# Soil $CO_2$ 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 $CO_2$ 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 $yr^{-1}$ broadleaved; 12.8 ± 1.0 t C $yr^{-1}$ 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. A 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 $CO_2$ efflux, autotrophic soil respiration, heterotrophic soil respiration, incubation, temperature sensitivity, moisture sensitivity

## 1 Introduction

Carbon dioxide ($CO_2$) efflux from soil (= soil respiration; Rs) is one of the major fluxes in the global C cycle, affects atmospheric $CO_2$ 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 sink or source 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 $CO_2$, 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 km$^2$ 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 m$^2$ 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 m$^2$ 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 m$^2$ (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 10-30 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 $CO_2$ 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 $CO_2$ 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 $CO_2$ 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 $cm^3$ 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 $CO_2$ efflux (= Rh) was measured using a fully automated incubation system. During incubation, samples were put into 2 l containers and their $CO_2$ efflux was determined by a dynamic closed – chamber system (Pumpanen et al., 2009). For $CO_2$ 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 $CO_2$ enrichment. Wet tissues were put into containers in order to prevent samples from drying out during incubations; moisture loss was thereby negligible (< 2 vol. %). $CO_2$ concentration within connected containers were measured for 6 minutes with a recording interval of 10 sec. Rates of $CO_2$ efflux were calculated from the headspace $CO_2$ 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 $\mu mol\ CO_2\ kg\ C^{-1}\ s^{-1}$.

### 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):

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

where *R* (µmol $CO_2$ $m^{-2}$ $s^{-1}$) is the measured Rs, T (°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 ($Rs_{10}$) 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 °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 ($Rh_{10}$) were calculated for each site. Temperature sensitivity ($Q_{10}$) of Rh was calculated as follows:

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

where $Q_{10}$ is the factor by which Rh changes at a temperature change of 10 °C, and $\beta_1$ 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:

$$R = \beta_0 + \beta_1 \cdot VWC + \beta_2 \cdot VWC^2 \tag{3}$$

where *R* is the measured $CO_2$ efflux from soil samples (Rh), $\beta_i$ 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 Ra and Rh in the field. In a first approach, we used the trenching data, assuming that the $CO_2$ efflux from the trenched plots represented solely Rh, while the $CO_2$ efflux from adjacent control plots represented Rs, and accordingly, the difference between trenched and control plot $CO_2$ efflux represented Ra. 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 Rh derived during laboratory incubation together with field soil C stocks and field climate data. This allowed an alternative way to estimate the contribution of Rh 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 Rh 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 Rh from the mineral soil in 10 – 30 cm depth. Predicted Rh rates (µmol $CO_2$ kg $C^{-1}$) were multiplied by the C stocks (kg C $m^{-2}$) of the respective soil layer. Annual litter input (Table 1) was used as a proxy for litter C stocks. This procedure enabled us to upscale Rh to the whole soil profile in the field (Kutsch et al., 2010). To account for a moisture response as well, predicted Rh rates were also corrected for soil moisture conditions in the field. For that, model parameters derived from Eq. (3) were used to calculate Rh 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 Rh 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 ~ 4°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 $m^3$ $ha^{-1}$, at the mixed and broadleaved forest, respectively. Mineral soil organic C stocks down to 30 cm soil depth were 142 and 90 t $ha^{-1}$ 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 ± 0.7 µmol $CO_2$-C $m^{-2}$ $s^{-1}$, mixed: 4.0 ± 0.6 µmol $CO_2$-C $m^{-2}$ $s^{-1}$) but basal respiration rates ($Rs_{10}$) were higher at the mixed forest (Fig. 2a). Cumulative annual Rs were 14.3 ± 0.5 t C $ha^{-1}$ for the broadleaved and 13.0 ± 0.5 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 ± 1.2 t C $ha^{-1}$, broadleaved and 12.8 ± 1.0 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 Ra and Rh to Rs, 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 Rh and Ra 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 Rh was in the range of field Rs during the cold season (Fig. 3). The gap between Rh and Rs became larger during the growing season, implying highest contribution of Ra during the warm monsoon months at both sites (Fig. 3 and 4). The strong temporal fluctuation in sources (Ra, Rh) which was obtained from trenching was not confirmed by Rh model output (Fig. 3).

## 4. Discussion

Annual Rs of both forest sites (12.8 – 14.5 t C ha$^{-1}$) was in the range of values reported for similar ecosystems (10.1-13 t C ha$^{-1}$ (Dar et al., 2015); 10-12 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 ~ 140 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 ($Rs_{10}$) at the mixed forest explaining the comparatively high annual Rs rates at this cooler, higher altitude, site.

At both forests, Rs 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). Rs 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 Ra and simultaneously accelerating SOM decomposition by increased availability of labile C and rhizosphere priming (Kuzyakov, 2010; Bader and Cheng, 2007; Bengtson et al., 2012; Dijkstra and Cheng, 2007; Schindlbacher et al., 2009). Such processes would further increase Rs and Ra during the warm summer months. Our modelled Rh and Ra data suggests that this was also likely the case in the studied forests (significant increase in Ra contribution during the summer months; Fig. 3).

Our model generated wintertime Rh fluxes which were in the range of, or slightly below, Rs fluxes (Fig. 4). During frost periods, downward C-flux from the tree canopy is limited/disabled and the contribution of Ra to Rs is considered low during winter (Rey et al., 2002; Hanson et al., 2000). Our modelled wintertime (and overall) Rh therefore lay in a realistical range. There, however, is evidence that the contribution of Ra 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 Rh rather represents the upper edge of potential Rh 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 Rh and its temporal dynamics. C stocks from deeper soil layers (> 30 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 Rh 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. Although annual litter input should reflect the litter layer C in an ecosystem close to steady-state, litter input has temporal patterns and thereby affects litter decomposition dynamics. Such temporal patterns in litter input/decomposition were, however not reflected in our model. 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 $CO_2$ 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 $CO_2$ 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 $CO_2$ 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 $CO_2$ 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 $CO_2$ 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. Soil C input via aboveground litter-fall was almost similar between sites (~ 3.5 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. Assuming a mean fine root turnover time of one year (Brunner et al., 2013), the annual fine root litter input from 0-30 cm soil layer was ~ 2 and ~ 3 t C $ha^{-1}$ at the mixed and broadleaved forest, respectively. During 2015, the estimated soil C input (leaf litter and fine root litter of the top 30 cm soil) was, therefore, ~ 3 tons lower than the estimated annual gaseous soil C loss via Rh. This, however, is only a first rough approximation of the real soil C budget, since fine root turnover was not adequately determined and important C fluxes, such as for instance, DOC leaching, root litter production below 30 cm depth, and C input from vigorously growing herbaceous ground vegetation were not accounted for in our study, which primarily aimed at a detailed characterization of the soil $CO_2$ efflux.

## 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. Gratzer designed the larger-scale throughfall manipulation experiment. R. Jandl, G. Gratzer 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

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## 9. Disclaimer

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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 | *Tsuga dumosa (59.5%)*<br>*Quercus semecarpifolia (29.3%)*<br>*Picea spinulosa (6.3%)*<br>*Abies densa (4.1%)*<br>*Taxus baccata (0.3%)* | *Quercus lanata (63.5%)*<br>*Quercus griffithii (29.6%)* |
| Dominant Understory species | *Ilex dipreyana (0.2%)*<br>*Rhododendron arboreum (0.1%)* | *Symplocus sp. (0.8%)*<br>*Lyonia ovalifolia, (2.2%)*<br>*Rhododendron arboreum (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.%) | $Rh_{10}$ ($\mu$mol $CO_2$ kg $C^{-1}$ $s^{-1}$) | $Q_{10}$ |
|---|---|---|---|---|
| Broadleaved | | | | |
| Litter | 1 | 46±1 | 0.58±0.04 | 2.22±0.09 |
| Mineral | 1 | 35±2 | 0.22±0.03 | 2.31±0.06 |
| Mineral | 2 | dry (10±1) | 0.10±0.01 | 1.54±0.11a |
| Mineral | 2 | interm. (33±1) | 0.14±0.02 | 2.39±0.22b |
| Mineral | 2 | wet (56±1) | 0.18±0.03 | 2.12±0.25ab |
| Mixed | | | | |
| Litter | 1 | 46±2 | 1.05±0.24 | 1.93±0.06 |
| Mineral | 1 | 33±1 | 0.16±0.02 | 2.25±0.06 |
| Mineral | 2 | dry (9±1) | 0.08±0.01 | 1.55±0.18a |
| Mineral | 2 | interm. (29±1) | 0.10±0.01 | 2.63±0.39b |
| Mineral | 2 | wet (51±1) | 0.13±0.01 | 2.06±0.10ab |

**Table 2.** Basal respiration rates ($Rh_{10}$) and temperature sensitivity ($Q_{10}$) 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, Intem., 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 $Q_{10}$ between soil moisture levels of the mineral soil samples.

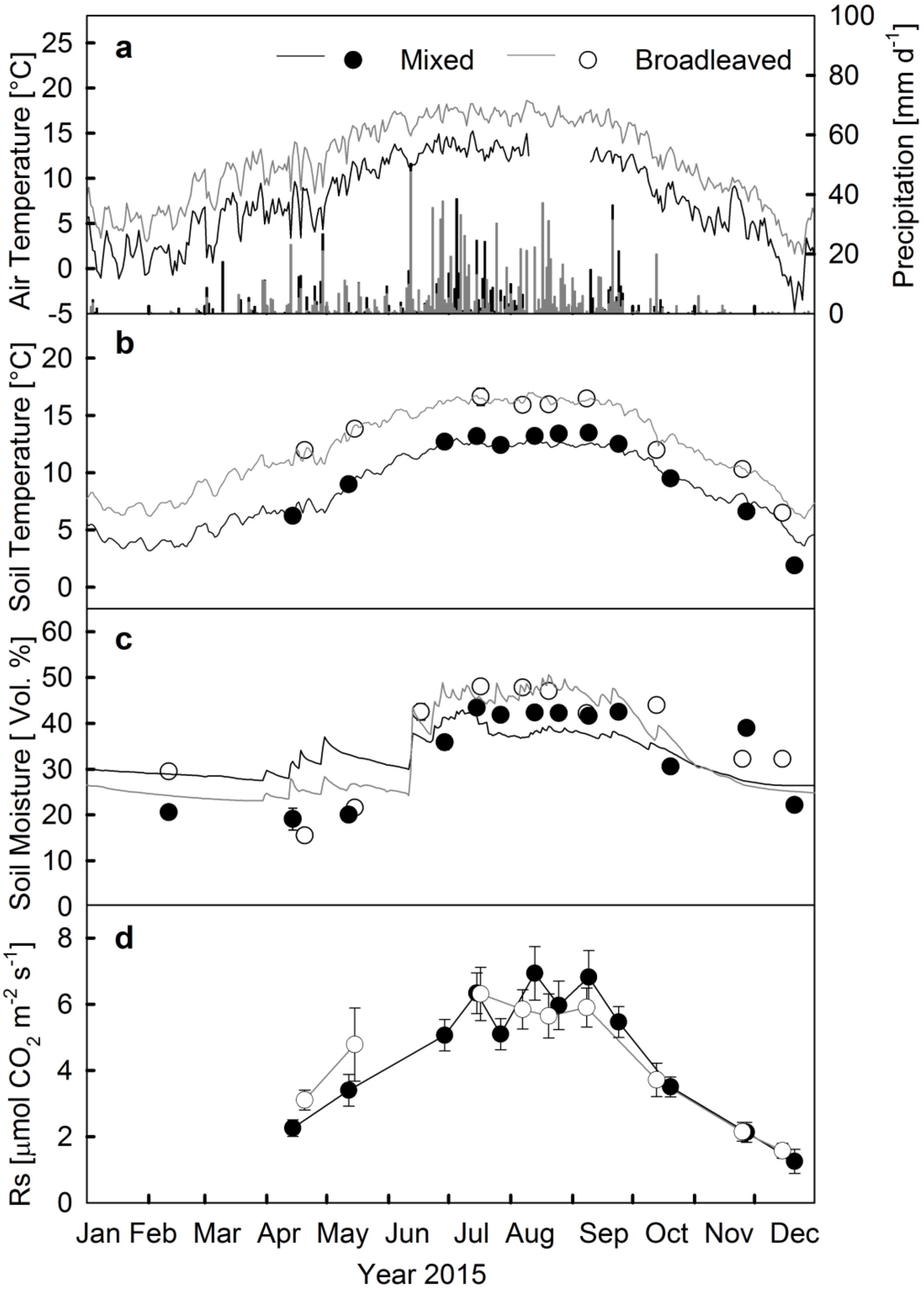

**Figure 1**. Seasonal course of air temperature and precipitation (a), soil temperature (b), volumetric soil water content (c), and soil respiration (d) measured at a mixed and a broadleaved forest in Bhutan Himalayas in 2015. Circles represent daily mean values of manual measurements. Solid lines (a,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

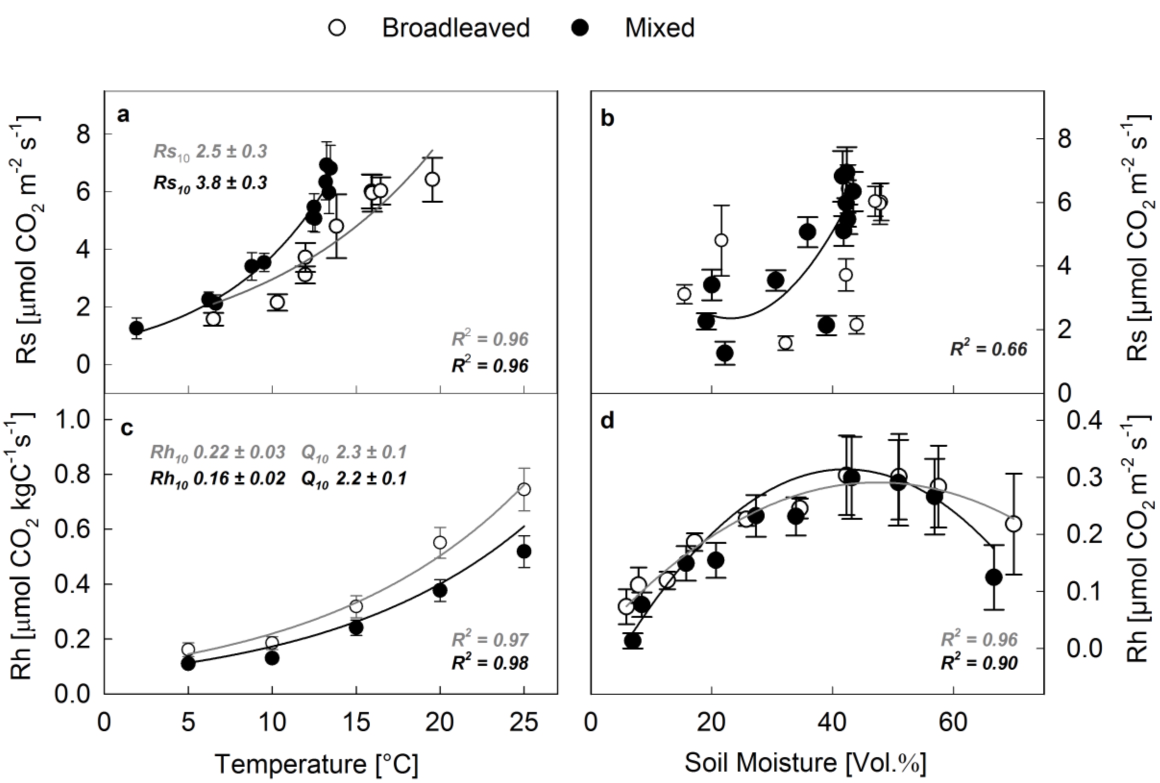

**Figure 2. (a)** Relationship between soil CO$_2$ efflux (Rs) and soil temperature, and **(b)** Rs and soil moisture (vol.%) at a broadleaved and a mixed forest in Bhutan Himalayas. **(c)** Relationship between heterotrophic soil respiration (Rh) and soil temperature, and **(d)** Rh and soil moisture (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 °C ($Rs_{10}$, $Rh_{10}$) and temperature sensitivity of Rh ($Q_{10}$) are given (mean ± SE).

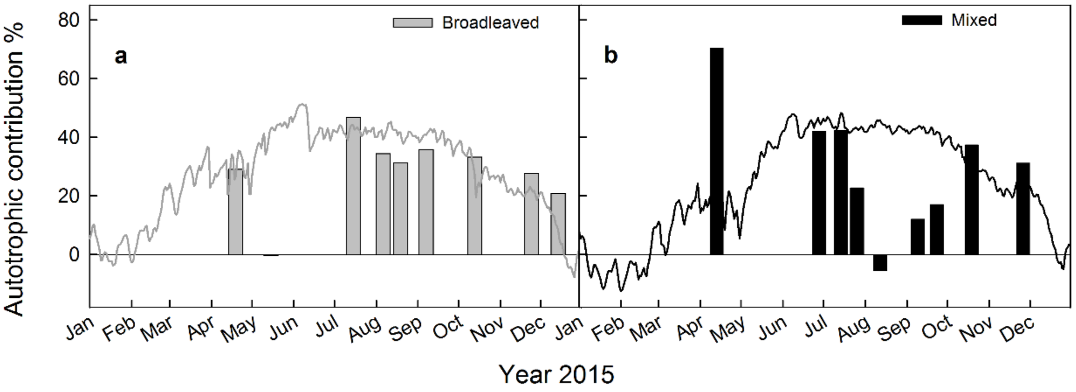

**Figure 3:** Contribution of autotrophic soil respiration (Ra) to total soil $CO_2$ efflux (Rs) at a **(a)** broadleaved and **(b)** mixed forest in Bhutan Himalayas. Autotrophic contribution was derived from the differences between Rs measured at control and trenched plots (bars) and from the differences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

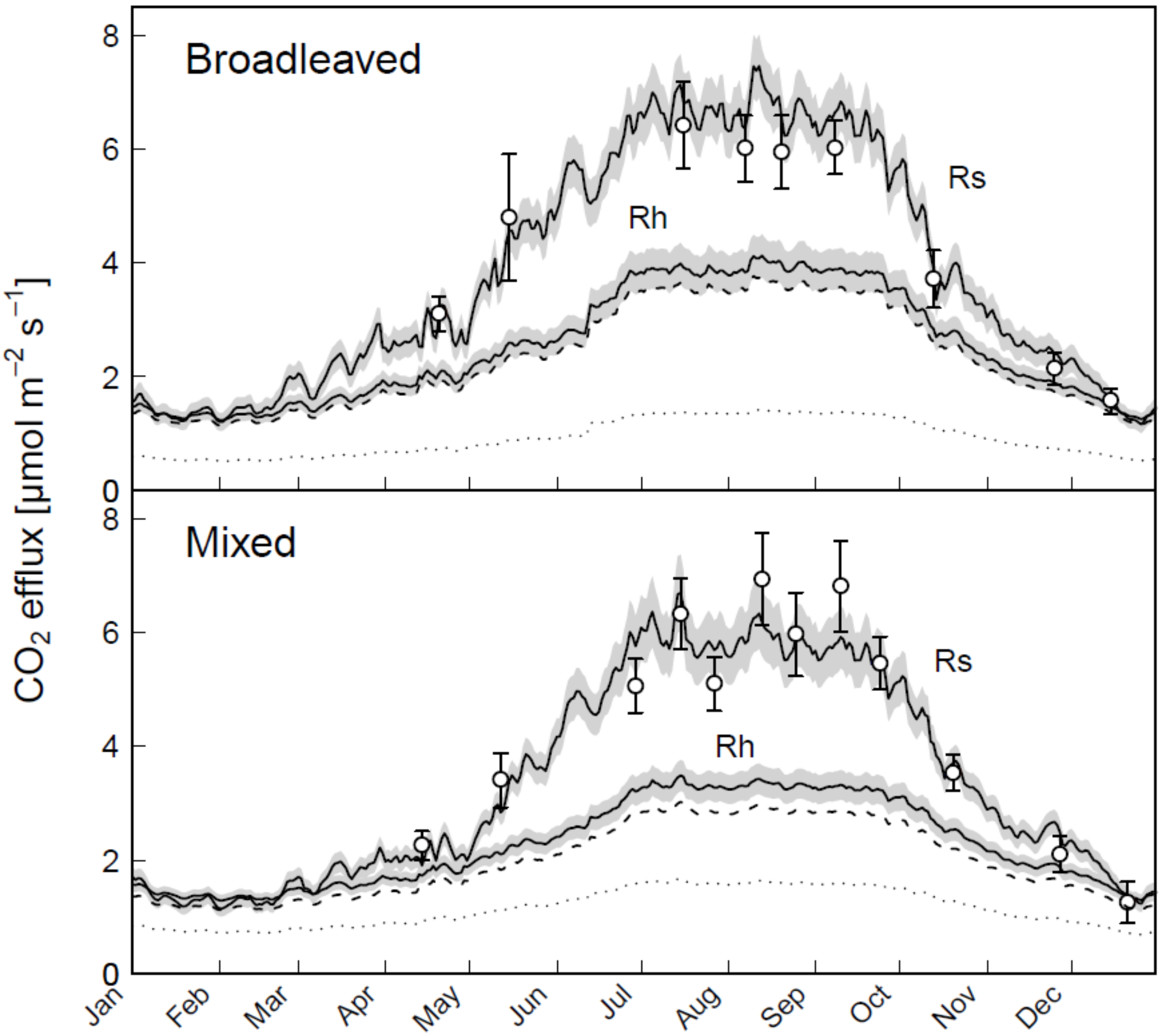

**Figure 4.** Seasonal course of modelled soil $CO_2$ efflux (Rs) and heterotrophic soil respiration rates (Rh) at a broadleaved and mixed forest in Bhutan Himalayas in 2015. Open circles are measured Rs rates. Error bars and shaded areas represent standard error of the daily mean. Dashed and dotted lines indicate the $CO_2$ 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.