

Anonymous Referee #1

General comments

This manuscript describes measurements of soil respiration (Rs) made in the field in two forests in Bhutan, supplemented by laboratory incubations, that looks at Rs fluxes, sources, seasonally-driven changes, as well as sensitivities to temperature and moisture. This is interesting and valuable, given the paucity of data from this region, if not groundbreaking. The ms is reasonably well written, although there are many minor English errors, and frequently insightful. I particularly liked the comparison between different techniques and measurements/models, even though this is not developed as fully as it could be. There are some problems. Aspects of the methods and results are unclear; in particular, the authors should be careful to distinguish between measured and modeled results, why and when each was performed, and when they're referring to each. I think the trenched plot results could be better discussed, particularly as the problems that occurred seem relatively straightforward to explain. Finally, and very importantly, the authors need in my opinion to post or include the data and code backing all their main results (see #9 below). In summary, this ms needs moderate to significant revisions in many places, but it's fundamentally a strong and interesting study.

We thank the anonymous referee for the constructive comments and suggestions. We revised the manuscript accordingly and incorporated all the comments and suggestions. The model code is also included as supplementary files to the manuscript as well as the data.

Specific comments

1. Lines 23-24: why does a discrepancy between modeled and measured Ra indicate trenching performed poorly? Clarify. Might also add “, probably because of the short time lag between trenching and measurement”?

AR: *We clarified that and added more discussion about the strengths and weaknesses of both methods (L259-303).*

2. L. 27: “preceding”?

AR: *Changed to “prevailing”*

3. L. 37: maybe “potentially feeds back on global climate change”. Also there are better citations for this, e.g. Frey et al. 2013 (10.1038/nclimate1796) or Wang et al. 2014 (10.1111/gcb.12620)

AR: *Changed and suggested citations added.*

4. L. 50: start a new paragraph

AR: *New paragraph set.*

5. L. 67: “would show decreases in Rs during”

AR: *Changed*

6. L. 118-: what was delay between trenching and starting measurements?

AR: *Plots were trenched in April 2014. The delay was 1 year accordingly. We stressed this in the revised manuscript (L80).*

7. L. 172: better to say “Effects of site” rather than “forest type” since you can’t actually test forest type (as n=1)

AR: *Changed as “Effects of site” and we consistently use this term in the revised manuscript.*

8. L. 190: perhaps “to calculate a projected daily field Rs” for clarity

AR: *Re-worded as suggested.*

9. Availability of code and data? It's 2016, and I expect all code and data (at least that backing the main results) to be included as supplementary info, or posted in a repository. It's not acceptable to produce results from a black box

AR: We have included the R-code as supplementary file and we will also upload the data to a repository.

10. L. 252-257: interesting!

AR: Thank you

11. L. 278: "any meaningful Rh values"?

Trenching values from additional (2015) trenching plots were taken out (as suggested by reviewers 2 and 3) and discussion was adapted accordingly.

12. L. 310-: "Q10 tends"; also should be "increase with decreasing temperatures"?

This discussion was taken out as we avoided Q10 for field Rs (suggested by reviewer 2 and 3).

13. L. 314: "than the ones"

Corrected

14. L. 327: "We intend to"

Corrected

15. L. 333: this is awkward English and unclear – why "ambivalent"?

Deleted.

16. L. 338: "Rs, falling well within"

Re-worded.

17. L. 345: "albeit"? What?

"besides" was the correct term

18. L. 348-353: interesting though unsurprising. Might mention this in abstract

In our opinion this is a little too specific for the abstract.

19. Figure 1: minor point but perhaps format x axis dates as "Apr 2014", "May 2014", or something like that to eliminate M/D/Y ambiguity (i.e. make consistent with Figures 4 and 5)

Incorporated in the final revised figures. Labels are consistent as we have removed the data for the year 2014 completely (suggested by reviewers 2 and 3).

20. Figure 3: necessary?

We removed the graph.

21. Figure 4: this is confusing. At the very least, clarify the caption, and perhaps re-think how these data are displayed

We revised the graph and simplified the caption and data display.

22. Figure 5: perhaps note in caption that the Rh lines are cumulative

We improved the caption, it should be clear now.

Anonymous Referee #2

The paper "Soil CO₂ efflux from two mountain forests in the Eastern Himalayas Bhutan: components and controls" by Wangdi et al. provides further information on a data poor environment, relevant to the Earths carbon budget. In this way the paper is a useful contribution to the cannon. Further lab-based incubations also appear useful for constraining modeled behaviors in the field, and the provided comparisons to in situ outcomes may be informative.

I have a number of concerns about the choice to include some of the provided data, as well as the exact equations and parameters that the model utilized to determine partitioning between respiration components. Overall, in agreement with the first reviewer, I believe that this study has some sound and useful information and analysis that should be published, but I would expect major revisions would be necessary to clear out the unnecessary components of the article and clarify others.

We highly appreciate all your constructive comments. All suggestions were taken into account and the revised manuscript is shorter and streamlined. 2014 data, which held some methodological bias were removed as suggested by reviewer 2 and 3, Rh-model R-code and all data are added as supplement. While revising the manuscript, we found a minor conversion error for Rh values per kgC-1, which we corrected for in the revised manuscript. Corrections did not affect the overall outcome of the study. Corrections resulted in slightly higher modeled Rh and minimal, insignificant deviations of Q₁₀ and R₁₀ values when compared to the values in the initial manuscript (without any effect on the study results!).

My broad concerns will be listed first with specific items listed afterwards:

1) The "coniferous forest" as described has a substantial component of broadleaved trees (~29% Quercus sp.), and is later described as, perhaps more appropriately, a "cool temperate mixed coniferous forest" (line 72/73). Perhaps describing as a "mixed forest" throughout the paper would be more helpful. This is likely to have some impact on respiratory fluxes (through litter quality, leaf economics, etc) and this, along with the potential impacts from soil type and understory plant types, density and behavior is not addressed in the text sufficiently in my mind.

We consistently use the term "mixed forest" in the revised manuscript. We discuss possible effects of litter dynamics on R_s and R_h (L250-252, L270-275)

2) I question the value of the 2014 field-based R_s results, considering that they are acknowledged by the authors to be influenced by pressure effects from chamber placement.

We have removed all 2014 data, as suggested. We did not lose important information by doing so, but it made the whole paper much easier to read.

3) I am uncomfortable with different mathematical functions being used to determine the same biological functionality (in particular the linear versus Gaussian response of soil water content to respiration rates). I would prefer that whichever function is used that there is some biological rationale that can be used to defend this choice.

That was a mistake. We use consistent functions in the revised manuscript. We also changed to a more simple mathematical function for the relationship between R_h and soil moisture.

4) I agree with the first reviewer that it would be better to have the model by which R_h and R_a components were calculated either explained through the primary equations in the text, or by incorporating the model as a supplementary material.

We explained the functions in the text more thoroughly and added the R-code of the R_h model as well as all data as supplement.

5) The use of the term Q₁₀ to describe the entire soil response to, effectively, seasonal changes is inappropriate to my mind. By definition Q₁₀ refers to the change in reaction rate of an enzyme or system to 10 degree changes in temperature, and on this basis the lab-based incubation Q₁₀s are appropriate and should be retained and used in the models, but calling the whole system response a Q₁₀ when the authors acknowledge (lines 301-303) that it incorporates water content, leaf litter availability and other co-variable parameters makes this use of the Q₁₀ term meaningless.

We agree that the relationship between seasonal Rs and seasonal soil temperature does not resemble the actual temperature sensitivity of Rs. We also agree that the use of Q10 actually is not desirable in this regard (although quite commonly done). We used another formulation for the exponential relationship in Eq. (1), avoiding the term Q10 already in the Rs function. We completely reworded the results and discussion section and removed the Q10 values for seasonal Rs from the graphs. We did not lose any relevant information by applying these changes, but shortened the ms and made it clearer and easier to read.

1) Line 25/26: see broader point 5 above. This is not in any way a Q10 with the number of conflating variables. Please use different terminology.

No Q10 used for Rs any more – see above.

2) Lines 64-67: These hypotheses are not all that useful and the final hypothesis is not addressed within the paper, leading to a question of whether these are needed in the paper at all.

We removed the hypotheses and defined broader research questions instead.

3) Line 78: *Acer campbelli* is listed as a dominant species in the cool, temperate mixed coniferous forest but is not listed in Table 1.

We removed *Acer campbelli* from the text as it was not dominant.

4) Lines 88-92: Climate can vary dramatically in mountainous regions over spatial scales of 1km. Is there evidence that these weather stations were recording appropriate data for these sites?

Especially rainfall can vary within small spatial scales. However, the climate station was at exactly the same altitude in the same valley/same slope/ same aspect, so that there is no indication of differences in climate at such fine scales. Soil moisture data at the site correspondingly fits very well with rainfall events measured at the weather station.

5) Line 123: By the nature of its close follow on after trenching this seems to refer to volumetric soil water measurements in the trenched plots but instead refers to the broader study plots (as shown in Figure 1). This could be more clear.

We clarified that. Moisture was measured at all plots, broader study plots, trenched plots, and control plots.

6) Lines 145-146: I would be interested in hearing more about the ventilation system used for the incubations. I am uncertain how much water might be lost by the soils during this process (e.g.- the ventilation process during the two-week waiting periods between soil moisture sampling) and how this water loss was addressed during periods between measurements.

We added (L107-109): “In the meanwhile, disconnected containers were ventilated by means of an air pump in order to prevent internal CO₂ enrichment. Wet tissues were put into containers in order to prevent samples from drying out during incubations; moisture loss was thereby negligible (< 2 vol. %).”

We also clarified that soil cores were only placed in the incubation chambers during actual incubation runs and that cores were stored in a storage room (+4°C) in-between the incubation runs.

7) Lines 143-148: I wonder about the effect of sieving on Rh considering the disruption placed on the soil/fungal community. It seems likely that this has significantly affected this component within this aspect of the study. (Datta et al Int. Agrophys., 2014, 28, 119-124)

We are aware that sieving disrupts fungal hyphae and has further unwanted effects, such as a disruption of soil aggregates, which could liberate bound SOM. We nevertheless decided sieving the soil. Incubating undisturbed cores, makes it difficult to be sure that root respiration is really excluded, as intact fine roots in the cores can maintain respiration for relatively long times. Correspondingly, root respiration could add to the core CO₂ efflux even after long equilibration times and thereby affect the temperature sensitivity. As we aimed to model Rh, we decided not to use intact soil cores. We added some lines to the discussion:

L 280-282: As a last point, soil sieving could have positively affected Rh rates during incubation by releasing physically protected SOM and/or providing additional C sources via disrupted fungal hyphae and fine root fragments (Datta et al., 2014) .

8) Agreed with reviewer #1 point 7

Changed accordingly throughout the revised manuscript.

9) Lines 188-194: The assumption that the temperature in the soil at 5cm depth is sufficiently predictive of Rs may work within this model but it assumes that the system is sufficiently co-variant that this one data point is essentially all that is needed. This seems to assume that the basal respiration from lower soil depths is effectively constant. Can the authors provide any evidence that this is true?

Most of Rs will be produced in the topsoil with highest SOM, microbial biomass, and fine root contents. Therefore topsoil temperature usually is a quite good predictor of total Rs. We actually do not assume that the basal respiration from deeper layers is constant, but that respiration rates from deeper layers co-varies with that from topsoil. We are aware that this very likely is not really the case as deeper soil temperature reacts somewhat delayed to topsoil temperature variations and as Rs, produced in deep soil, needs some time to diffuse to the surface. The very tight relationship between topsoil temperature and Rs however indicates that deeper soil Rs production is quantitatively not so relevant, or that deeper soil Rs still co-varies with topsoil Rs, at a scale that is mostly covered within the model. We discuss the shortcomings of the model approach in the revised manuscript (L259-284).

10) Line 200: I agree that a Gaussian distribution is probably the most appropriate here (and for appropriate biologically relevant reasons) but the linear fits later in figure 2 have no real biological rationale.

We changed to a more simple polynomial function which is consistently used now.

11) Lines 205-212: The trenching experiment not only affects water retention in the soil but also provides further litter availability and there are likely non-linear effects that are not well addressed in this section. I am also unconvinced that the correction for soil moisture is precise and accurate based upon the data reported. Perhaps it would be more useful to report a range of possible outcomes instead of the firm values reported here.

We more intensively discuss the problems associated with trenching (L285-303). Soil moisture correction should have been fine as we used the moisture measurements directly obtained from trenching and control plots. This was somewhat unclear in the original ms and has been clarified.

12) Line 220: It is unclear if the lack of specific moisture response function is due to a lack of (or no) collected data or a poor linear or Gaussian fit was obtained from the collected data.

This was matter of a misleading formulation. We simply did not obtain litter CO₂ efflux data under different moisture levels. Accordingly, no response function was available for litter, and the function for mineral soil was used instead. We clarified that in the text.

13) Line 246-247: The method for assessing fine root biomass is not reported. Either the method should be discussed or a reference to the data would be helpful.

We added the method (L66-70): Fine root (≤ 2 mm) biomass was estimated by soil-core method (Makkonen and Helmisaari, 1999) once in spring 2014 at both sites. We used a cylindrical soil corer (7.5 cm diameter) for sampling. The extracted core samples were divided into three depth sections of 0-10 cm, 10-20 cm and 20-30 cm. After washing and sorting (live roots and necromass), roots were dried at 70 °C to constant mass before weighing dry biomass. Contribution of fine root C was estimated as 50 % of the plant tissue.

14) Lines 252-254: Given the potentially compromised nature of the Rs data from 2014 I would prefer that it not be reported at all, especially given the successful campaign run through 2015. The nature of pressure pumping and its effects on fluxes is sufficiently well established that this doesn't add much value to the paper.

We removed all 2014 data as suggested.

15) Line 259: This is somewhat self-fulfilling. You measured once every three weeks and find that 3 week sampling density is sufficient. In order to truly test this you would need a higher density sampling rate that you are then able to sub-sample at the 3 week frequency. I would suggest this comment (and others similar) be removed from the text.

This is true. We removed that.

16) Line 277-278: Again, given the nature of the trenched plots in 2015 (errors in strategy that are explainable and understandable) I am uncertain why this is discussed in the methods section and here. If I understand correctly not including this would save space and would not affect your analysis.

We removed the additional 2015 trench plot data completely.

17) Lines 280-287: The model should be made clearer, in agreement with point 9 from reviewer #1.

We added the complete code and data as supplement.

18) Lines 301-319: I find this justification of the "field Q10" values to be unconvincing and suggest that this section be reworked or removed from the text. There are too many other variables that are not addressed beyond the already tenuous soil moisture correction for this to be adequately compared to a true Q10.

We re-worked this chapter. Actually, we deleted most of it as we decided not to use Q10 for Rs (as suggested). The whole chapter now is much clearer and only the important information is provided/discussed.

I agree that Figure 3 seems to serve little purpose and any lost detail can be described quickly and easily in the text.

We removed the graph.

Anonymous Referee #3

This manuscript entitled "Soil CO₂ efflux from two mountain forests in the Eastern Himalayas Bhutan: components and controls" by Wangdi et al. provides interesting, relevant and valuable information on a poorly studied region. Manuscript is mostly well written and easy to read. The use and comparison of different techniques of measurements and different models is interesting. Nevertheless, aspects of the methods and then of the results remained unclear because it was not easy to distinguish and understand when and also why measured or modeled results were used to suit the purpose.

Major revisions would be necessary to clarify the manuscript and to develop more explicitly the objectives of the comparison between different measurements/models.

We highly appreciate the constructive comments which largely aligned with suggestions from reviewers 1 and 2. We better distinguish between modeled Rh and trenching results in the revised manuscript and we better explained why these methods were used. All other suggestions have been followed as well. While revising the manuscript, we found a minor conversion error for Rh values per kgC⁻¹, which we corrected for in the revised manuscript. Corrections did not affect the overall outcome of the study. Corrections resulted in slightly higher modeled Rh and minimal, insignificant deviations of Q10 and R10 values when compared to the values in the initial manuscript (without any effect on the study results!).

General comments:

I am not convinced that 2014 field Rs data should be presented in the ms as they are not relevant because influenced by pressure effects. In the same way given the trenched plots in 2015 didn't produced meaningful values, what does these data bring to the analysis? If retained, the trenched plot results could be better discussed. Important care must be given to distinguish between measured and modeled results. Authors should explain why and when each was performed and also why and when they are referring to each.

As suggested, we removed the 2014 Rs data as well as the data from 2015 trenching plots. The text is now easier to read and we did not lose relevant information.

Specific comments:

1) L23-24 : unclear. I can't see why the variability of Ra indicates a methodological issue with the trenching

We removed this from the abstract. We further refined the discussion and point at shortcomings of both methods (model, trenching) in the discussion section (L259-303).

2) I.272 : prefer effect of sites rather than of forest type

Changed to “sites” in the whole manuscript

3) I.190 : discuss how constraining the model with the temperature in the soil at 5cm depth is sufficient and relevant. What about the deepest contributions to Rs?

We actually used soil temperatures from different soil layers (mineral soil 5 cm, and mineral soil 20 cm depth) for modeling (L180-183) of CO₂ efflux from the corresponding layers. CO₂ efflux from < 30 cm depth was neglected in our model. We discussed this in terms of the Rh model outcome. We extended the discussion accordingly (L259-284).

4) I.190 : The same parameters (of Eq1) are used to model Rs over the year without any discussion whether or not the Q10 could vary with the temperature range over the year.

We alternatively fitted a Gaussian function (where Q10 changes with temperature). The fit of the simple exponential function was slightly better. We therefore decided to stick to this function.

5) I.205-212 : agreed with reviewer #2 point 11. Indicate the uncertainties rather than that corrected value.

As both methods have some different sources of uncertainty, they are quite difficult to quantify. We therefore stuck to the graph, but better discuss uncertainties in the text.

6) I.218: what is Fig S1 ?

Supporting Figure 1 is a supplement. We deleted this figure as this is a common procedure in model anyway.

7) I.246 : report and discuss the method used to estimate fine root biomass

We added the method (L66-70).

8) I.259 : How can you be convinced that it ‘indicates that a three-week interval is sufficient’ although you didn’t measured with a higher frequency ? Restrain the purpose.

That’s true. We deleted this sentence.

9) I.278 : useful ?

Deleted.

10) I.308-319: I have issues with the analysis presented here because I am concerned about the definition for the terms intrinsic and apparent sensitivities. Recently, Sierra et al. 2015, JAMES 7: 335-356 proposed consistent and formal definitions for intrinsic and apparent sensitivity. It would be nice if the authors referred to that definition or explained how they defined these conceptual sensitivities.

We completely revised the section. According to reviewer 2, we don’t use Q10 for field Rs. The text passage is shorter and much easier to read now. We refer to Sierra et.al. in the discussion section with regard to moisture effects on temp sensitivity.

11) I.345: albeit ?

Should be “besides” – changed.

12) Figure 4: The figure is really confusing. Caption doesn’t help

We adapted the figure. Should be easy to understand now.

13) Figure 5: not easy to understand that the lines are cumulative. Indicate by filling with different colors that the bottom area is Rh (10 – 30), the second area is Rh (0 –10), the third (upper) one Rh litter and the highest Ra.

We adapted the figure and caption. It should be clear now.

4. Associate Editor's Comments

General Comments

Many thanks for your revised manuscript. You have managed to address the referees' comments well, and I'm happy in principle for this study to be published. I am also glad to see that you have made your source data available via figshare. Could I kindly ask you to address a number of remaining, mostly minor points that I list below? These are mainly clarifications in the text.

Specific Comments

Abstract: Please include a real reference when quoting annual Rs figures, i.e. "14.5 ± 1.2 t C ha⁻¹ broadleaved; 12.8 ± 1.0 t C ha⁻¹".

AR: Added.

Line 6: Either "... serve as a C sink or source...", or "... serve as C sinks or sources...".

AR: Changed to "serve as C sinks or sources".

Line 61: Should this be "0-10, 10-20 and 20-30 cm"?

AR: Sorry, yes, it was a typo. It should be "0-10, 10-20 and 20-30 cm"

Line 184: This use of input as a proxy for stock is unclear. Do you have data to back this up? (see also comment below).

AR: Due to a strong seasonal variation in litter input/decomposition (at both sites, but especially at the broadleaved site), litter layer depth and C stocks will vary with time. We think that thoroughly measured total annual litter input rates represent a reasonable estimation for this year's litter stocks and is more accurate than a single point in time measurement of the litter layer depth/stock. A thorough assessment of litter C stocks (multiple-time assessment throughout the seasons) was not carried out during this study. We therefore decided to stick to the litter input as proxy. Nevertheless, a rough estimate during spring 2015 showed that stocks roughly matched annual 2015 litter input rates. We added this to the method text and better explained the effects on uncertainty in the discussion (see below).

Methods (L183-187): We used the litter Q_{10} together with continuous temperature at 5 cm soil depth to model daily Rh from the litter layer. In order to scale to field fluxes, we used the annual litter input (Table 1) as a proxy for field litter C stocks. A first rough litter assessment in March 2015 showed that litter stocks were in a similar range as the annual litter input at both sites.

Line 258: I'm not sure the word "disabled" works here. Stating that belowground allocation of C by trees is limited should be appropriate to make this point.

AR: We removed the word "disabled".

Line 260: Better: "However, there is..."

AR: Corrected.

Line 269: This is unclear to me. In steady state, litter C input is balanced by litter C losses, but the pool size of litter is not necessarily equal to one year's amount of litter. That depends on turnover rates. Please clarify.

AR: We agree, that annual litter input is not necessarily equal to the actual amount of litter on the forest floor. However, both, litter input rates and litter decomposition rates underlie a strong seasonal variation (especially in the broadleaved forest); depending on the time of the year, an exact quantification of annual litter stocks can thus be quite challenging (e.g. spring VS. fall measurements of litter layer thickness). We therefore think that total litter input rates as a rough proxy for the C stocks of this year's litter constitutes fair a compromise. We are aware that our upscaling approach of annual heterotrophic respiration rates to the field holds a lot of uncertainties; the estimation of litter C stocks is recognized as one of them (please see discussion section). However, the respiratory contribution from the litter layer to total heterotrophic respiration rates was comparably low at both sites. Although the magnitude of predictions seems to be overestimated, we nevertheless think that our method represents an applicable and easy tool to investigate the seasonal course of heterotrophic and autotrophic soil respiration rates. We changed the discussion to:

L 276-279: Using annual litter input as proxy for litter C stocks is a further source of uncertainty. Litter input has temporal patterns and thereby affects litter decomposition dynamics. Such temporal patterns in litter input/decomposition were not reflected in our model. The modeled contribution of the litter layer to total soil Rh was, however, small (Fig. 4), and therefore, the uncertainty related to temporal litter layer dynamics can also be considered as small.

Line 310: It was either similar or not... Do you mean "almost identical"?

AR: Changed to "almost identical".

Lines 315-322: I'm not sure why you give a very approximate soil C budget when stating that you don't actually have the data to do so confidently. This was not your aim, and I don't see that this is a meaningful contribution at this point.

AR: We deleted this chapter and moved the root and litter discussion (L317-323) upwards (now L249-254).

Below you find the revised manuscript. All major changes are marked in blue and red

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Soil CO₂ efflux from two mountain forests in the Eastern Himalayas Bhutan: components and controls

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Abstract

The biogeochemistry of mountain forests in the Hindu Kush-Himalaya range is poorly studied although climate change is expected to disproportionally affect the region. We measured the soil CO₂ efflux (Rs) at a high elevation (3260 m) mixed, and a lower elevation (2460 m) broadleaved forest in Bhutan, eastern Himalayas, during 2015. Trenching was applied to estimate the contribution of autotrophic (Ra) and heterotrophic (Rh) soil respiration. The temperature (Q_{10}) and the moisture sensitivities of Rh were determined under controlled laboratory conditions and were used to model Rh in the field. The higher elevation mixed forest had a higher standing tree stock, reflected in higher soil C stocks and basal soil respiration. Annual Rs was similar between the two forest sites (14.5 ± 1.2 t C ha⁻¹ broadleaved; 12.8 ± 1.0 t C ha⁻¹ mixed). Modelled annual contribution of Rh was ~ 65 % of Rs at both sites with a higher heterotrophic contribution during winter and lower contribution during the monsoon season. Rh, estimated from trenching, was in the range of modelled Rh but showed higher temporal variability. Measured temperature sensitivity of Rh was similar at the mixed and broadleaved forest site (Q_{10} 2.2- 2.3) under intermediate soil moisture but decreased (Q_{10} 1.5 at both sites) in dry soil. Rs closely followed the annual course of field soil temperature at both sites. Co-variation between soil temperature and moisture (cold-dry winters, warm-wet summers) likely was the main cause for this tight relationship. Under the prevailing weather conditions, a simple temperature-driven model was able to explain more than 90 % of the temporal variation in Rs. Longer time series and/or experimental climate manipulations are required to understand the effects of eventually occurring climate extremes such as monsoon failures.

Keywords: Himalaya, soil CO₂ efflux, autotrophic soil respiration, heterotrophic soil respiration, incubation, temperature sensitivity, moisture sensitivity

1 Introduction

Carbon dioxide (CO₂) efflux from soil (= soil respiration; Rs) is one of the major fluxes in the global C cycle, affects atmospheric CO₂ concentrations and [potentially](#) feeds back on global climate change (Reichstein et al., 2003; [Frey et al., 2013](#); [Wang et al., 2014](#); Hashimoto et al., 2015). Counteracting to C uptake via photosynthesis, Rs primarily determines whether forest ecosystems serve as C sinks or sources to the atmosphere (Bolstad et al., 2004; Dixon et al., 1994; Schlesinger and Andrews, 2000). The current function of forests as global C sink (Stocker, 2014; Janssens et al., 2003) could weaken or even turn into the opposite if climate change disproportionally accelerates respiratory processes such as Rs (Cox et al., 2000). Rs consists of an autotrophic component (Ra; root and rhizosphere respiration), which is closely linked to C gain by photosynthesis and a heterotrophic component (Rh), which is the respiratory product of soil organic matter (SOM) decomposition. While the source of Ra is recently assimilated CO₂, Rh can release stored soil C to the atmosphere. For better prediction of the response of forest C cycling to climate change, it is crucial to understand how Rs and its components are affected by changing environmental parameters such as temperature and moisture (Davidson and Janssens, 2006; [Sierra et al., 2015](#)). Rates and climate sensitivity of Rs, Ra and Rh can vary among forest ecosystem type and climatic region (Hashimoto et al., 2015). So far, research has focused on the temperate and boreal areas of the northern hemisphere whereas remote forested areas are still largely uninvestigated (Bond-Lamberty and Thomson, 2010).

The Hindu Kush-Himalaya range represents a region, where research on forest biogeochemistry is gaining momentum (Pandey et al., 2010; Sundarapandian and Dar, 2013; Sharma et al., 2010b; Dorji et al., 2014b; Ohsawa, 1991; Wangda and Ohsawa, 2006a; Tashi et al., 2016; Verma et al., 2012). It extends over 4.3 million km² across eight countries with an average forest cover of approximately 20 % (Schild, 2008), ranging from lowland tropical forest to high altitudinal forests up to ~ 4900 m (Liang et al., 2016; Schickhoff, 2005). Situated in the eastern Himalayas, Bhutan shows a forest cover of 70 % (DoFPS, 2011). Most forests in Bhutan are natural old growth (Ohsawa, 1987), store high amounts of C in biomass and soil (Dorji et al., 2014a; Sharma and Rai, 2007) and serve as an important regional C sink (FAO, 2010). As climate change is expected to intensify in the Himalaya region (Shrestha et al., 2012; Singh, 2011; Xu and Grumbine, 2014; Tsering et al., 2010; Xu et al., 2009), the effects on forest C cycling could have implications not only regionally, but also on a global scale.

[With the objective of a better understanding of soil C cycling of mountain forest ecosystems, we studied Rs, its components \(Ra, Rh\), as well as the effects of environmental drivers such as temperature and moisture at a moderately high altitude cool temperate mixed forest and a lower altitude cool temperate broadleaved forest in Bhutan. These forest types cover large areas of the eastern Himalayas.](#)

2 Materials and methods

2.1 Site description

Two representative forest ecosystems for the eastern Himalayas (Wikramanayake, 2002), a cool temperate conifer dominated mixed forest and a cool temperate broadleaved forest, were studied at Thimphu and Wangduephodrang districts, Bhutan. The cool temperate mixed forest (Grierson and Long, 1983) was situated on a south-east facing slope close to the top of a mountain ridge (elevation 3260 m a.s.l.). The cool temperate broadleaved forest was situated on an east facing gentle slope along the same mountain ridge ~ 11 km eastwards (elevation 2640 m a.s.l.). Sites will be referred to as “mixed forest” and “broadleaved forest” in the further text. The mixed forest was dominated by *Tsuga dumosa* along with *Picea spinulosa*, *Quercus semecarpifolia*, *Abies densa*, and *Taxus baccata*. The broadleaved forest was dominated by *Quercus lanata* and *Quercus griffithii*. Soils at the mixed forest were Cambisols. Soils at the broadleaved forest were Luvisols. A detailed site and soil description and the comparison are given in Table 1. The current study was aligned within a larger-scale throughfall manipulation experiment, which consisted of control and temporarily roofed areas within each forest type. For this study, we randomly distributed all our plots within the control areas (~ 1500 m² each) of the throughfall manipulation experiment.

2.2 Field measurements

Basic climate parameters were measured using automatic weather stations located at a distance of approx. one kilometer from the sites at the same elevation. Data was recorded at 15 min intervals on a Decagon-EM50 data logger (Decagon Devices Inc., Pullman, WA, USA). The automatic weather stations recorded precipitation with an ECRN-100 rain gauge (Decagon Devices Inc., Pullman, WA, USA), and air temperature and relative humidity with a VP-3 vapor pressure, temperature and relative humidity sensor (Decagon Devices Inc., Pullman, WA, USA).

Stand and soil inventories were carried out in March and April 2014 at both sites covering an area of ~ 1500 m² each. The location, height and the diameter at breast height of all trees having a dbh > 10 cm were assessed. The basal area was calculated for each tree species. Standing volume was estimated based on species-specific volume equations developed by Paul Lawmans (1994), Forest Survey of India (1996) and Department of Forests and Park Services, Bhutan (2005). Aboveground litter-fall was collected monthly using mesh-traps (n = 10) per site, with an area of 1.0 m² (100 × 100 cm). Litter was dried at 80 °C and the C content was assumed to be 50 % of the dry weight (de Wit et al., 2006). Soil samples were collected from the 0-10, 10-20 and 20-30 cm mineral soil layers of four locations at both sites in May 2014. Soil samples were sieved (2 mm) and dried (105 °C, 48 h). Soil organic C (SOC) of a ground (Pulverisette 5, Fritsch, Germany), 0.1 g subsample was measured by means of the dry combustion technique using a CN Analyser (TruSpec® CN, LECO Inc., Michigan, USA). Soil organic C stocks (t ha⁻¹) were calculated for each horizon by multiplying the SOC concentration (%) by the bulk density (g cm⁻³) and the depth of the horizon (cm). Fine root (≤ 2 mm) biomass was estimated by the soil-core method (Makkonen and Helmisaari, 1999) in spring 2014 at both sites. We used a cylindrical soil corer (7.5 cm diameter) for sampling. The extracted samples were divided into three depth sections of 0-10, 10-20 and 20-30 cm. After washing and

sorting (live roots and necromass), roots were dried at 70 °C to constant mass before weighing dry biomass. Contribution of fine root C was estimated as 50 % of the plant tissue.

Rs was measured at both sites once every three weeks from April 2015 to December 2015 at 10 randomly chosen plots (n = 10) at each. To cover the within-plot variability, Rs was measured at four positions within each plot (total 40 positions per site). We used a portable infrared gas analyzer (EGM-4, PP-Systems, Amesbury, USA) with an attached soil respiration chamber (SRC-1, PP-Systems, Amesbury, USA) for Rs measurements. Prior to measurements (March 2015), we installed permanent collars (total height 5 cm, 2-3 cm inserted into the soil, diameter 10 cm) at each plot which served as a base for Rs measurements. Rs was estimated by a linear fit to the increasing headspace CO₂ concentration over time (chamber closure time 90 seconds). A soil respiration measurement campaign lasted for ~ 5 h at each site. Measurement order among plots and collars was fully random to avoid bias from temporal variations in Rs.

We installed two trenching plots at each site in April 2014 (1 yr prior soil efflux CO₂ measurements) to estimate the relative contributions of Ra and Rh. Trenches (1.5 x 1.5 m) were dug to ~ 1 m depth, and all roots within the trenches were cut. The trenches were sealed with double layered plastic foil in order to restrict tree root ingrowth. Adjoining to each trenched plot, a corresponding control plot of the same size was established. Each trenched and control plot hosted three collars for Rs measurements. We measured soil CO₂ efflux at trenched and corresponding control plots after finishing regular Rs measurements (same day).

Volumetric soil water content (0-20 cm soil depth; (vol. %)) was measured in the center of each plot (Rs plots, trenched plots, control plots) using a portable Field Scout TDR meter (Spectrum Technologies, Inc. Aurora, USA) during Rs measurements. Soil temperature at 5 cm soil depth was measured with a handheld thermometer probe (Hanna Instruments, Germany) at each Rs measurement location. Soil temperature and soil moisture were measured continuously at soil profile pits (two pits per site) with five combined soil temperature-moisture sensors (TM-5; Decagon Devices, Inc., Pullman, WA, USA) at soil depths ranging from 5 to 120 cm. Data was recorded at 15 min intervals on Decagon-EM50 data loggers (Decagon Devices, Inc., Pullman, WA, USA).

2.3 Laboratory incubation

About 500 g of mineral soil (0-10 cm depth) and approximately 250 g of forest floor litter were sampled at six random locations (n = 6) at each site in mid-September 2015. The mineral soil was homogenized and sieved (2 mm mesh) and stored at 4 °C at field moisture for one week prior to transport from Bhutan to Austria for further processing. Forest floor litter was not sieved. Upon arrival in Austria, mineral soil samples were further divided into 3 sub-samples to account for potential soil heterogeneity at individual sampling locations. Samples were filled into 200 cm³ stainless steel cylinders at approximate field bulk density (~ 0.5 g dry weight cm⁻³ for mineral soil; ~ 0.1 g dry weight cm⁻³ for forest floor). In total, we incubated 36 sub-samples (cylinders) for mineral soil and 12 sub-samples for the forest floor litter. Filled cylinders were kept at 4 °C for 5 days for equilibration before incubation. Soil CO₂ efflux (= Rh) was measured using a fully automated incubation system. During incubation,

samples were put into 2 l containers and their CO₂ efflux was determined by a dynamic closed – chamber system (Pumpanen et al., 2009). For CO₂ measurements, containers were sequentially connected to an infrared gas analyzer (SBA-4, PP Systems International Inc., Amesbury, MA, USA) by means of a tubing system. In the meanwhile, disconnected containers were ventilated by means of an air pump in order to prevent internal CO₂ enrichment. Wet tissues were put into containers in order to prevent samples from drying out during incubations; moisture loss was thereby negligible (< 2 vol. %). CO₂ concentration within connected containers were measured for 6 minutes with a recording interval of 10 sec. Rates of CO₂ efflux were calculated from the headspace CO₂ increase during 2 – 6 minutes, after Pumpanen et al. (2009).

Incubations proceeded in two steps. We first incubated at different soil temperatures to assess the temperature sensitivity of Rh. In a second step, we incubated under different soil moisture contents to assess the sensitivity of Rh to changes in soil moisture. In addition, we repeated the temperature-runs with wet (140 % gravimetric water content (grav. %)) and dry (30 grav. %) soil in order to test for effects of soil moisture on the temperature sensitivity of Rh. In-between incubations, soil cores were stored in a cold room (+ 4 °C). During storage, soil moisture was kept constant by periodical water addition.

Temperature-incubation started with mineral soil. Soil temperature was increased from 5 °C until 25 °C in 5 °C steps, with each temperature step lasting for 6 h. At each temperature step, efflux measurements were repeated three times for each cylinder; to account for a warm up period between the individual temperature steps only a calculated mean value of the latter two measurements was used for further analysis. After finishing the temperature run, we re-measured Rh at 10 °C to assess and correct for potential effects of labile C loss during the ~ 30 h incubation. The forest floor litter was incubated under the same procedure as mineral soil.

After the temperature-incubation, we set soil moisture of all mineral soil sub-samples to 80 grav. %, incubated at constant 15 °C for 6 h and measured Rh as described above. Afterwards, the three sub-samples from each sampling location were split into (i) a sub-sample that was kept at constant soil moisture (80 grav. %), (ii) a sub-sample that was allowed to dry out (60 to 15 grav. %), and (iii) a sub-sample that was progressively watered (100 to 160 grav. %). In-between repeated incubations (all at 15 °C for 6 h) cylinders were taken out from incubation containers and were stored at 4 °C. The whole moisture-incubation procedure lasted for 10 weeks with ~ two-weekly intervals between incubations (time limiting step was soil drying). We used Rh from the sub-samples which had been kept at constant moisture to correct for potential decreases in Rh due to a loss in labile C throughout the experiment. After finishing all incubations, samples were dried and actual bulk density, as well as actual gravimetric (grav. %) and volumetric soil moisture (vol. %) of each sub-sample (cylinder), was calculated and their total C content was determined (TruSpec® CN, LECO Inc., Michigan, USA). Rh rates were expressed as $\mu\text{mol CO}_2 \text{ kg C}^{-1} \text{ s}^{-1}$.

2.4 Data analysis

Effects of site on field Rs, soil temperature and moisture were tested by means of repeated-measures ANOVA with a mixed-effects model structure (Pinheiro and Bates, 2000). The significance level for this and all other analyses

was set at $P < 0.05$. The relationship between soil temperature and Rs was fitted by an exponential function (Buchmann, 2000):

$$R = \beta_0 \cdot e^{(\beta_1 \cdot T)} \quad (1)$$

where R ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) is the measured Rs, T ($^{\circ}\text{C}$) is the soil temperature at 5 cm depth, and b_i are model parameters. Equation (1) was fitted to the daily averages of each site as well as to the individual plot data. Basal respiration rates at 10°C soil temperature (R_{s10}) were subsequently calculated (using Eq. (1)) for each site. One sampling date (2015 Jul 16) was excluded from this analysis because heavy rain occurred during measurements. The relationship between Rs and soil moisture was tested by fitting a polynomial function obtained from lab incubation (see further below). Cumulative annual Rs of both sites and both years were calculated by linear interpolation of field Rs between measurement dates of each individual plot (the area beneath the curves in Fig. 1 d). In addition, model parameters of Eq. (1), together with daily field soil temperatures at 5 cm depth were used to calculate a projected daily field Rs. To account for a spatial variation in soil temperature, continuously measured data were adjusted to discontinuously measured plot-data by linear modelling. Cumulative annual Rs rates were calculated by averaging the summed-up daily plot Rs values.

Average Rh rates from laboratory incubations were calculated for each site, soil horizon (mineral soil, forest floor litter) and temperature step ($5 - 25^{\circ}\text{C}$), respectively. Equation 1 was fitted to the temperature-incubation data separately for each site and soil horizon. Basal heterotrophic respiration rates at 10°C (R_{h10}) were calculated for each site. Temperature sensitivity (Q_{10}) of Rh was calculated as follows:

$$Q_{10} = e^{(10 \cdot \beta_1)} \quad (2)$$

where Q_{10} is the factor by which Rh changes at a temperature change of 10°C , and β_1 is the model parameter derived from Eq. (1). To determine the relationship between soil moisture and Rh, we fitted a polynomial function to the moisture-incubation data:

$$R = \beta_0 + \beta_1 \cdot VWC + \beta_2 \cdot VWC^2 \quad (3)$$

where R is the measured CO_2 efflux from soil samples (R_h), β_i are model parameters and VWC is the volumetric water content of the samples. Effects of soil moisture on Q_{10} values were tested by means of one-way ANOVA and Tukey's post-hoc tests.

We followed two approaches to estimate the contribution of R_a and R_h in the field. In a first approach, we used the trenching data, assuming that the CO_2 efflux from the trenched plots represented solely R_h , while the CO_2 efflux from adjacent control plots represented R_s , and accordingly, the difference between trenched and control plot CO_2 efflux represented R_a . As trenched plots lack water uptake by tree roots, they were regularly wetter than control plots. We accounted for that by correcting the soil CO_2 efflux for the difference in soil moisture by using Eq. (3) (see Schindlbacher et al. (2009) for details).

In a second approach, we applied the response functions of R_h derived during laboratory incubation together with field soil C stocks and field climate data. This allowed an alternative way to estimate the contribution of R_h in the field (Gough et al., 2007; Kutsch et al., 2010). Model parameters derived from Eq. (1) together with continuously measured temperature data from 5 cm soil depth were used to model daily R_h from the litter and from the mineral soil in 0 – 10 cm depth respectively. Model parameters for mineral soils together with continuous measurements of soil temperature in 20 cm depth were further used to model daily R_h from the mineral soil in 10 – 30 cm depth. Predicted R_h rates ($\mu\text{mol CO}_2 \text{ kg C}^{-1}$) were multiplied by the C stocks (kg C m^{-2}) of the respective soil layer. We used the litter Q_{10} together with continuous temperature at 5 cm soil depth to model daily R_h from the litter layer. In order to scale to field fluxes, we used the annual litter input (Table 1) as a proxy for field litter C stocks. A first rough litter assessment in March 2015 showed that litter stocks were in a similar range as the annual litter input at both sites. This procedure enabled us to upscale R_h to the whole soil profile in the field (Kutsch et al., 2010). To account for a moisture response as well, predicted R_h rates were also corrected for soil moisture conditions in the field. For that, model parameters derived from Eq. (3) were used to calculate R_h rates at actual moisture conditions in the field (from continuous moisture data) and at initial moisture conditions of the soil samples during incubation (mixed forest: 33 vol. %, broadleaved forest: 35 vol. %, litter: 46 vol. %); their relative difference was subsequently used to correct R_h rates predicted with Eq. (1). Since litter soil moisture was not regularly measured in the field, we applied the same moisture parameters and continuous soil moisture records as for mineral soil (0-10 cm). The R code of the empirical model is provided in the supplement information (S1).

3. Results

Air and soil temperatures were $\sim 4^{\circ}\text{C}$ higher at the lower elevation broadleaved forest (Table 1) with a stable trend throughout both study years (Fig. 1a). Air temperatures reached a maximum of 29.6°C and 22.6°C at the broadleaved and mixed forest, respectively. Winter air temperatures dropped slightly below freezing at the mixed forest which showed ephemeral snow cover. Soil temperatures remained above freezing at both sites during the full study period (Fig. 1b). Annual precipitation in 2015 was similar at both sites (mixed 1167 mm, broadleaved 1120 mm). Both sites received the maximum rainfall (60-75 % of annual precipitation) during the peak monsoon months (Jun, Jul and Aug). Soil moisture was significantly higher at the broadleaved forest during summer (Fig. 1c). During the dry season (Nov – Apr), manually measured soil moisture decreased to < 20 vol. % at both sites. Continuous soil moisture records indicated accelerated drying at the broadleaved forest (Fig. 1c).

Aboveground and below-ground C stocks were markedly higher in the mixed forest (Table 1). Standing volume was 1066 and $464\text{ m}^3\text{ ha}^{-1}$, at the mixed and broadleaved forest, respectively. Mineral soil organic C stocks down to 30 cm soil depth were 142 and 90 t C ha^{-1} and leaf litter inputs (2015) were 3.5 and 3.4 t C ha^{-1} at the mixed and broadleaved forest, respectively. Fine root biomass (0-30 cm mineral soil) was lower at the mixed forest (2.3 t C ha^{-1}) when compared to the broadleaved forest (3.2 t C ha^{-1}).

Rs did not differ significantly between the two sites (mean Rs broadleaved: $4.2 \pm 0.7\text{ }\mu\text{mol CO}_2\text{-C m}^{-2}\text{ s}^{-1}$, mixed: $4.0 \pm 0.6\text{ }\mu\text{mol CO}_2\text{-C m}^{-2}\text{ s}^{-1}$) but basal respiration rates (Rs_{10}) were higher at the mixed forest (Fig. 2a). Cumulative annual Rs were $14.3 \pm 0.5\text{ t C ha}^{-1}$ for the broadleaved and $13.0 \pm 0.5\text{ t C ha}^{-1}$ for the mixed forest when calculated by linear interpolation between measurement dates. These values were very close to the ones obtained by the modelling approach (Eq. (1), $14.5 \pm 1.2\text{ t C ha}^{-1}$, broadleaved and $12.8 \pm 1.0\text{ t C ha}^{-1}$, mixed). Rs showed a higher spatial variability at the mixed forest (21 - 87 % coefficient of variation (CV)) than at the broadleaved forest (23 - 46 % CV). Between 89 and 96 % of the annual temporal variation in measured Rs was explained by field soil temperature (Eq. (1), Fig. 2a). Rs showed a weak relationship with soil moisture at the broadleaved forest site, whereas there was no significant correlation between Rs and soil moisture at the mixed forest site (Fig. 2b).

Laboratory incubations showed a strong positive, exponential, relationship between soil temperature and Rh (Fig. 2c). Temperature sensitivity of mineral soil Rh was similar between sites (mixed $Q_{10} = 2.2$, broadleaved $Q_{10} = 2.3$; Fig. 2c, Table 2) and slightly lower for forest floor litter (mixed $Q_{10} = 1.9$; broadleaved $Q_{10} = 2.2$; Table 2). Q_{10} values of dry soil (mixed $Q_{10} = 1.6$; broadleaved $Q_{10} = 1.5$) were significantly lower than Q_{10} from the soil which remained at intermediate moisture content ($P < 0.05$, Table 2). Q_{10} values obtained from dry and wet soil did not differ significantly (Table 2). Rh and soil moisture showed a unimodal relationship with highest rates of Rh at intermediate soil moisture (40 - 50 vol. %) and decreasing rates at lower and higher moisture levels (Fig. 2d). Soil from both sites responded overall similarly to changes in soil moisture. Mixed forest soil showed a slightly sharper decrease in Rh at lower and at higher soil moisture (Fig. 2d).

Trenching plots indicated an average autotrophic and heterotrophic contribution of 29 and 27 % and 71 and 73 % at the mixed and broadleaved forest sites during the whole 2015 season, respectively (Fig. 3). The contribution of R_a and R_h to R_s , obtained by trenching, showed high temporal variability and strong fluctuations between individual measurement dates at the mixed forest site (Fig. 3).

The modelling approach yielded annual heterotrophic contributions of 67 % in mixed forest and 63 % in broadleaved forest. Modelled cumulative annual R_h and R_a were 8.6 and 4.2 t C ha⁻¹ at the mixed and 9.5 and 5.0 t C ha⁻¹ at the broadleaved forest respectively. Modelled R_h was in the range of field R_s during the cold season (Fig. 3). The gap between R_h and R_s became larger during the growing season, implying highest contribution of R_a during the warm monsoon months at both sites (Fig. 3 and 4). The strong temporal fluctuation in sources (R_a , R_h) which was obtained from trenching was not confirmed by R_h model output (Fig. 3).

4. Discussion

Annual R_s of both forest sites ($12.8 - 14.5 \text{ t C ha}^{-1}$) was in the range of values reported for similar ecosystems ($10.1-13 \text{ t C ha}^{-1}$ (Dar et al., 2015); $10-12 \text{ t C ha}^{-1}$ (Li et al., 2008); 13.7 t C ha^{-1} (Yang et al., 2007) and 14.7 t C ha^{-1} (Wang et al., 2010)). The higher altitude mixed forest had double tree basal area and standing stock, indicating that this specific site is exceptionally productive (Singh et al., 1994; Sharma et al., 2010a; Tashi et al., 2016; Wangda and Ohsawa, 2006b). Soil C stocks of $\sim 140 \text{ t ha}^{-1}$ (0-30 cm depth mineral soil) indicate that these mixed forests are likely among those ecosystems with the highest C storage capacity in the eastern Himalayas (Wangda and Ohsawa, 2006a; Sheikh et al., 2009; Dorji et al., 2014a; Tashi et al., 2016). High soil C contents and stocks were reflected in generally higher basal respiration (R_{s10}) at the mixed forest explaining the comparatively high annual R_s rates at this cooler, higher altitude, site. Soil C input via aboveground litter-fall was almost identical between sites ($\sim 3.5 \text{ t C ha}^{-1}$) although tree basal area was substantially lower at the broadleaved forest. This can be attributed to a generally higher leaf litter production in broadleaved ecosystems (Tiwari and Joshi, 2015; Bisht et al., 2014). Fine root stocks at both sites fall within the upper range of estimates from other surveys in the Himalayan region (Adhikari et al., 1995; Usman et al., 1999; Garkoti, 2008; Rana et al., 2015), especially if it is considered that fine root contents in this study were estimated solely for 0-30 cm mineral soil depth.

At both forests, R_s tightly followed the seasonal course of soil temperature because soil temperature and soil moisture co-varied with dry and cold winters and optimal soil moisture during the warm summer months (Fig. 1b, c; Fig 2a, b). R_s can also be affected by labile C allocation to soil (Gu et al., 2004). During the growing season, trees tend to allocate higher amounts of labile C belowground, thereby potentially increasing the contribution of R_a and simultaneously accelerating SOM decomposition by increased availability of labile C and rhizosphere priming (Kuznyakov, 2010; Bader and Cheng, 2007; Bengtson et al., 2012; Dijkstra and Cheng, 2007; Schindlbacher et al., 2009). Such processes would further increase R_s and R_a during the warm summer months. Our modelled R_h and R_a data suggests that this was also likely the case in the studied forests (significant increase in R_a contribution during the summer months; Fig. 3).

Our model generated wintertime R_h fluxes which were in the range of, or slightly below, R_s fluxes (Fig. 4). During frost periods, downward C-flux from the tree canopy is limited and the contribution of R_a to R_s is considered low during winter (Rey et al., 2002; Hanson et al., 2000). Our modelled wintertime (and overall) R_h therefore lay in a realistic range. However, there is evidence that the contribution of R_a can be significant even during cold winters (Schindlbacher et al., 2007; Tucker et al., 2014). Roots in deeper and warmer soil layers can remain active and add to the soil CO_2 efflux. Accordingly, modelled R_h rather represents the upper edge of potential R_h at our site. Our modelling approach was based on a relatively simple set of soil C stocks combined with temperature and moisture sensitivities, and holds corresponding uncertainty with regard to quantity of R_h and its temporal dynamics. C stocks from deeper soil layers ($> 30 \text{ cm}$ depth) were not accounted for and a single Q_{10} (obtained from 0-10 cm depth) was used for the whole mineral soil layer. Stabilization of SOC is usually increasing with soil depth (Fontaine et al., 2007). Our R_h predictions for deeper layers (10-30cm) might therefore overestimate the real rate.

Using annual litter input as proxy for litter C stocks is a further source of uncertainty. Litter input has temporal patterns and thereby affects litter decomposition dynamics. Such temporal patterns in litter input/decomposition were not reflected in our model. The modeled contribution of the litter layer to total soil Rh was, however, small (Fig. 4), and therefore, the uncertainty related to temporal litter layer dynamics can also be considered as small. We further used a constant Q_{10} throughout the year, although the Q_{10} may vary with season due to changes in substrate supply and quality (Davidson and Janssens, 2006; Gu et al., 2004) and/or interactions with soil moisture (Sierra et al., 2015). We showed that soil moisture affected the temperature sensitivity of Rh by significantly lower Q_{10} under dry conditions (lab incubation, Table 2). Such dry conditions were, however, not observed in the field. We therefore assume that ignoring potential moisture effects on Q_{10} in our model had only minimal effects on the Rh estimate. Rhizosphere priming could have affected Rh dynamics as well, but we were not able to account for that in our model. Moreover, soil sieving could have positively affected Rh rates during incubation by releasing physically protected SOM and/or providing additional C sources via disrupted fungal hyphae and fine root fragments (Datta et al., 2014). Nevertheless, the modelled annual ~ 65 % contribution of Rh falls well within estimates from similar forests (Lee et al., 2010). Even if we overestimated the real contribution of Rh, we are confident that the model relatively robustly reflected the temporal dynamics of Rh/Ra throughout the year.

In contrast to the modelling approach, trenching was applied as an attempt to estimate Ra *in situ*. The trenching method, although highly invasive, was shown to provide reasonable estimates of Ra for several forest types (Hanson et al., 2000; Subke et al., 2006). Trenching suggested slightly higher contributions of Rh at both sites (average 72 % both sites) but showed much stronger temporal variations in Rh/Ra, especially at the mixed forest (Fig. 3). Trenching has several drawbacks. Soil moisture is usually higher in trenched plots because water uptake by roots is interrupted. This bias was accounted for as we used the moisture response function (Eq. (3)) for correction. However, trenched fine roots can maintain respiration for a comparatively long time after cutting (Lee et al., 2003) and when fine roots finally die, their decomposition can add to the soil CO₂ efflux from the trenched plots (Hanson et al., 2000). Assuming a dead fine root mass loss of roughly one-third during the second year after trenching (Díaz-Pinés et al., 2010) and accounting for the corresponding effects on soil CO₂ efflux (additional efflux ~ 1 t C ha⁻¹), the estimated annual contribution of Rh decreases to ~ 65 % of Rs, which is in the range of our modelling results. Potential effects of root decomposition, however, do not explain the atypically strong temporal variation in Ra at the mixed forest site. Soil CO₂ efflux from trenched plots was similar or even higher than from corresponding control plots, suggesting a steep decrease in Ra between July and September (Fig. 3). We do not have a straightforward explanation for this pattern. Probably we did not trench deep enough and missed a larger proportion of roots which added to the summertime CO₂ efflux from trenched plots. A further explanation could be altered nutrient availability to decomposers in the trenched plots. In trenched plot soil, roots do not compete any more for nutrients, potentially increasing nutrient availability to decomposers. This could accelerate SOM decomposition and soil CO₂ efflux. In summary, trenching showed a less clear outcome at the two study sites when compared to other forests. Therefore, other methods, such as girdling or isotope labeling might be alternatively applied in the forest types studied.

Our simple empirical temperature-driven Rs model explained most of the temporal variation in Rs under the typical monsoon weather patterns during 2015. However, monsoon failures and drought periods have occurred in the past and may even increase in frequency and/or severity of climate change (Schewe and Levermann, 2012; Menon et al., 2013; Cook et al., 2010; Sharmila et al., 2015). To model drought effects, it is necessary to further develop the model by integrating potential soil moisture response of Rs. To do so, longer Rs time series including dry years and/or data from artificial drought experiments are needed for model parameterization and testing.

5. Conclusion

The monsoon climate allows for highly productive mountain forests in the eastern Himalayas. Such forests can store high amounts of C in plant biomass and soil, which was particularly evident in the high altitude mixed forest in our study. At both forests studied, a simple temperature-driven model was sufficient to explain most of the temporal variation in Rs during the study year. The sites experienced typical monsoon climate with dry and cold winters and monsoon rain during the warm season. Further research and model development is, however, warranted to better understand how infrequent/extreme events such as monsoon failure and drought affect soil/ecosystem C cycling and Rs in these forest ecosystems.

6. Author contribution

N. Wangdi carried out the field research, analyzed data and drafted the manuscript. M. Mayer performed modelling and contributed to writing the manuscript. M. P. Nirola carried out the incubation experiment and analysed the data. N. Zangmo and K. Orong collected the data and continuously monitored the research sites. I.U Ahmed carried out the root and the soil analyses. G. Gratzner designed the larger-scale throughfall manipulation experiment. R. Jandl, G. Gratzner and A. Darabant designed this study and provided feedback on the manuscript. A. Schindlbacher supervised the overall work, designed the experiment and critically revised the manuscript.

7. Data Availability

All relevant soil respiration, soil moisture, and soil temperature data from the field and the laboratory incubations are freely available from open source figshare repository (<https://figshare.com>) via <https://dx.doi.org/10.6084/m9.figshare.4239122>

8. Acknowledgements

We are highly grateful to the management and staff of the Ugyen Wangchuck Institute for Conservation and Environment, Bumthang for supporting the study. This study was part of the work package I of the BC-CAP project (Climate Change Adaptation potentials of forests in Bhutan –Building human capacities and knowledge base) jointly implemented by the Department of Forest and Park Services, Bhutan and University of Natural Resources and Life Sciences (BOKU), Austria with funding by the Austrian Ministry of Agriculture, Forestry, Environment and Water Management.

9. Disclaimer

The views and opinions expressed in this article are those of the authors and do not necessarily reflect the views of any institutions of the Royal Government of Bhutan or the Government of Austria.

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Table 1 Site characteristics of the two studied forests

Parameter	Mixed forest	Broadleaved forest
Elevation (m)	3260	2460
Latitude	27°28' 00" N	28°28'51.06" N
Longitude	89°44'30.79" E	89°51'27.73" E
Annual Precipitation 2015 (mm)	1167	1120
Mean Air Temperature 2015 (°C)	7.8	12.0
Dominant Overstorey species	<i>Tsuga dumosa</i> (59.5%) <i>Quercus semecarpifolia</i> (29.3%) <i>Picea spinulosa</i> (6.3%) <i>Abies densa</i> (4.1%) <i>Taxus baccata</i> (0.3%)	<i>Quercus lanata</i> (63.5%) <i>Quercus griffithii</i> (29.6%)
Dominant Understorey species	<i>Ilex dipreyana</i> (0.2%) <i>Rhododendron arboreum</i> (0.1%)	<i>Symplocos sp.</i> (0.8%) <i>Lyonia ovalifolia</i> , (2.2%) <i>Rhododendron arboreum</i> (3.4%)
Tree density (No. ha ⁻¹)	364 ± 50	569 ± 19
Mean Tree height (m) Overstorey	24.4 ± 2.1	23.6 ± 1.4
Mean Tree Height (m) Understorey	7.8 ± 3.5	9.8 ± 0.4
Mean DBH (cm) Overstorey	50.7 ± 5.8	37.8 ± 2.3
Mean DBH (cm) Understorey	13.8 ± 1.4	16.1 ± 0.9
Tree basal area (m ² ha ⁻¹)	77.5 ± 4.6	39.9 ± 4.4
Standing volume (m ³ ha ⁻¹)	1066 ± 2.3	464 ± 25
Soil organic C (t ha ⁻¹) 0-30 cm	142.0 ± 25.4	90.1 ± 9.0
Soil organic C (t ha ⁻¹) 0-10 cm	61.9 ± 5.3	55.5 ± 6.9
Soil organic C (t ha ⁻¹) 10-30 cm	80.1 ± 8.0	34.6 ± 2.4
Soil N (t ha ⁻¹) 0-30 cm	7.4 ± 0.5	4.3 ± 0.4
Soil N (t ha ⁻¹) 0-10 cm	3.2 ± 0.2	2.4 ± 0.3
Soil N (t ha ⁻¹) 10-30 cm	4.2 ± 0.4	1.9 ± 0.1
pH (0-10 cm)	5.2 ± 0.1	5.0 ± 0.1
Bulk density (g cm ⁻³) 0-10 cm	0.61 ± 0.02	0.61 ± 0.01
Fine Root biomass (t C ha ⁻¹) 0-30 cm	2.3 ± 0.3	3.2 ± 0.5
Litter input (t C ha ⁻¹ yr ⁻¹)	3.5 ± 0.10	3.4 ± 0.03

*All stand and soil parameters are expressed as the mean ± standard error.

Layer	Incubation	Moisture (vol.%)	Rh ₁₀ ($\mu\text{mol CO}_2 \text{ kg C}^{-1} \text{ s}^{-1}$)	Q ₁₀
<u>Broadleaved</u>				
Litter	1	46 \pm 1	0.58 \pm 0.04	2.22 \pm 0.09
Mineral	1	35 \pm 2	0.22 \pm 0.03	2.31 \pm 0.06
Mineral	2	dry (10 \pm 1)	0.10 \pm 0.01	1.54 \pm 0.11a
Mineral	2	interm. (33 \pm 1)	0.14 \pm 0.02	2.39 \pm 0.22b
Mineral	2	wet (56 \pm 1)	0.18 \pm 0.03	2.12 \pm 0.25ab
<u>Mixed</u>				
Litter	1	46 \pm 2	1.05 \pm 0.24	1.93 \pm 0.06
Mineral	1	33 \pm 1	0.16 \pm 0.02	2.25 \pm 0.06
Mineral	2	dry (9 \pm 1)	0.08 \pm 0.01	1.55 \pm 0.18a
Mineral	2	interm. (29 \pm 1)	0.10 \pm 0.01	2.63 \pm 0.39b
Mineral	2	wet (51 \pm 1)	0.13 \pm 0.01	2.06 \pm 0.10ab

Table 2. Basal respiration rates (Rh₁₀) and temperature sensitivity (Q₁₀) of litter and mineral soil (0-10 cm depth) samples derived from laboratory incubations. Incubations took place initially after sampling (Incubation 1) using a set of 3 samples per plot (6 plots per site). Subsequently, sets were split and the moisture sensitivity of Rh was tested (Fig. 2d). Subsequent to moisture incubations, the different subsets (Dry, Interm., Wet) were re-incubated to test temperature sensitivities at different moisture contents (Incubation 2). The time-lag between Incubation 1 and Incubation 2 was approximately 10 weeks. Different letters indicate significant differences in Q₁₀ between soil moisture levels of the mineral soil samples.

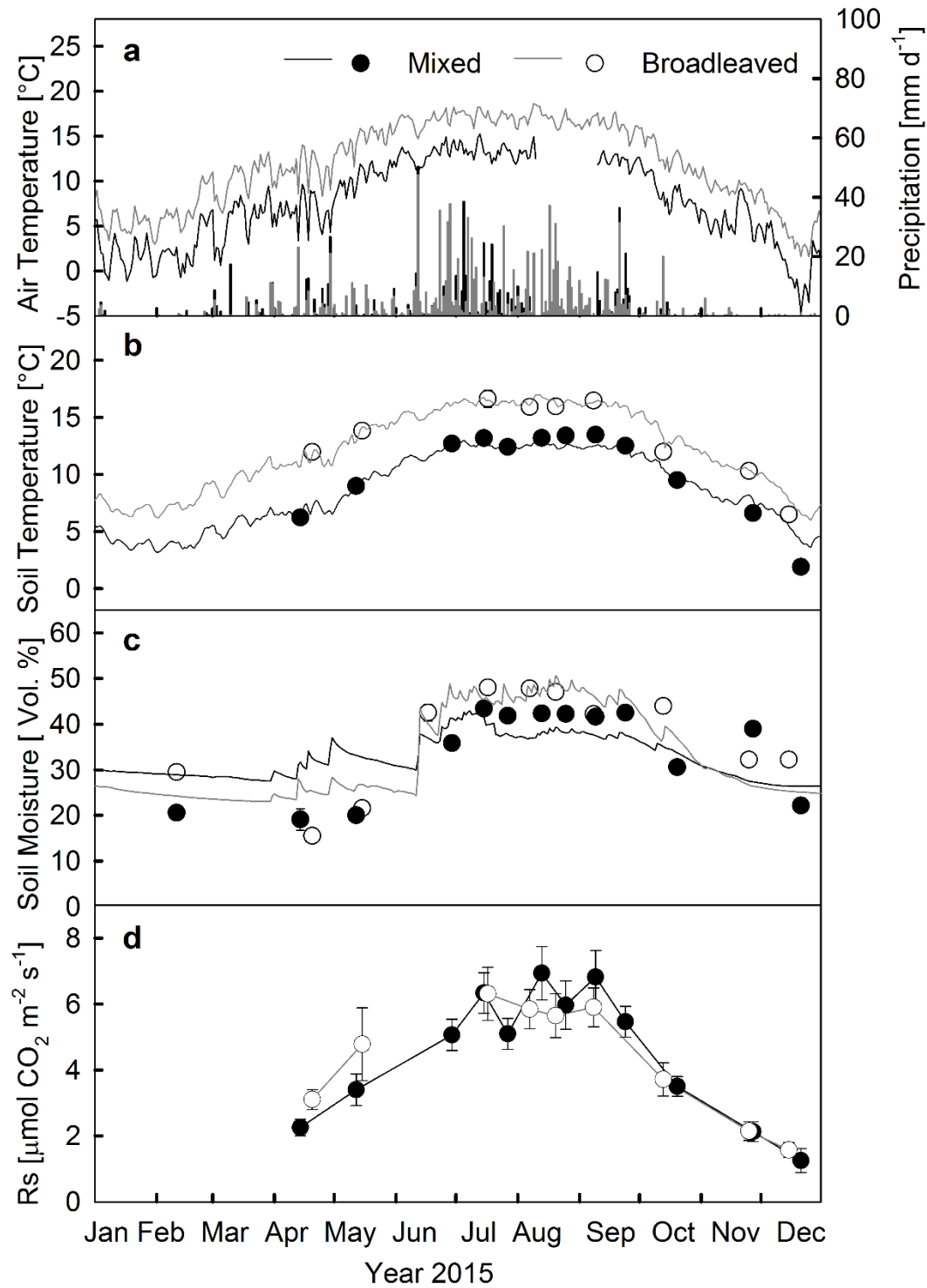


Figure 1. Seasonal course of air temperature and precipitation (a), soil temperature (b), volumetric soil water content (c), and soil respiration (d) measured at a mixed and a broadleaved forest in Bhutan Himalayas in 2015. Circles represent daily mean values of manual measurements. Solid lines (a, b, c) represent daily mean values of continuous measurements. Error bars indicate standard error of the mean.

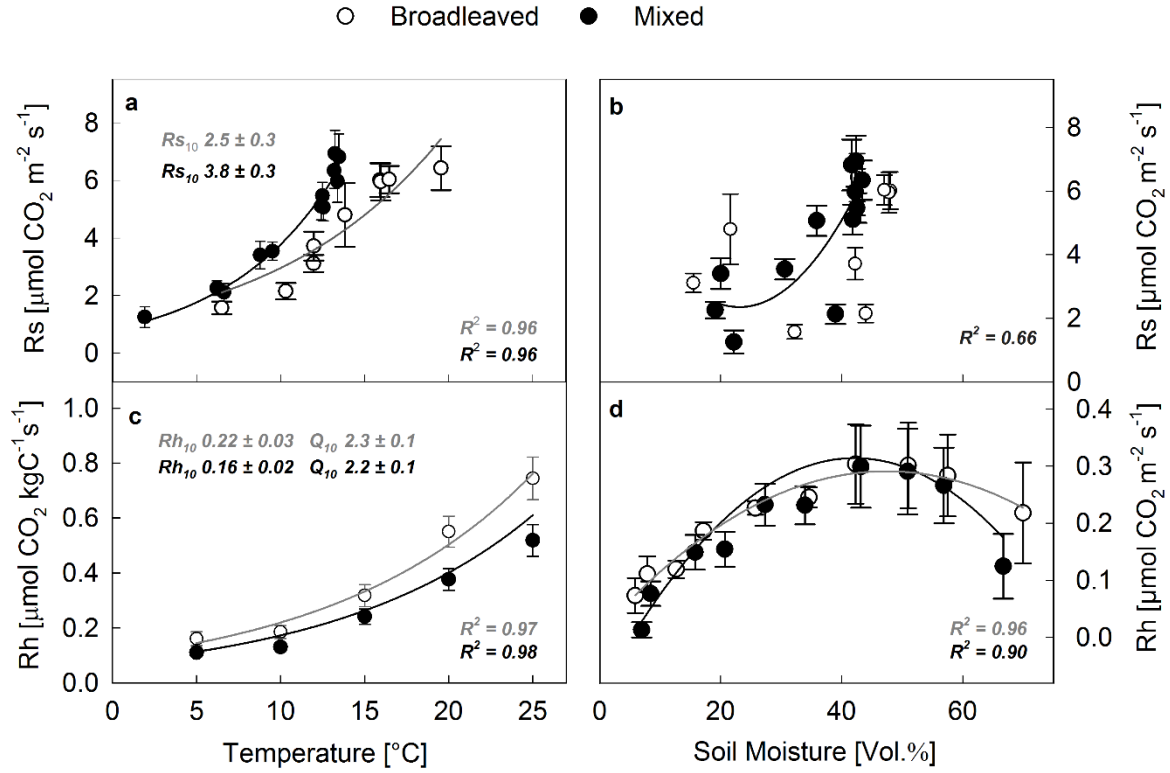


Figure 2. (a) Relationship between soil CO₂ efflux (R_s) and soil temperature, and (b) R_s and soil moisture (vol.%) at a broadleaved and a mixed forest in Bhutan Himalayas. (c) Relationship between heterotrophic soil respiration (R_h) and soil temperature, and (d) R_h and soil moisture (vol. %) as determined during a laboratory incubation. A temperature response was fitted with an exponential function (Eq. (1)) and a moisture response was fitted with a polynomial function (Eq. (3)). Error bars represent standard error of the mean (SE). Basal respiration rates at 10 $^{\circ}\text{C}$ (R_{s10} , R_{h10}) and temperature sensitivity of R_h (Q_{10}) are given (mean \pm SE).

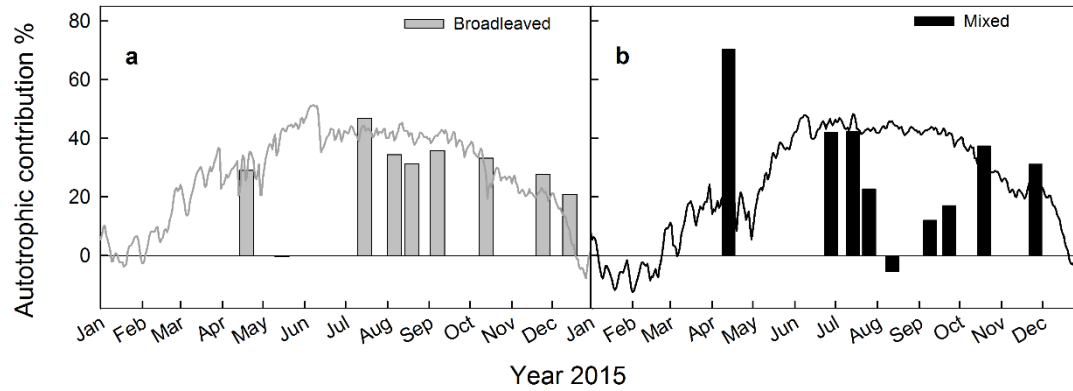


Figure 3: Contribution of autotrophic soil respiration (R_a) to total soil CO_2 efflux (R_s) at a (a) broadleaved and (b) mixed forest in Bhutan Himalayas. Autotrophic contribution was derived from the differences between R_s measured at control and trenched plots (bars) and from the differences between modelled R_s and heterotrophic soil respiration rates (lines), respectively.

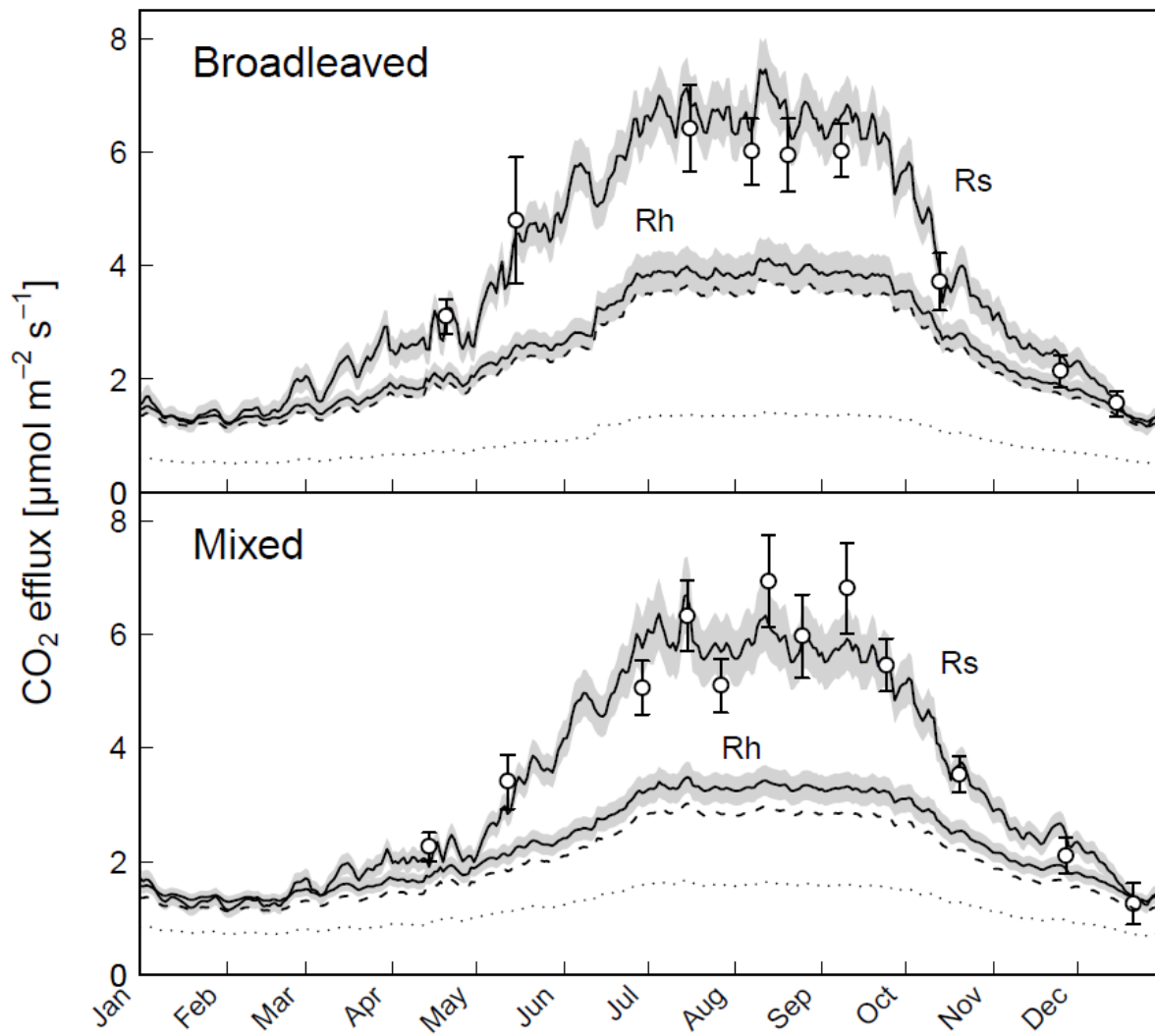


Figure 4. Seasonal course of modelled soil CO₂ efflux (Rs) and heterotrophic soil respiration rates (Rh) at a broadleaved and mixed forest in Bhutan Himalayas in 2015. Open circles are measured Rs rates. Error bars and shaded areas represent standard error of the daily mean. Dashed and dotted lines indicate the CO₂ contributions of litter and mineral soil layers to Rh. The area between the full line (total Rh) and the dashed line represents the contribution from litter, the area between dashed and dotted line represents the contribution of the topsoil (0-10 cm), and the area below the dotted line represents the contribution from the 10-30 cm mineral soil layer.