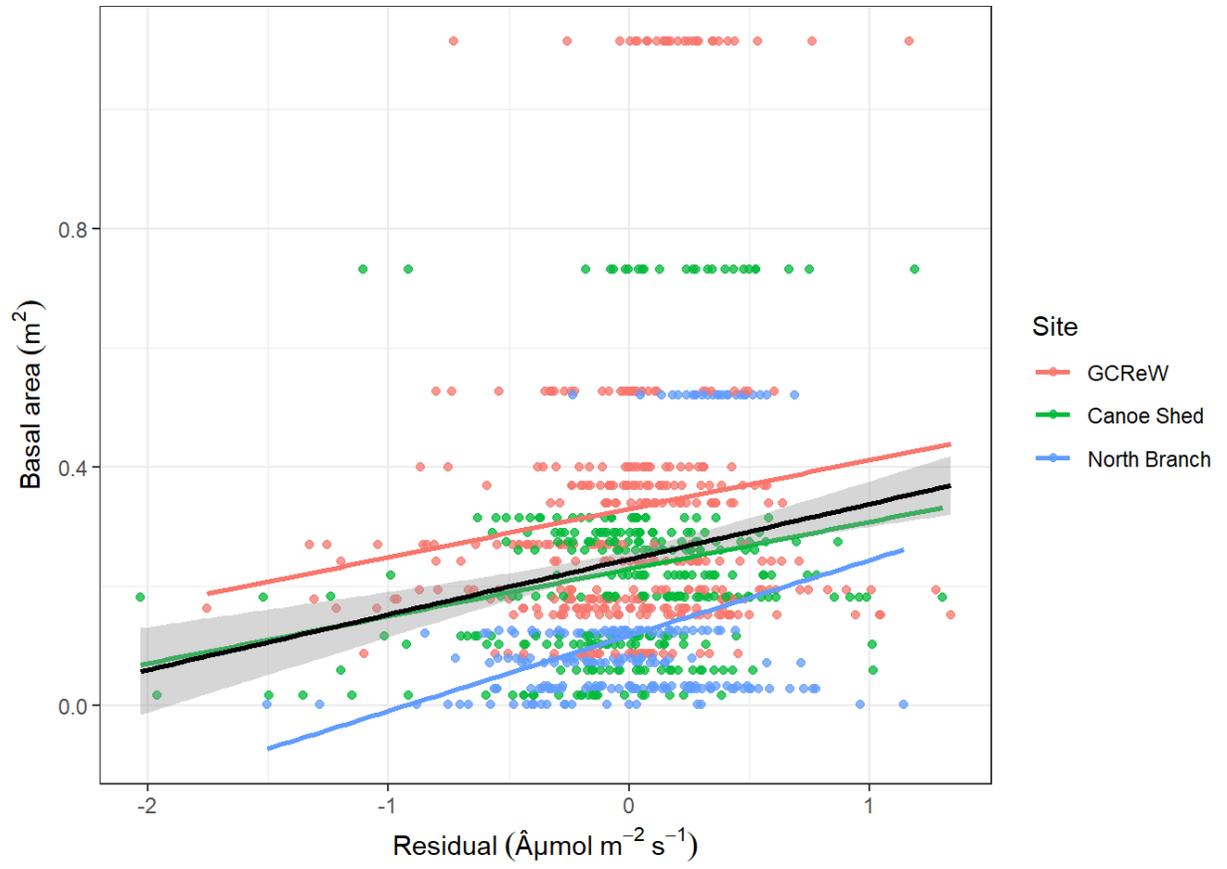
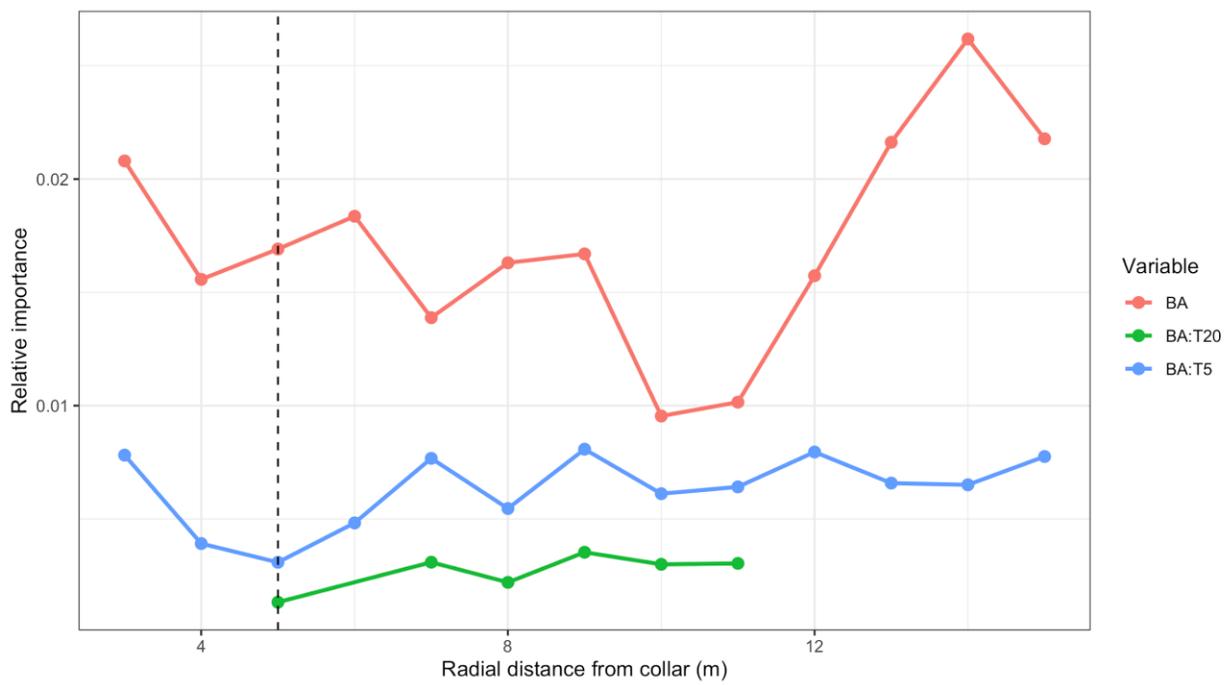
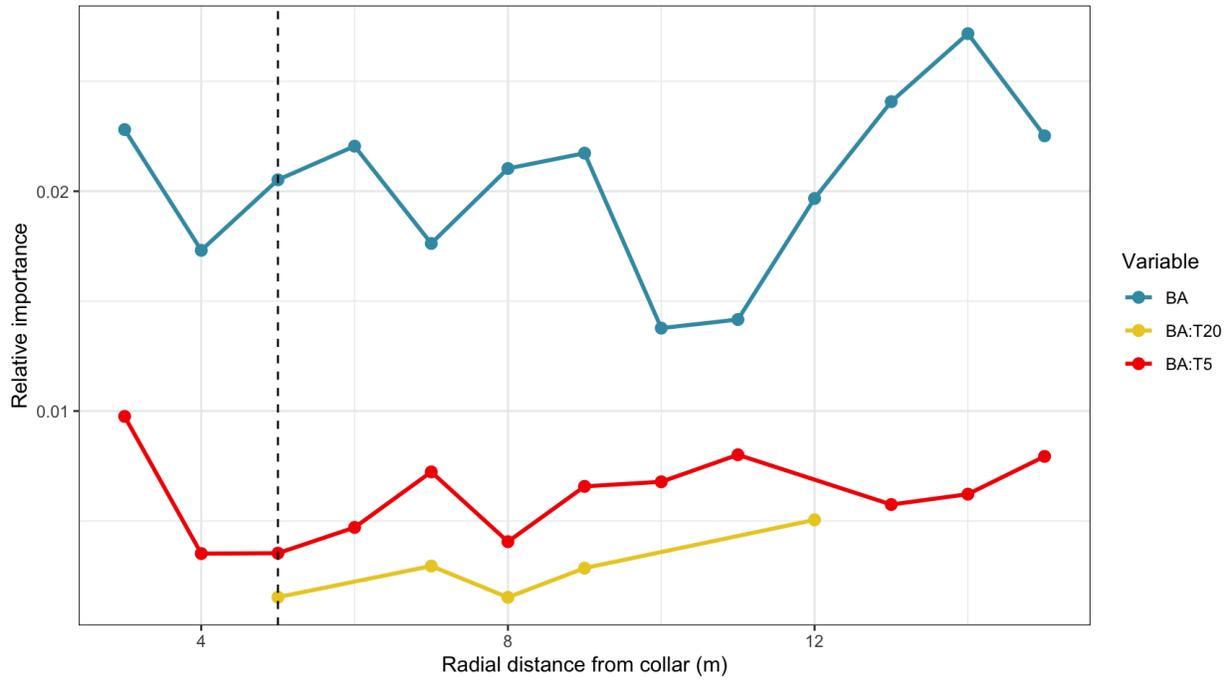


Figure 5. Test of robustness of results, run at various distances from soil respiration measurement collars (x axis). Lines shows the variable importance (calculated as R² partitioned by averaging over orders; see Methods) significance (chi square p-value from Type III ANOVA of the linear mixed effects model, y axis; note logarithmic scale) of basal area (BA), as well as the interaction of BA and temperatures at 5 and 20 cm (T₅ and T₂₀ respectively). Horizontal dashed line shows the standard 0.05 significance cutoff; vertical dashed line shows the 5 m radius used in **Table 3** and **Figure 4** results. Note that 'missing' BA:T20 (in yellow)~~green and blue~~ dots at distances < 5 m and >12 m mean that the terms were dropped from the model and are thus not significant.



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