Associate Editor 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 quiet 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).

Soil CO_2 efflux from two mountain forests in the Eastern Himalayas Bhutan: components and controls

Norbu Wangdi*[1,2,], Mathias Mayer*[1], Mani Prasad Nirola[1,4], Norbu Zangmo[2], Karma Orong[2], Iftekhar Uddin Ahmed[1], Andras Darabant[1], Robert Jandl [3], Georg Gratzer[1], Andreas Schindlbacher[3]

[1]Institute of Forest Ecology, University of Natural Resources and Life Sciences, 1180 Peter Jordan Strasse, Vienna, Austria

[2] Ugyen Wangchuck Institute for Conservation and Environmental Research, Department of Forests and Park Services Lamai Goempa, Bumthang, Bhutan

[3]Federal Research and Training Centre for Forests, Natural Hazards and Landscape – BFW, A-1131 Vienna, Austria

[4]National Biodiversity Center, Ministry of Agriculture and Forests, Thimphu, Bhutan

*These authors contributed equally to this work.

Correspondence to: Norbu Wangdi (norwangs@gmail.com)

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 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 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 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 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 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 ($\leq$ 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

6

69   sorting (live roots and necromass), roots were dried at 70 °C to constant mass before weighing dry biomass.

70   Contribution of fine root C was estimated as 50 % of the plant tissue.

71   Rs was measured at both sites once every three weeks from April 2015 to December 2015 at 10 randomly chosen

72   plots (n = 10) at each. To cover the within-plot variability, Rs was measured at four positions within each plot (total

73   40 positions per site). We used a portable infrared gas analyzer (EGM-4, PP-Systems, Amesbury, USA) with an

74   attached soil respiration chamber (SRC-1, PP-Systems, Amesbury, USA) for Rs measurements. Prior to

75   measurements (March 2015), we installed permanent collars (total height 5 cm, 2-3 cm inserted into the soil,

76   diameter 10 cm) at each plot which served as a base for Rs measurements. Rs was estimated by a linear fit to the

77   increasing headspace CO_2 concentration over time (chamber closure time 90 seconds). A soil respiration

78   measurement campaign lasted for ~ 5 h at each site. Measurement order among plots and collars was fully random

79   to avoid bias from temporal variations in Rs.

80   We installed two trenching plots at each site in April 2014 (1 yr prior soil efflux CO_2 measurements) to estimate the

81   relative contributions of Ra and Rh. Trenches (1.5 x 1.5 m) were dug to ~ 1 m depth, and all roots within the

82   trenches were cut. The trenches were sealed with double layered plastic foil in order to restrict tree root ingrowth.

83   Adjoining to each trenched plot, a corresponding control plot of the same size was established. Each trenched and

84   control plot hosted three collars for Rs measurements. We measured soil CO_2 efflux at trenched and corresponding

85   control plots after finishing regular Rs measurements (same day).

86   Volumetric soil water content (0-20 cm soil depth; (vol. %)) was measured in the center of each plot (Rs plots,

87   trenched plots, control plots) using a portable Field Scout TDR meter (Spectrum Technologies, Inc. Aurora, USA)

88   during Rs measurements. Soil temperature at 5 cm soil depth was measured with a handheld thermometer probe

89   (Hanna Instruments, Germany) at each Rs measurement location. Soil temperature and soil moisture were

90   measured continuously at soil profile pits (two pits per site) with five combined soil temperature-moisture sensors

91   (TM-5; Decagon Devices, Inc., Pullman, WA, USA) at soil depths ranging from 5 to 120 cm. Data was recorded at

92   15 min intervals on Decagon-EM50 data loggers (Decagon Devices, Inc., Pullman, WA, USA).

93

94   **2.3 Laboratory incubation**

95   About 500 g of mineral soil (0-10 cm depth) and approximately 250 g of forest floor litter were sampled at six

96   random locations (n = 6) at each site in mid-September 2015. The mineral soil was homogenized and sieved (2 mm

97   mesh) and stored at 4 °C at field moisture for one week prior to transport from Bhutan to Austria for further

98   processing. Forest floor litter was not sieved. Upon arrival in Austria, mineral soil samples were further divided

99   into 3 sub-samples to account for potential soil heterogeneity at individual sampling locations. Samples were filled

100   into 200 cm^3 stainless steel cylinders at approximate field bulk density (~ 0.5 g dry weight cm^{-3} for mineral soil; ~

101   0.1 g dry weight cm^{-3} for forest floor). In total, we incubated 36 sub-samples (cylinders) for mineral soil and 12

102   sub-samples for the forest floor litter. Filled cylinders were kept at 4 °C for 5 days for equilibration before

103   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 μmol 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

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

142 $$R = \beta_0 \cdot e^{(\beta_1 \cdot T)} \tag{1}$$

144 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
145 parameters. Equation (1) was fitted to the daily averages of each site as well as to the individual plot data. Basal
146 respiration rates at 10°C soil temperature (Rs_{10}) were subsequently calculated (using Eq. (1)) for each site. One
147 sampling date (2015 Jul 16) was excluded from this analysis because heavy rain occurred during measurements.
148 The relationship between Rs and soil moisture was tested by fitting a polynomial function obtained from lab
149 incubation (see further below). Cumulative annual Rs of both sites and both years were calculated by linear
150 interpolation of field Rs between measurement dates of each individual plot (the area beneath the curves in Fig. 1
151 d). In addition, model parameters of Eq. (1), together with daily field soil temperatures at 5 cm depth were used to
152 calculate a projected daily field Rs. To account for a spatial variation in soil temperature, continuously measured
153 data were adjusted to discontinuously measured plot-data by linear modelling. Cumulative annual Rs rates were
154 calculated by averaging the summed-up daily plot Rs values.

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

160 $$Q_{10} = e^{(10 \cdot \beta_1)} \tag{2}$$

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

166 $$R = \beta_0 + \beta_1 \cdot VWC + \beta_2 \cdot VWC^2 \tag{3}$$

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

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

177 In a second approach, we applied the response functions of Rh derived during laboratory incubation together with
178 field soil C stocks and field climate data. This allowed an alternative way to estimate the contribution of Rh in the
179 field (Gough et al., 2007; Kutsch et al., 2010). Model parameters derived from Eq. (1) together with continuously
180 measured temperature data from 5 cm soil depth were used to model daily Rh from the litter and from the mineral
181 soil in 0 – 10 cm depth respectively. Model parameters for mineral soils together with continuous measurements of
182 soil temperature in 20 cm depth were further used to model daily Rh from the mineral soil in 10 – 30 cm depth.
183 Predicted Rh rates (μmol CO_2 kg C^{-1}) were multiplied by the C stocks (kg C m^{-2}) of the respective soil layer. We
184 used the litter Q_{10} together with continuous temperature at 5 cm soil depth to model daily Rh from the litter layer.
185 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
186 rough litter assessment in March 2015 showed that litter stocks were in a similar range as the annual litter input at
187 both sites. This procedure enabled us to upscale Rh to the whole soil profile in the field (Kutsch et al., 2010). To
188 account for a moisture response as well, predicted Rh rates were also corrected for soil moisture conditions in the
189 field. For that, model parameters derived from Eq. (3) were used to calculate Rh rates at actual moisture conditions
190 in the field (from continuous moisture data) and at initial moisture conditions of the soil samples during incubation
191 (mixed forest: 33 vol. %, broadleaved forest: 35 vol. %, litter: 46 vol. %); their relative difference was subsequently
192 used to correct Rh rates predicted with Eq. (1). Since litter soil moisture was not regularly measured in the field, we
193 applied the same moisture parameters and continuous soil moisture records as for mineral soil (0-10 cm). The R
194 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).

229   Trenching plots indicated an average autotrophic and heterotrophic contribution of 29 and 27 % and 71 and 73 % at

230   the mixed and broadleaved forest sites during the whole 2015 season, respectively (Fig. 3). The contribution of Ra

231   and Rh to Rs, obtained by trenching, showed high temporal variability and strong fluctuations between individual

232   measurement dates at the mixed forest site (Fig. 3).

233   The modelling approach yielded annual heterotrophic contributions of 67 % in mixed forest and 63 % in

234   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

235   C ha^{-1} at the broadleaved forest respectively. Modelled Rh was in the range of field Rs during the cold season

236   (Fig. 3). The gap between Rh and Rs became larger during the growing season, implying highest contribution of Ra

237   during the warm monsoon months at both sites (Fig. 3 and 4). The strong temporal fluctuation in sources (Ra, Rh)

238   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. Soil C input via aboveground litter-fall was almost identical 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.

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 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. However, there 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.

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

290 In contrast to the modelling approach, trenching was applied as an attempt to estimate Ra *in situ*. The trenching
291 method, although highly invasive, was shown to provide reasonable estimates of Ra for several forest types
292 (Hanson et al., 2000; Subke et al., 2006). Trenching suggested slightly higher contributions of Rh at both sites
293 (average 72 % both sites) but showed much stronger temporal variations in Rh/Ra, especially at the mixed forest
294 (Fig. 3). Trenching has several drawbacks. Soil moisture is usually higher in trenched plots because water uptake
295 by roots is interrupted. This bias was accounted for as we used the moisture response function (Eq. (3)) for
296 correction. However, trenched fine roots can maintain respiration for a comparatively long time after cutting (Lee
297 et al., 2003) and when fine roots finally die, their decomposition can add to the soil CO_2 efflux from the trenched
298 plots (Hanson et al., 2000). Assuming a dead fine root mass loss of roughly one-third during the second year after
299 trenching (Díaz-Pinés et al., 2010) and accounting for the corresponding effects on soil CO_2 efflux (additional
300 efflux ~ 1 t C ha^{-1}), the estimated annual contribution of Rh decreases to ~ 65 % of Rs, which is in the range of our
301 modelling results. Potential effects of root decomposition, however, do not explain the atypically strong temporal
302 variation in Ra at the mixed forest site. Soil CO_2 efflux from trenched plots was similar or even higher than from
303 corresponding control plots, suggesting a steep decrease in Ra between July and September (Fig. 3). We do not
304 have a straightforward explanation for this pattern. Probably we did not trench deep enough and missed a larger
305 proportion of roots which added to the summertime CO_2 efflux from trenched plots. A further explanation could be
306 altered nutrient availability to decomposers in the trenched plots. In trenched plot soil, roots do not compete any
307 more for nutrients, potentially increasing nutrient availability to decomposers. This could accelerate SOM
308 decomposition and soil CO_2 efflux. In summary, trenching showed a less clear outcome at the two study sites when
309 compared to other forests. Therefore, other methods, such as girdling or isotope labeling might be alternatively
310 applied in the forest types studied.

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

317 **5. Conclusion**
318

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

326

327 **6. Author contribution**
328

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

335

341

350

351 **9. Disclaimer**
352

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

355 **References**

356

357   Adhikari, B., Rawat, Y., and Singh, S.: Structure and function of high altitude forests of central Himalaya I. Dry
358   matter dynamics, Ann. Bot., 75, 237-248, 1995.

359   Bader, N. E., and Cheng, W.: Rhizosphere priming effect of *Populus fremontii* obscures the temperature sensitivity
360   of soil organic carbon respiration, Soil Biol. Biochem., 39, 600-606, 2007.

361   Bengtson, P., Barker, J., and Grayston, S. J.: Evidence of a strong coupling between root exudation, C and N
362   availability, and stimulated SOM decomposition caused by rhizosphere priming effects, Ecology and Evolution, 2,
363   1843-1852, 10.1002/ece3.311, 2012.

364   Bisht, V. K., Nautiyal, B. P., Kuniyal, C. P., Prasad, P., and Sundriyal, R. C.: Litter Production, Decomposition,
365   and Nutrient Release in Subalpine Forest Communities of the Northwest Himalaya, J. Ecosyst., 2014, 2014.

366   Bolstad, P., Davis, K., Martin, J., Cook, B., and Wang, W.: Component and whole-system respiration fluxes in
367   northern deciduous forests, Tree Physiol., 24, 493-504, 2004.

368   Bond-Lamberty, B., and Thomson, A.: A global database of soil respiration data, Biogeosciences, 7, 1915-1926,
369   10.5194/bg-7-1915-2010, 2010.

370   Buchmann, N.: Biotic and abiotic factors controlling soil respiration rates in Picea abies stands, Soil Biology and
371   Biochemistry, 32, 1625-1635, 2000.

372   Cook, E. R., Anchukaitis, K. J., Buckley, B. M., D'Arrigo, R. D., Jacoby, G. C., and Wright, W. E.: Asian
373   monsoon failure and megadrought during the last millennium, Science, 328, 486-489, 2010.

374   Cox, P. M., Betts, R. A., Jones, C. D., Spall, S. A., and Totterdell, I. J.: Acceleration of global warming due to
375   carbon-cycle feedbacks in a coupled climate model, Nature, 408, 184-187, 2000.

376   Dar, J. A., Ganie, K. A., and Sundarapandian, S.: Soil CO2 efflux among four coniferous forest types of Kashmir
377   Himalaya, India, Environmental monitoring and assessment, 187, 715, 10.1007/s10661-015-4927-2, 2015.

378   Davidson, E. A., and Janssens, I. A.: Temperature sensitivity of soil carbon decomposition and feedbacks to
379   climate change, Nature, 440, 165-173, 2006.

380   de Wit, H. A., Palosuo, T., Hylen, G., and Liski, J.: A carbon budget of forest biomass and soils in southeast
381   Norway calculated using a widely applicable method, For. Ecol. Manage., 225, 15-26, 2006.

382   Datta, R., Vranová, V., Pavelka, M., Rejšek, K., Formánek, P.: Effect of soil sieving on respiration induced by low-
383   molecular-weight substrates, International Agrophysics, 28, 119-124, 2014.

384   Díaz-Pinés, E., Schindlbacher, A., Pfeffer, M., Jandl, R., Zechmeister-Boltenstern, S., and Rubio, A.: Root
385   trenching - A useful tool to estimate autotrophic soil respiration? Case study in an Austrian mountain forest,
386   European Journal of Forest Research, 129, 101-109, 2010.

387   Dijkstra, F. A., and Cheng, W.: Interactions between soil and tree roots accelerate long-term soil carbon
388   decomposition, Ecology Letters, 10, 1046-1053, 10.1111/j.1461-0248.2007.01095.x, 2007.

389   Dixon, R. K., Solomon, A., Brown, S., Houghton, R., Trexier, M., and Wisniewski, J.: Carbon pools and flux of
390   global forest ecosystems, Science, 263, 185-190, 1994.

391   Dorji, T., Odeh, I., and Field, D.: Vertical Distribution of Soil Organic Carbon Density in Relation to Land
392   Use/Cover, Altitude and Slope Aspect in the Eastern Himalayas, Land, 3, 1232-1250, 10.3390/land3041232,
393   2014a.

394   Dorji, T., Odeh, I. O., Field, D. J., and Baillie, I. C.: Digital soil mapping of soil organic carbon stocks under
395   different land use and land cover types in montane ecosystems, Eastern Himalayas, For. Ecol. Manage., 318, 91-
396   102, 2014b.

397   FAO: Global Forest Resources Assessment :Country Report -Bhutan, Food and Agriculture Organization of the
398   United Nations, Rome, 56, 2010.

399   Fontaine, S., Barot, S., Barre, P., Bdioui, N., Mary, B., and Rumpel, C.: Stability of organic carbon in deep soil
400   layers controlled by fresh carbon supply, Nature, 450, 277-280,
401   http://www.nature.com/nature/journal/v450/n7167/suppinfo/nature06275_S1.html, 2007.

402   FRDD: Local Volume Table, Forest Resources Development Division, Department of Forests and Park Services,
403   Bhutan, 2005.

404   Frey, S. D., Lee, J., Melillo, J. M., and Six, J.: The temperature response of soil microbial efficiency and its
405   feedback to climate, Nature Climate Change, 3, 395-398, 2013.

406   FSI: Volume Equations for Forests of India, Nepal and Bhutan, Ministry of Environment and Forests, Govt. of
407   India, 249 pp., 1996.

408   Garkoti, S.: Estimates of biomass and primary productivity in a high-altitude maple forest of the west central
409   Himalayas, Ecol. Res., 23, 41-49, 2008.

410   Gough, C. M., Vogel, C. S., Harrold, K. H., George, K., and Curtis, P. S.: The legacy of harvest and fire on
411   ecosystem carbon storage in a north temperate forest, Global Change Biology, 13, 1935-1949, 2007.

412   Grierson, A. J. C., and Long, D. G.: Flora of Bhutan, Royal Botanical Garden Edinburgh, Edinburgh, U.K., 1983.

413   Gu, L., Post, W. M., and King, A. W.: Fast labile carbon turnover obscures sensitivity of heterotrophic respiration
414   from soil to temperature: a model analysis, Global Biogeochem. Cycles, 18, 2004.

415   Hanson, P., Edwards, N., Garten, C., and Andrews, J.: Separating root and soil microbial contributions to soil
416   respiration: a review of methods and observations, Biogeochemistry, 48, 115-146, 2000.

417   Hashimoto, S., Carvalhais, N., Ito, A., Migliavacca, M., Nishina, K., and Reichstein, M.: Global spatiotemporal
418   distribution of soil respiration modeled using a global database, Biogeosciences, 12, 4121-4132, 10.5194/bg-12-
419   4121-2015, 2015.

420   Janssens, I. A., Freibauer, A., Ciais, P., Smith, P., Nabuurs, G.-J., Folberth, G., Schlamadinger, B., Hutjes, R. W.,
421   Ceulemans, R., and Schulze, E.-D.: Europe's terrestrial biosphere absorbs 7 to 12% of European anthropogenic
422   CO_2 emissions, Science, 300, 1538-1542, 2003.

423   Kutsch, W. L., Persson, T., Schrumpf, M., Moyano, F. E., Mund, M., Andersson, S., and Schulze, E.-D.:
424   Heterotrophic soil respiration and soil carbon dynamics in the deciduous Hainich forest obtained by three
425   approaches, Biogeochemistry, 100, 167-183, 2010.

426   Kuzyakov, Y.: Priming effects: Interactions between living and dead organic matter, Soil Biology and
427   Biochemistry, 42, 1363-1371, http://dx.doi.org/10.1016/j.soilbio.2010.04.003, 2010.

428   Laumans, P.: Height -Diameter Functions form a Country Level Site classification and Local Volume Table
429   Selection., UNDP/FAO Forest Resources Management and Institutional

430   Development Project,Thimphu, Bhutan, 1994.
431
432   Lee, M.-s., Nakane, K., Nakatsubo, T., and Koizumi, H.: Seasonal changes in the contribution of root respiration to
433   total soil respiration in a cool-temperate deciduous forest, in: Roots: The Dynamic Interface between Plants and the
434   Earth: The 6th Symposium of the International Society of Root Research, 11–15 November 2001, Nagoya, Japan,
435   edited by: Abe, J., Springer Netherlands, Dordrecht, 311-318, 2003.

436   Lee, N.-y., Koo, J.-W., Noh, N. J., Kim, J., and Son, Y.: Autotrophic and heterotrophic respiration in needle fir and
437   Quercus-dominated stands in a cool-temperate forest, central Korea, J. Plant Res., 123, 485-495, 10.1007/s10265-
438   010-0316-7, 2010.

439   Li, H.-j., Yan, J.-x., Yue, X.-f., and Wang, M.-b.: Significance of soil temperature and moisture for soil respiration
440   in a Chinese mountain area, Agric. For. Meteorol., 148, 490-503, 2008.

441   Liang, E., Wang, Y., Piao, S., Lu, X., Camarero, J. J., Zhu, H., Zhu, L., Ellison, A. M., Ciais, P., and Peñuelas, J.:
442   Species interactions slow warming-induced upward shifts of treelines on the Tibetan Plateau, Proceedings of the
443   National Academy of Sciences, 113, 4380-4385, 10.1073/pnas.1520582113, 2016.

444   Makkonen, K., and Helmisaari, H.-S.: Assessing fine-root biomass and production in a Scots pine stand–
445   comparison of soil core and root ingrowth core methods, Plant Soil, 210, 43-50, 1999.

446   Menon, A., Levermann, A., Schewe, J., Lehmann, J., and Frieler, K.: Consistent increase in Indian monsoon
447   rainfall and its variability across CMIP-5 models, Earth Syst. Dynam. Discuss., 4, 1-24, 10.5194/esdd-4-1-2013,
448   2013.

449   Pandey, R., Sharma, G., Singh, T., and Tripathi, S.: Factors influencing soi l CO2 efflux in a north eastern Indian
450   oak forest and plantation, Afr. J. Plant Sci., 4, 280-289, 2010.

451   Pinheiro, J. C., and Bates, D. M.: Mixed-Effects Models in S and S-Plus, Springer - Verlag, New York Berlin
452   Heidelberg, 530 pp., 2000.

453   Pumpanen, J., Longdoz, B., and Kutsch, W.: Field measurements of soil respiration: principles and constraints,
454   potentials and limitations of different methods, in: Soil Carbon Dynamics - An Integrated Methodology, edited by:
455   Kutsch, W., Bahn, M., and Heinemeyer, A., Cambridge University Press, Cambridge, 16-33, 2009.

456   Rana, S., Bargali, K., and Bargali, S.: Assessment of plant diversity, regeneration status, biomass and carbon stock
457   in a Central Himalayan cypress forest, Int. J. Biodivers. Conserv., 7, 321-329, 2015.

458   Reichstein, M., Rey, A., Freibauer, A., Tenhunen, J., Valentini, R., Banza, J., Casals, P., Cheng, Y., Grünzweig, J.
459   M., and Irvine, J.: Modeling temporal and large-scale spatial variability of soil respiration from soil water
460   availability, temperature and vegetation productivity indices, Global Biogeochem. Cycles, 17, 2003.

461   Rey, A., Pegoraro, E., Tedeschi, V., De Parri, I., Jarvis, P. G., and Valentini, R.: Annual variation in soil respiration
462   and its components in a coppice oak forest in Central Italy, Global Change Biol., 8, 851-866, 2002.

463   Schewe, J., and Levermann, A.: A statistically predictive model for future monsoon failure in India, Environ. Res.
464   Lett., 7, 044023, 2012.

465   Schickhoff, U.: The upper timberline in the Himalayas, Hindu Kush and Karakorum: a review of geographical and
466   ecological aspects, in: Mountain Ecosystems, Springer, 275-354, 2005.

467   Schild, A.: ICIMOD's Position on Climate Change and Mountain Systems, Mountain Research and Development,
468   28, 328-331, 10.1659/mrd.mp009, 2008.

469 Schindlbacher, A., Zechmeister-Boltenstern, S., Glatzel, G., and Jandl, R.: Winter soil respiration from an Austrian
470 mountain forest, Agricultural and Forest Meteorology 146, 205-215, 2007.

471

472 Schindlbacher, A., Zechmeister-Boltenstern, S., and Jandl, R.: Carbon losses due to soil warming: Do autotrophic
473 and heterotrophic soil respiration respond equally?, Global Change Biology, 15, 901-913, doi: 10.1111/j.1365-
474 2486.2008.01757.x, 2009.

475 Schlesinger, W. H., and Andrews, J. A.: Soil respiration and the global carbon cycle, Biogeochemistry, 48, 7-20,
476 2000.

477 Sharma, C. M., Baduni, N. P., Gairola, S., Ghildiyal, S. K., and Suyal, S.: Tree diversity and carbon stocks of some
478 major forest types of Garhwal Himalaya, India, For. Ecol. Manage., 260, 2170-2179, 2010a.

479 Sharma, E., Chettri, N., and Oli, K. P.: Mountain biodiversity conservation and management: a paradigm shift in
480 policies and practices in the Hindu Kush-Himalayas, Ecol. Res., 25, 909-923, 10.1007/s11284-010-0747-6, 2010b.

481 Sharma, P., and Rai, S. C.: Carbon sequestration with land-use cover change in a Himalayan watershed, Geoderma,
482 139, 371-378, 10.1016/j.geoderma.2007.02.016, 2007.

483 Sharmila, S., Joseph, S., Sahai, A. K., Abhilash, S., and Chattopadhyay, R.: Future projection of Indian summer
484 monsoon variability under climate change scenario: An assessment from CMIP5 climate models, Global Planet.
485 Change, 124, 62-78, 10.1016/j.gloplacha.2014.11.004, 2015.

486 Sheikh, M. A., Kumar, M., and Bussmann, R. W.: Altitudinal variation in soil organic carbon stock in coniferous
487 subtropical and broadleaf temperate forests in Garhwal Himalaya, Carbon balance and management, 4, 1-6, 2009.

488 Shrestha, U. B., Gautam, S., and Bawa, K. S.: Widespread climate change in the Himalayas and associated changes
489 in local ecosystems, PLoS One, 7, e36741, 10.1371/journal.pone.0036741, 2012.

490 Sierra, C. A., Trumbore, S. E., Davidson, E. A., Vicca, S., and Janssens, I.: Sensitivity of decomposition rates of
491 soil organic matter with respect to simultaneous changes in temperature and moisture, Journal of Advances in
492 Modeling Earth Systems, 7, 335-356, 2015.

493 Singh, S. B. K., Isabella; Singh Karky, Bhaskar; Sharma, Eklabya: Climate change in the Hindu Kush-Himalayas:
494 the state of current knowledge, ICIMOD, 88 2011.

495 Singh, S. P., Adhikari, B. S., and Zobel, D. B.: Biomass, productivity, leaf longevity, and forest structure in the
496 central Himalaya, Ecol. Monogr., 401-421, 1994.

497 Stocker, T. F.: Climate change 2013: the physical science basis: Working Group I contribution to the Fifth
498 assessment report of the Intergovernmental Panel on Climate Change, Cambridge University Press, 2014.

499 Subke, J.-A., Inglima, I., and Cotrufo, F. M.: Trends and methodological impacts in soil CO_2 efflux partitioning: A
500 metaanalytical review, Global Change Biology, 12, 921-943, doi: 10.1111/j.1365-2486.2006.01117.x, 2006.

501 Sundarapandian, S., and Dar, J.: Variation in Soil CO_2 Efflux in Pinus Wallichiana and Abies Pindrow Temperate
502 Forests of Western Himalayas, India. Forest Res, 3, 2, 2013.

503 Tashi, S., Singh, B., Keitel, C., and Adams, M.: Soil carbon and nitrogen stocks in forests along an altitudinal
504 gradient in the eastern Himalayas and a meta-analysis of global data, Global Change Biol., 2016.

505 Tiwari, S., and Joshi, R.: Litter-fall production in cool-temperate forests of the Nanda Devi Biosphere Reserve,
506 Uttarakhand Himalaya, India, Braz. J. Biolo. Sci., 2, 147-154, 2015.

507   Tsering, K., Sharma, E., Chettri, N., and Shrestha, A.: Climate Change Impact and Vulnerability in the Eastern
508   Himalayas – Synthesis Report. ICIMOD, ICIMOD, Kathmandu,Nepal, 2010.

509   Tucker, C.L., Young, J.M., Williams, D.G., and Ogle, K.: Process-based isotope partitioning of winter soil
510   respiration in a subalpine ecosystem reveals importance of rhizospheric respiration, Biogeochemistry, 121, 389-
511   408, 2014.

512

513   Usman, S., Singh, S., and Rawat, Y.: Fine root productivity and turnover in two evergreen central Himalayan
514   forests, Ann. Bot., 84, 87-94, 1999.

515   Verma, A., Tewari, A., and Shah, S.: Carbon storage capacity of high altitudeQuercus semecarpifolia, forests of
516   Central Himalayan region, Scand. J. For. Res., 27, 609-618, 10.1080/02827581.2012.689003, 2012.

517   Wang, X., Jiang, Y., Jia, B., Wang, F., and Zhou, G.: Comparison of soil respiration among three temperate forests
518   in Changbai Mountains, China, Can. J. For. Res, 40, 788-795, 2010.

519   Wang, X., Liu, L., Piao, S., Janssens, I. A., Tang, J., Liu, W., Chi, Y., Wang, J., and Xu, S.: Soil respiration under
520   climate warming: differential response of heterotrophic and autotrophic respiration, Global Change Biol., 20, 3229-
521   3237, 2014.

522   Wangda, P., and Ohsawa, M.: Gradational forest change along the climatically dry valley slopes of Bhutan in the
523   midst of humid eastern Himalaya, Plant Ecol., 186, 109-128, 2006a.

524   Wangda, P., and Ohsawa, M.: Structure and regeneration dynamics of dominant tree species along altitudinal
525   gradient in a dry valley slopes of the Bhutan Himalaya, For. Ecol. Manage., 230, 136-150, 2006b.

526   Wikramanayake, E. D.: Terrestrial ecoregions of the Indo-Pacific: a conservation assessment, Island Press, 2002.

527   Xu, J., Grumbine, R. E., Shrestha, A., Eriksson, M., Yang, X., Wang, Y., and Wilkes, A.: The melting Himalayas:
528   cascading effects of climate change on water, biodiversity, and livelihoods, Conserv. Biol., 23, 10.1111/j.1523-
529   1739.2009.01237.x, 2009.

530   Xu, J., and Grumbine, R. E.: Building ecosystem resilience for climate change adaptation in the Asian highlands,
531   Wiley Interdisciplinary Reviews: Climate Change, 5, 709-718, 10.1002/wcc.302, 2014.

532   Yang, Y.-S., Chen, G.-S., Guo, J.-F., Xie, J.-S., and Wang, X.-G.: Soil respiration and carbon balance in a
533   subtropical native forest and two managed plantations, Plant Ecol., 193, 71-84, 2007.

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%)* *Quercus semecarpifolia (29.3%)* *Picea spinulosa (6.3%)* *Abies densa (4.1%)* *Taxus baccata (0.3%)*	*Quercus lanata (63.5%)* *Quercus griffithii (29.6%)*
Dominant Understory species	*Ilex dipreyana (0.2%)* *Rhododendron arboreum (0.1%)*	*Symplocus sp. (0.8%)* *Lyonia ovalifolia, (2.2%)* *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} (μmol 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.
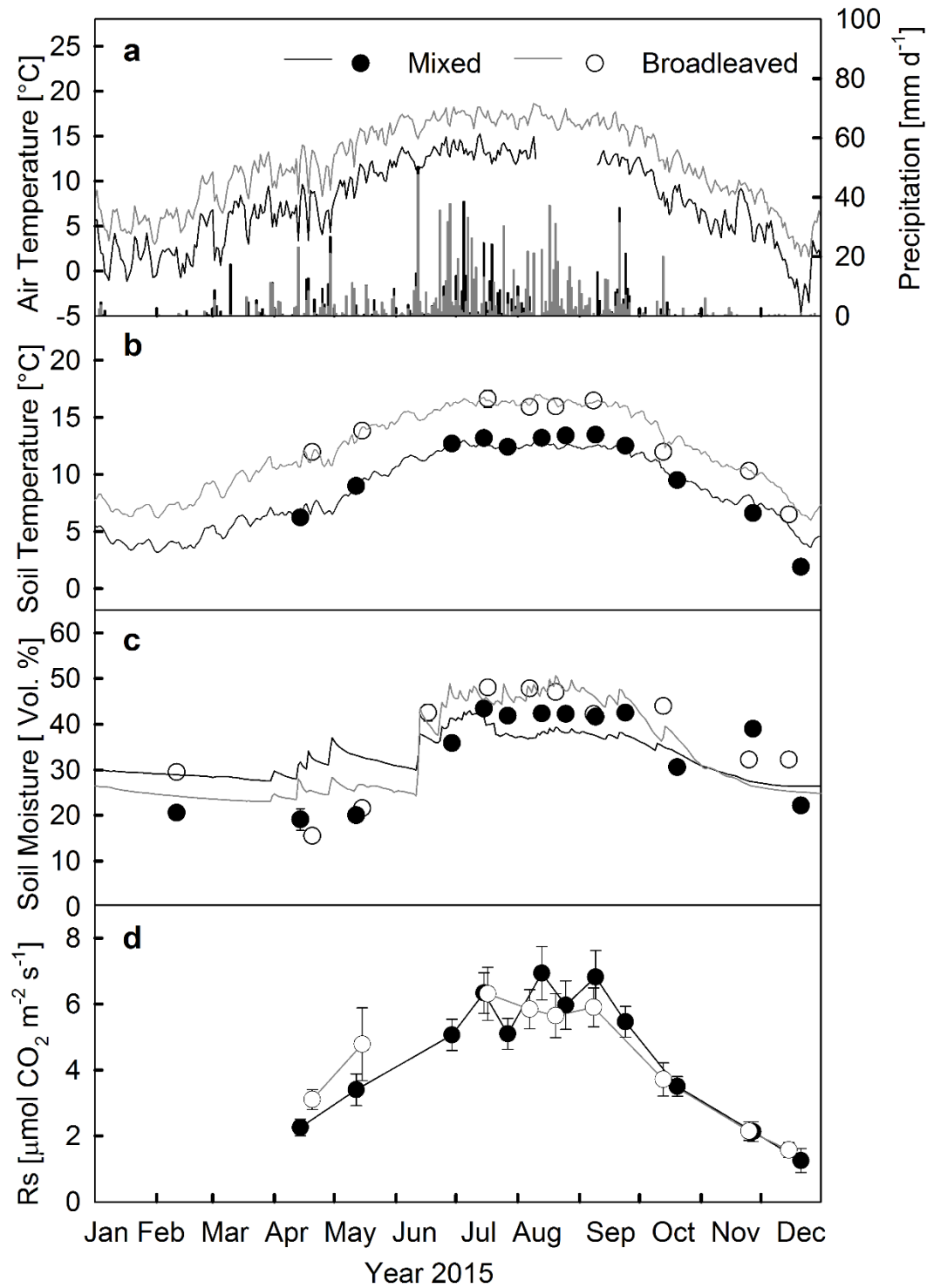
Figure 1. Seasonal course of air temperature and precipitation (a), soil temperature (b), volumetric soil water content (c), and soil respiration (d) measured at a mixed and a broadleaved forest in Bhutan Himalayas in 2015. Circles represent daily mean values of manual measurements. Solid lines (a, b, c) represent daily mean values of continuous measurements. Error bars indicate standard error of the mean.
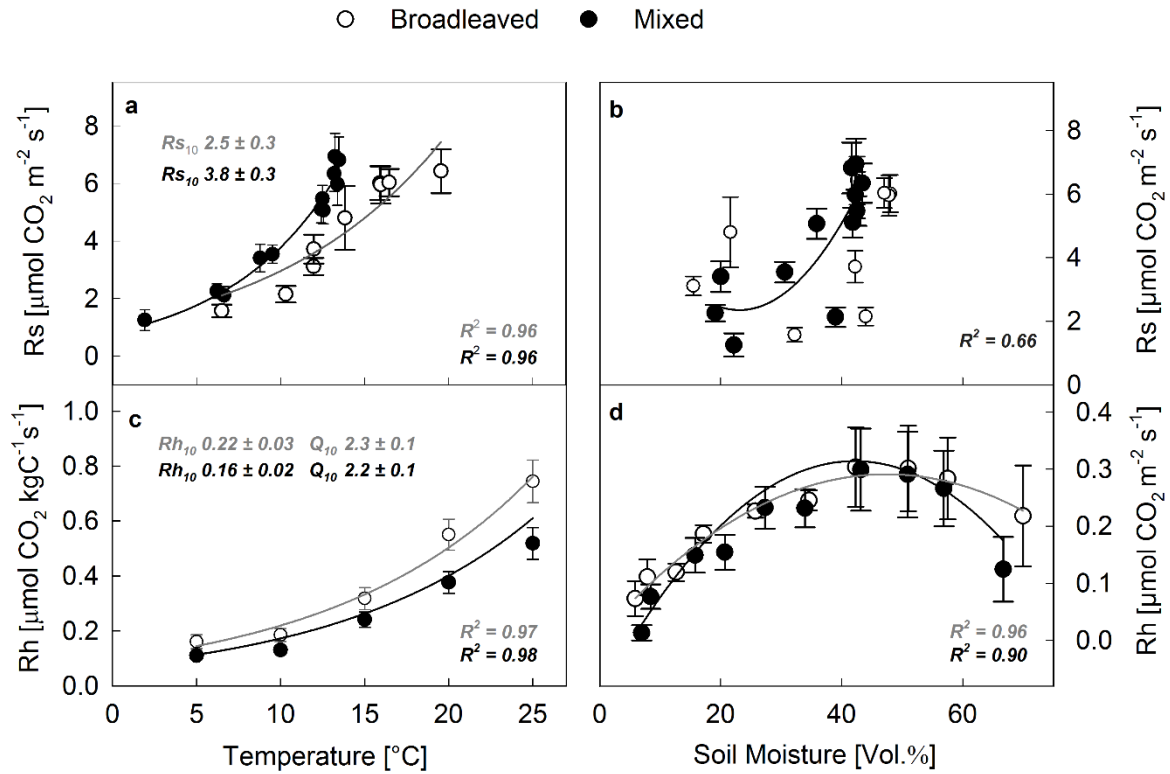
Figure 2. (a) Relationship between soil CO_2 efflux (Rs) and soil temperature, and **(b)** Rs and soil moisture (vol.%) at a broadleaved and a mixed forest in Bhutan Himalayas. **(c)** Relationship between heterotrophic soil respiration (Rh) and soil temperature, and **(d)** Rh and soil moisture (vol. %) 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).
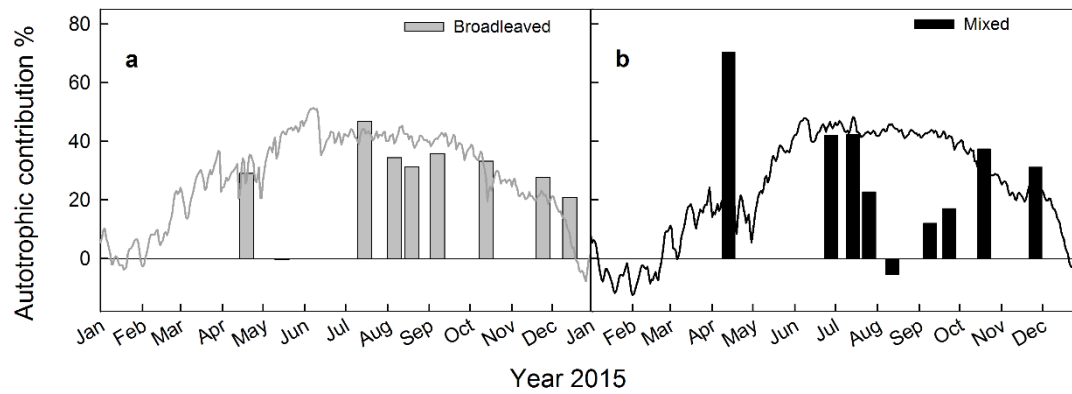
Figure 3: Contribution of autotrophic soil respiration (Ra) to total soil CO_2 efflux (Rs) at a **(a)** broadleaved and **(b)** mixed forest in Bhutan Himalayas. Autotrophic contribution was derived from the differences between Rs measured at control and trenched plots (bars) and from the differences between modelled Rs and heterotrophic soil respiration rates (lines), respectively.
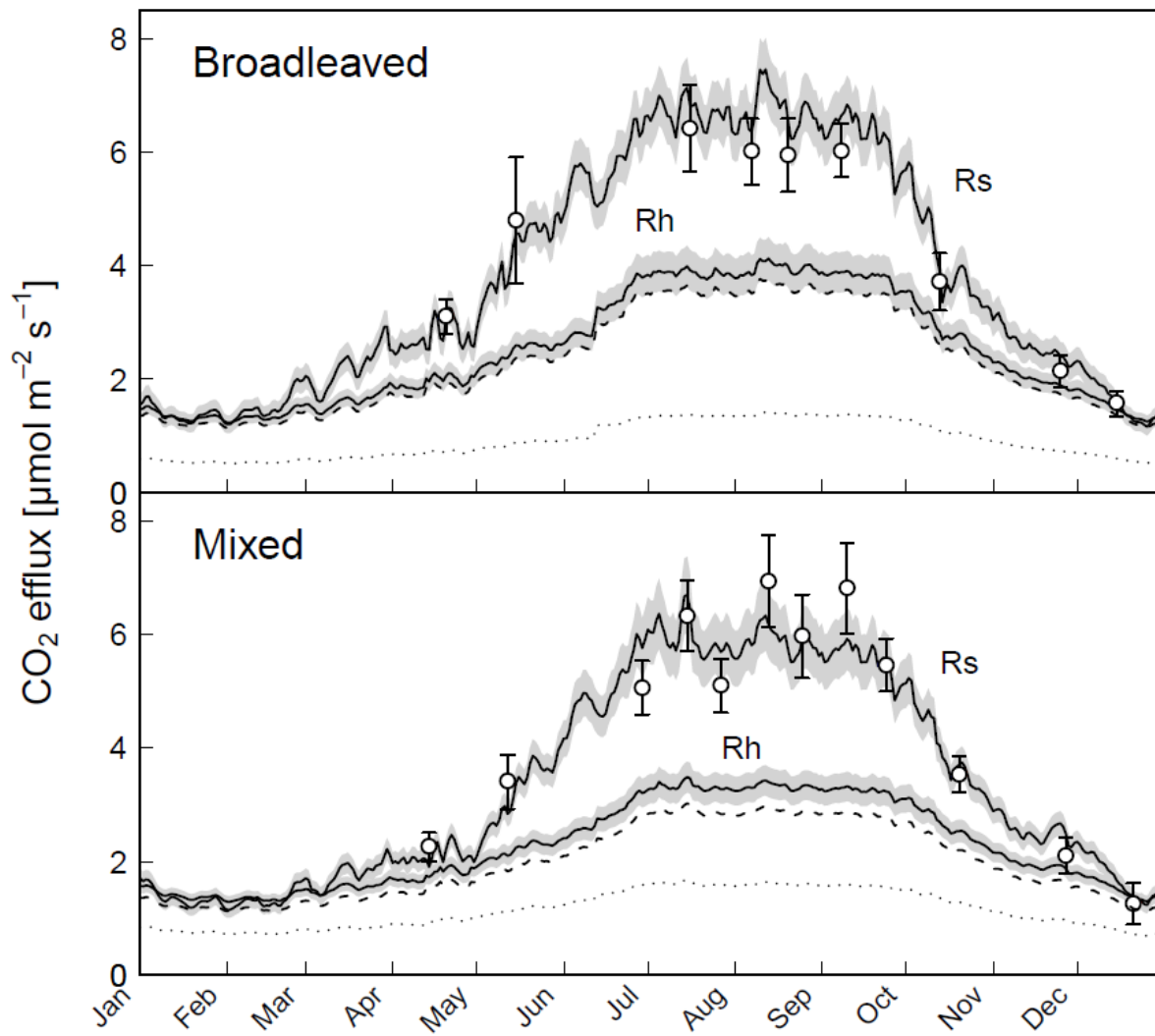
Figure 4. Seasonal course of modelled soil CO_2 efflux (Rs) and heterotrophic soil respiration rates (Rh) at a broadleaved and mixed forest in Bhutan Himalayas in 2015. Open circles are measured Rs rates. Error bars and shaded areas represent standard error of the daily mean. Dashed and dotted lines 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.