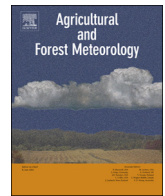




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# Soil respiration in a tropical montane grassland ecosystem is largely heterotroph-driven and increases under simulated warming

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## ABSTRACT

Soil respiration, a major source of atmospheric carbon (C), can feed into climate warming, which in turn can amplify soil CO<sub>2</sub> efflux by affecting respiration by plant roots, arbuscular mycorrhizal fungi (AMF) and other heterotrophic organisms. Although tropical ecosystems contribute > 60% of the global soil CO<sub>2</sub> efflux, there is currently a dearth of data on tropical soil respiration responses to increasing temperature. Here we report a simulated warming and soil respiration partitioning experiment in tropical montane grasslands in the Western Ghats in southern India. The study aimed to (a) evaluate soil respiration responses to warming, (b) assess the relative contributions of autotrophic and heterotrophic components to soil respiration, and (c) assess the roles of soil temperature and soil moisture in influencing soil respiration in this system. Soil respiration was tightly coupled with instantaneous soil moisture availability in both the warmed and control plots, with CO<sub>2</sub> efflux levels peaking during the wet season. Soil warming by ~1.4 °C nearly doubled soil respiration from 0.62 g CO<sub>2</sub> m<sup>-2</sup> hr<sup>-1</sup> under ambient conditions to 1.16 g CO<sub>2</sub> m<sup>-2</sup> hr<sup>-1</sup> under warmed conditions. Warming effects on soil CO<sub>2</sub> efflux were dependent on water availability, with greater relative increases in soil respiration observed under conditions of low (with a minimum of 2.6%), compared to high (with a maximum of 64.3%), soil moisture. Heterotrophs contributed to the majority of soil CO<sub>2</sub> efflux, with respiration remaining unchanged when roots and/or AMF hyphae were excluded as the partitioning treatments were statistically indistinguishable. Overall, our results indicate that future warming is likely to substantially increase the largely heterotroph-driven soil C fluxes in this tropical montane grassland ecosystem.

## 1. Introduction

Soils are substantial carbon (C) sinks, storing about 2157–2293 Pg C, ~3 times as in aboveground vegetation (Batjes, 1996; Cartmill, 2011; Ciais et al., 2013). The soil-to-atmosphere C flux of 64–94 Pg C yr<sup>-1</sup> globally, or soil respiration, also makes them significant C sources. This is ~30% of the total terrestrial and marine atmospheric C contribution, and ~10 times the C contribution from anthropogenic sources such as fossil fuel combustion (Raich and Schlesinger, 1992; Baggs, 2006; Hashimoto et al., 2015; Le Quéré et al., 2017; Zhao et al., 2017; Bond-Lamberty, 2018). Tropical ecosystems are estimated to contribute > 60% of the global soil CO<sub>2</sub> efflux (Bond-Lamberty and Thomson, 2010; Hashimoto et al., 2015), suggesting that even slight increases in soil respiration levels in these regions can translate to large additions to global atmospheric CO<sub>2</sub> pools.

Increased atmospheric CO<sub>2</sub> levels are a major contributor to global

warming (IPCC, 2013), which in turn can feed back to influence soil CO<sub>2</sub> efflux. Many studies have reported warming-induced increases in soil respiration in subtropical, temperate and boreal ecosystems (e.g. Buchmann, 2000; Rustad et al., 2001; Conant et al., 2004; Bronson et al., 2007; Lu et al., 2013; Li et al., 2016; Wangdi et al., 2017), and it is estimated that warming has accounted for a 3% increase in soil respiration levels from 1989 to 2008 in tropical ecosystems as well (Bond-Lamberty and Thomson, 2010). Warmer conditions can influence CO<sub>2</sub> fluxes by affecting both autotrophic respiration, from plant roots and plant-associated symbionts such as arbuscular mycorrhizal fungi (AMF), and heterotrophic respiration due to microbial (fungal and bacterial) and animal decomposers. Increasing temperatures can lead to altered rates of metabolism in plant roots (Atkin et al., 2000), as well as increased plant C investment in AMF leading to changes in root colonization levels, greater hyphal growth and increased mycorrhizal respiration (Hawkes et al., 2008; Rudgers et al., 2014; Birgander et al.,

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2017). Heterotrophic respiration can be affected under warmer conditions by changed soil microbial biomass, community composition, bacterial:fungal ratios (Singh et al., 2010; DeAngelis et al., 2015; Auffret et al., 2016), and microbial metabolism leading to altered decomposition rates (see Classen et al. (2015) and references therein for a review of soil microbial (including AMF) responses to warming).

The contributions of roots, AMF and microbial decomposers to soil respiration differ across ecosystems. For instance, root respiration can contribute anything between 5 to > 90% of the total CO<sub>2</sub> efflux from soils. Microbial decomposers have also been reported to contribute between ~30% and > 90% of the CO<sub>2</sub> efflux from soils, and may be correlated with the autotrophic respiration contribution (Hanson et al., 2000; Bond-Lamberty et al., 2004). Ecosystems also differ in soil temperature and soil moisture controls on soil respiration, with CO<sub>2</sub> efflux responding to changes in either or both (e.g. Cartmill, 2011; Wu et al., 2011; Liu et al., 2016; Hoover et al., 2016). While there are a number of reports of CO<sub>2</sub> efflux measurements from tropical ecosystems (e.g. Bond-Lamberty and Thomson (2010) and studies referred therein), there is a paucity of studies that have evaluated soil respiration responses to experimental warming in these ecosystems (Aronson and McNulty, 2009; Lu et al., 2013). Consequently, there is a dearth of data on tropical soil respiration responses, relative contributions of the autotrophic and heterotrophic components, and abiotic controls on CO<sub>2</sub> efflux under increasing temperature regimes.

We evaluated soil respiration responses to simulated warming in a tropical montane grassland ecosystem in the Western Ghats biodiversity hotspot, India, and assessed the relative contributions of roots, AMF and microbial decomposers to soil CO<sub>2</sub> efflux, over 2 years. These montane grasslands support high biodiversity but are also threatened as land use change has greatly reduced their extent, and the remaining grasslands are believed to be particularly vulnerable to climate change (Sukumar et al., 1995; Arasumani et al., 2018). In particular, we tested the prediction that soil respiration will be higher under simulated warming than under ambient (control) conditions. In addition, we quantified autotrophic and heterotrophic contributions to soil respiration in this ecosystem by measuring CO<sub>2</sub> efflux with and without plant roots and/or AMF hyphal components. We also assessed the roles of instantaneous soil temperature and soil moisture in influencing instantaneous soil respiration in this ecosystem.

## 2. Methods

### 2.1. Study area

The experiment was conducted in tropical montane grasslands of the shola-grassland ecosystem, a unique mosaic of grassland interspersed with pockets of stunted evergreen forests (sholas), found in the higher reaches of the Western Ghats (Robin and Nandini, 2012). These grasslands support several species of grasses and herbs, and a variety of wild herbivores such as sambar (*Rusa unicolor*), gaur (*Bos gaurus*), Asiatic elephant (*Elephas maximus*) and the endemic Nilgiri tahr (*Nilgiritragus hylocrius*). These grasslands are representative of other montane grassland and forest-grassland mosaics globally, such as Afromontane ecosystems (Kotze and Samways, 2001; Parr et al., 2014), Campos-Araucaria forest mosaics in southern Brazil (Overbeck et al., 2007), and forest-patana grassland mosaics in Sri Lanka (Gunatilleke et al., 2008).

Our experiment was located in the Avalanche area of the Nilgiris Biosphere Reserve (11.27°N 76.55°E, elevation: ~2300 m), in the state of Tamil Nadu in southern India. The average annual temperature in the region is 14.4°C, and the average annual rainfall is 1847 mm (<https://en.climate-data.org/location/24046/>). The majority of the precipitation in these grasslands occurs during the South-West monsoon season from early June to early September, and the North-East monsoon season from early October to early December, accounting for ~905 mm and ~528 mm rainfall on average, respectively. Summer precipitation

from early March to late May averages ~200 mm, while the winter months from late December to late February are the driest (District Statistical Handbook, The Nilgiris, 2015–2016; <https://nilgiris.nic.in/documents/>). Temperatures peak around May (average minimum and maximum temperatures are 12.07°C and 21.7°C, respectively), and are lowest around January (with average minimum and maximum temperatures of 5.85°C and 20.7°C, respectively), with winter temperatures frequently dropping below 0°C.

### 2.2. Experimental setup

#### 2.2.1. Open top chambers (OTCs)

To study soil respiration responses to simulated increasing temperature, we used 9 open top chambers (OTCs), which are passive warming structures (Aronson and McNulty, 2009; Godfree et al., 2011), and adjacent paired control plots (1 m<sup>2</sup>) experiencing ambient temperature conditions. Three OTCs and control plots each were set up within three 10 m × 20 m fences located in areas of similar slope and aspect, in May and June 2014. The OTCs were hexagonal structures, 3 m in diameter and ~50 cm tall (design modified from Godfree et al. (2011)). Iron frames supported the pyramidal structures, each with five sides having acrylic/polycarbonate walls placed at an inclination of ~60° to the ground and the sixth side left open after initial trials at our field site showed us that OTCs with all six sides closed increased temperatures up to 11°C, as opposed to up to 4°C in the 5-sided OTCs (data not shown).

#### 2.2.2. Respiration partitioning treatments

To assess autotrophic and heterotrophic contributions to soil respiration in our system and to measure their responses to warming, we set up respiration collars within the OTCs and adjacent to the control plots. Soils within these collars were 'partitioned' to measure respiration contributions of 'full soil', soil without roots, and soil without roots and AMF (referred to here on as 'partitioning treatments'; protocol adapted from Marthews et al. (2014); Fig. 1). Each OTC/control plot

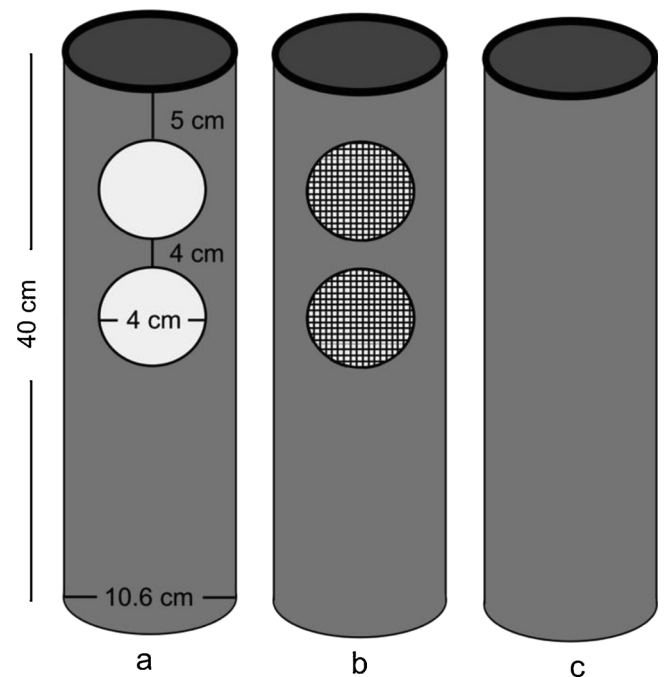


Fig. 1. A representation of the design and dimensions of the PVC pipe collars used for the soil partitioning treatments. (a) Full soil treatment, with circles representing the holes made on one side of the collars, (b) Soil without roots treatment, with circles representing holes covered by nylon meshes to keep out fine roots, and (c) Soil without roots and AMF treatment.

had three collars, one each for the three soil partitioning treatments, for a total of 54 collars. The partitioning treatments were set up in the first week of November 2014.

The partitioning treatments consisted of polyvinyl carbonate (PVC) pipe collars (length: 40 cm, diameter: 10.6 cm) buried in the soil to a depth of 35 cm with 5 cm remaining above the ground. Pits 35 cm deep were made at each collar location, and were re-filled with the same soil after inserting the collar and sifting through the soil to remove all severed roots and other organic debris. The 'full soil' treatment had collars with 4 circular holes of 4 cm diameter, with 2 pairs of holes drilled along opposite sides of the collars (Fig. 1a). These holes allowed roots and AMF hyphae in the top 12 cm of the soil to freely grow into the collars, and contribute to CO<sub>2</sub> efflux. Collars for the 'soil without roots' treatment had similar holes drilled, but were covered with nylon meshes with 40µ pores to allow the growth of AMF extraradical mycelium (ERM) into the collars, but not fine roots (Fig. 1b). The 'soil without roots and AMF' treatment had collars with no holes, preventing the growth of roots or AMF hyphae into them, thus allowing for CO<sub>2</sub> efflux measurement from root- and AMF-free soil (Fig. 1c).

We tested the efficacy of the partitioning treatments using additional treatment collars set up in early October 2015, from which we collected soils and measured the amounts of roots, AMF hyphae and microbial biomass in November 2016. We found that the treatments were successful in allowing/preventing the growth of roots and/or AMF hyphae within the collars (detailed methods and results in Supplementary Information A). Further, to ensure that soil disturbance during the setting up of the collars did not affect soil respiration over the period of our study, we set up two types of 'method control' collars that were installed along with the treatment collars, within an OTC-control plot pair in each fence. One of these (designated as C1) consisted of PVC collars set up exactly as the other treatment collars, but without removing severed roots and other debris from the soils before filling in the collars after installation. The second (designated as C2) had PVC collars hammered into the ground to a depth of ~30 cm without displacing the soil before installation. We found that, after an initial spike, soil respiration in these 'method control' collars was indistinguishable from the 'soil without roots and mycorrhizae' treatment (details of methods and results in Supplementary Information A). We therefore report only results from the three partitioning treatment collars.

### 2.3. Soil respiration measurement and calculations

Soil respiration in the partitioning treatment and control collars were measured at approximately 15-day intervals from late November 2014 to late January 2017, for a total of 48 sampling days. We used a portable IR-based gas analyser (Environmental Gas Monitor; EGM-4, PP Systems, USA), to measure CO<sub>2</sub> flux. Alongside CO<sub>2</sub> flux measurements, we also measured ambient atmospheric temperature within each OTC and control plot, and collar height (averaged across three measurements per collar) at each measurement time point. These data were then used to calculate CO<sub>2</sub> efflux following Marthews et al. (2014), as:

$$r_{uc} = \left( \frac{C_n - C_1}{t_n - t_1} \right) \left( \frac{P}{T_a} \right) \left( \frac{V_d}{A} \right) \left( \frac{44.01 \times 0.36}{R} \right) \text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1} \quad (1)$$

$$r_c = r_{uc} \left( \frac{V_d + V_{added}}{V_d} \right) \text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1} \quad (2)$$

where  $r_{uc}$  denotes soil CO<sub>2</sub> efflux calculated without correcting for the added volume of the respiration collar, and  $r_c$  denotes CO<sub>2</sub> efflux corrected for volume in g CO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup>;  $C_n - C_1$  is the CO<sub>2</sub> flux difference, typically between the last 10 readings per measurement, or between the first and last flux values if the measurement had less than 10 readings, in ppmv;  $t_n - t_1$  is the difference in time, in seconds, over which the difference in CO<sub>2</sub> flux was calculated;  $P$  is ambient atmospheric

pressure, in mb, averaged over  $t_n - t_1$  as measured by the EGM;  $T_a$  is atmospheric temperature in Kelvin;  $V_d$  is volume within the EGM respiration chamber;  $A$  is the area of soil over which CO<sub>2</sub> flux was measured;  $R$  is the Universal Gas Constant, 8.314 J K<sup>-1</sup> mol<sup>-1</sup>; and  $V_{added}$  is the volume of the respiration collar above the soil surface at the time of measurement. A more detailed discussion of the method for measurement and calculation of CO<sub>2</sub> efflux can be found in Marthews et al. (2014).

To account for potential measurement errors in CO<sub>2</sub> flux while using the EGM in the field, we assessed linearity of CO<sub>2</sub> accumulation for each collar for each sampling day using linear models of CO<sub>2</sub> accumulation versus time, and only those measurements that satisfied the criteria that  $R^2 \geq 0.9$  (Savage et al., 2008), and had a positive slope, were used for further analyses. Further, since some values of measured CO<sub>2</sub> efflux were found to be unusually high or low, we excluded values that fell beyond 3 SDs of the mean CO<sub>2</sub> efflux from the analyses. Our final analyses were based on 80.9% of the original data collected.

### 2.4. Temperature and soil moisture measurements

Air temperatures were measured from December 2014 to January 2017 by placing iButtons (Thermochron Temperature Data Loggers, Maxim Integrated, USA) 2–3 cm above the ground within all 9 OTCs, and 3 control plots, one in each fence. Soil temperatures were measured from May 2015 to January 2016, by placing iButtons just below the soil surface in an OTC and control plot in each fence. Data for some months are missing due to loss of iButton, or due to logging errors. We also measured instantaneous soil temperature and soil moisture when quantifying soil respiration. Instantaneous soil temperature measurements were done at 12.5 cm depth using a temperature probe (HI145-00 and HI145-01, Hanna Instruments, USA), and instantaneous soil moisture measurements were done over the top 12 cm of soil using a soil moisture meter (FieldScout TDR 100 Soil Moisture Meter, Spectrum Technologies, USA), with 3 replicates in the vicinity of each soil respiration collar.

### 2.5. Data analysis

We used linear mixed effects models (LMMs) to test whether (a) soil respiration in warmed plots differed from control plots, (b) CO<sub>2</sub> efflux was different in treatments where roots and/or AMF were excluded from 'full soil' respiration levels, and (c) partitioning treatment effects were different in warmed versus control plots. Warming (OTC/control), partitioning treatments (full soil, soil without roots, soil without roots and AMF) and their interaction were used as fixed factors and collars nested within plots, which were in turn nested within fences were used as random factors to account for multiple measurements across time from the same respiration collars (Baayen et al., 2008; Zuur, 2009; Cunnings and Finlayson, 2015). Soil respiration, measured at approximately 15-day intervals from November 2014 to January 2017 per warming and partitioning treatment, was the response variable. In all, there were 310–348 individual respiration measures per partitioning treatment per OTC/control plot (median = 339.5), for a total of 1994 values. Soil CO<sub>2</sub> efflux values were log transformed before analyses to meet model assumptions.

We then tested whether instantaneous soil temperature and soil moisture individually or together best explained variation in soil respiration in the OTC and control plots using LMMs in conjunction with AIC based model selection. Instantaneous soil temperature and soil moisture, warming treatment and their interactions were as fixed factors and as in the previous analysis, collars nested within plots, which were in turn nested within fences were the random factors. We only used soil respiration and instantaneous soil moisture and soil temperature data from the 'full soil' collars for these analyses. The fixed effects in the three candidate LMMs were (a) soil temperature × soil moisture × warming treatment, (b) soil temperature × warming

treatment, and (c) soil moisture  $\times$  warming treatment. We also computed marginal and conditional  $R^2$  values that give an indication of the variation explained by only the fixed effects and the fixed and random effects, respectively, for all three candidate models (Nakagawa and Schielzeth, 2013). Again, soil  $\text{CO}_2$  efflux values were log transformed before analyses to meet model assumptions.

We used the R package *lme4* to conduct all the mixed effects models (Bates, 2010; Bates et al., 2014; Kuznetsova et al., 2015; Bates et al., 2017), the *lmerTest* package to conduct *t*-tests using Satterthwaite approximations for the degrees of freedom, and the *car* package to conduct Type II Wald chi-square tests to assess the statistical significance of the fixed effects (Bates et al., 2014, 2017). Marginal and conditional  $R^2$  values were computed using the *piecewiseSEM* package (Lefcheck, 2016). All analyses were conducted using R version 3.2.4 (The R Foundation for Statistical Computing, 2016). The data and the R code are available in Supplementary Information B and C.

### 3. Results

#### 3.1. Temperature and soil moisture between treatments

Average daily soil temperatures of control and OTC plots over the period of the study was  $16.10 \pm 0.13^\circ\text{C}$  and  $17.53 \pm 0.15^\circ\text{C}$ , respectively (over 277 measures from 146 days each). The difference in mean daily temperature between OTC and control plots averaged  $1.41 \pm 0.08^\circ\text{C}$  overall (Fig. 2a), with a maximum temperature increase of  $3.43^\circ\text{C}$  ( $t = 16.751$ ,  $df = 145$ ,  $P < 0.001$ , 95% CI = 1.24, 1.57; results from a one-sample *t*-test, with  $H_0$  that the true mean = 0). Monthly averages of soil temperatures ranged from  $14.55$  to  $21.67^\circ\text{C}$  in the controls and  $16.09$  to  $22.93^\circ\text{C}$  in the OTCs (Fig. 2b).

Average daily air temperature responses were smaller than soil temperature responses to warming, with the difference in mean air temperatures of OTCs and control plots per day averaging  $0.10 \pm 0.04^\circ\text{C}$  (details in Supplementary Information A and Fig. S1).

Soil moisture was lower in the OTCs than in the control plots (Fig. 2c), with averages of  $23.74 \pm 0.76\%$  and  $25.98 \pm 0.81\%$ , respectively (from 421 and 429 estimates, respectively, across 27 months). The average difference in soil moisture levels between control and OTC plots was  $2.22\%$  ( $t = 11.36$ ,  $df = 420$ ,  $P < 0.001$ , 95% CI = 1.84, 2.61; results from a one-sample *t*-test, with  $H_0$  that the true mean = 0). Soil moisture levels ranged from 3.26 to 64.30% and 2.6058.88% on average in the controls and OTCs, respectively (Fig. 2d).

#### 3.2. Effects of warming and partitioning treatments on soil respiration

Warming significantly increased soil respiration by 55–89% compared to control levels in all three partitioning treatments ( $P < 0.05$ ). The three partitioning treatments, however, were statistically indistinguishable from each other in both controls and OTCs (Table 1, Fig. 3). Average soil respiration over the entire duration of the experiment and across partitioning treatments was  $0.62 \pm 0.01 \text{ g CO}_2 \text{ m}^{-2} \text{ hr}^{-1}$  in the controls and  $1.16 \pm 0.03 \text{ g CO}_2 \text{ m}^{-2} \text{ hr}^{-1}$  under warmed conditions. Mixed effects model estimates of the average  $\text{CO}_2$  efflux levels (and 95% CIs) in the three partitioning treatments were  $0.51$  (0.40, 0.65),  $0.56$  (0.44, 0.72) and  $0.46$  (0.36, 0.59)  $\text{g CO}_2 \text{ m}^{-2} \text{ hr}^{-1}$ , respectively, in the control treatment, and  $0.79$  (0.62, 1.02),  $0.94$  (0.73, 1.20) and  $0.87$  (0.68, 1.12)  $\text{g CO}_2 \text{ m}^{-2} \text{ hr}^{-1}$ , respectively, in the OTCs.

Soil respiration also differed by month mirroring the seasonality of our study system (Fig. 4). Overall, control plots recorded minimum soil respiration of  $0.16 \pm 0.02 \text{ g CO}_2 \text{ m}^{-2} \text{ hr}^{-1}$  in March 2015, while respiration peaked to  $1.10 \pm 0.12 \text{ g CO}_2 \text{ m}^{-2} \text{ hr}^{-1}$  in September 2016; while the OTCs recorded minimum and maximum soil respiration levels of  $0.63 \pm 0.07 \text{ g CO}_2 \text{ m}^{-2} \text{ hr}^{-1}$  and  $1.84 \pm 0.36 \text{ g CO}_2 \text{ m}^{-2} \text{ hr}^{-1}$ , in February 2015 and April 2016, respectively (Fig. 4). Responses per partitioning treatment were similar to this overall warming effect

(Supplementary Information A, Fig. S3).

#### 3.3. Effects of instantaneous soil temperature and moisture on soil respiration

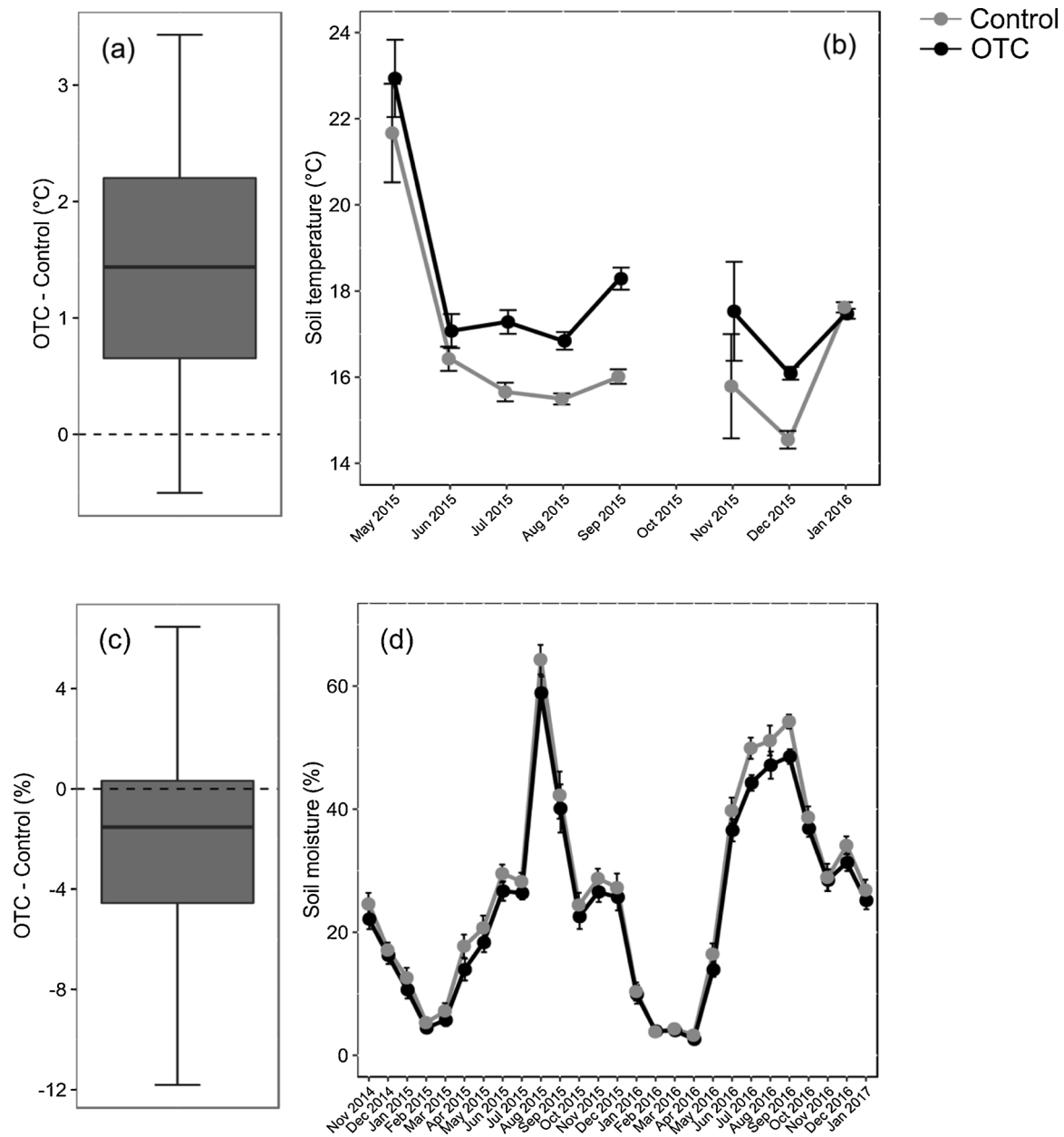
The most parsimonious model predicting soil respiration in our system was the model that included warming treatment, instantaneous soil moisture and their interaction as predictors (Table 2). The addition of instantaneous soil temperature to the model does not improve marginal and conditional  $R^2$  values by much (Table 2). Soil respiration was higher in the warmed plots ( $P = 0.002$ ; Table 1), and increased as soil moisture increased ( $P < 0.001$ ; Table 1). However, the effect of warming on soil respiration was more pronounced under low soil moisture conditions (soil moisture  $\times$  warming:  $P = 0.023$ ; Table 1; Fig. 5). Given that the partitioning treatments were statistically indistinguishable, only data from the ‘full soil’ treatment were used for these analyses.

### 4. Discussion

Our study shows that even small increases in soil temperature ( $1.41^\circ\text{C}$ ) greatly influence soil respiration rates in a tropical montane grassland ecosystem in the Western Ghats. Further, soil respiration was largely heterotrophic, and increased with soil moisture in these grasslands. Warming effects on soil respiration were more pronounced in drier soils, while soil respiration is unrelated to instantaneous soil temperature in the region.

Soil respiration in the study site was largely heterotroph-driven. Heterotroph-dominant soil respiration, as observed in this study system, has been reported from several non-forest ecosystems, such as grasslands, croplands and oak savannas, and also some temperate forests, although autotrophs generally contribute ~50% of the soil respiration in forest ecosystems (Kelting et al., 1998; Buchmann, 2000; Hanson et al., 2000; Melillo et al., 2002; Scott-Denton et al., 2006; Cartmill, 2011). Heterotrophic contributions to soil respiration have been shown to correlate strongly with soil detritus levels (Bond-Lamberty et al., 2004) and increase with increasing soil nitrogen availability (Rodeghiero and Cescatti, 2006). Heterotroph contributions to soil respiration are also potentially influenced by other factors such as vegetation and soil microbial community composition, net primary production and litter quality, though which of these factors underlie heterotroph dominated respiration in these montane grasslands is unclear.

Another potential reason for the lack of differences in soil respiration levels among partitioning treatments in this study is soil microbial biomass changes following loss of plant roots and AMF hyphae. Plants and microbes compete for soil resources (such as N), and removal of plant roots can lead to increases in decomposer biomass, which in turn can increase soil  $\text{CO}_2$  efflux levels, masking the loss of the autotrophic contribution to soil respiration. In this study, while microbial biomass carbon (MBC) increases with root exclusion, there are no increases in microbial biomass with AMF hyphal exclusion (Supplementary Information A, Fig. S2). This suggests that the lack of differences in soil respiration levels between treatments in this study is not entirely a consequence of decomposer biomass increases in the root- and AMF-free soil. In other words, MBC responses to root and AMF hyphal exclusion in this study further supports the conclusion that soil respiration in our system is heterotroph dominated. Another potential reason for the lack of differences in soil respiration we see between the root exclusion and ‘full soil’ treatments is diffusion of  $\text{CO}_2$  from below the root exclusion layer. While root exclusion to the depth of 20–40 cm is common in respiration partitioning literature, the absence of roots (and mycorrhizal) contributions has been shown to create a  $\text{CO}_2$  gradient due to respiration by the small amounts of fine roots that may exist in deeper soil layer. This can in turn lead to increased  $\text{CO}_2$  diffusion to the upper layers, masking, in part, the full extent of  $\text{CO}_2$  depletion due to root (and AMF) exclusion (Jassal and Black, 2006).



**Fig. 2.** Differences between OTCs and control plots for (a) daily averages of soil temperature and (c) fortnightly measures of soil moisture. Monthly averages of (b) air temperature and (d) soil moisture over replicate plots in the control (grey dots) and OTC plots (black dots). Error bars in (b) and (d) are 1SE around the mean.

Soil  $\text{CO}_2$  efflux levels in this experiment nearly doubled, from  $0.62 \text{ g m}^{-2} \text{ hr}^{-1}$  under ambient temperature conditions to  $1.16 \text{ g m}^{-2} \text{ hr}^{-1}$  within the OTCs. This is in agreement with empirical findings from other ecosystems including grasslands, as well as theoretical studies suggesting increases in soil respiration under climate change in the tropics (Schindlbacher et al., 2009; Bond-Lamberty and Thomson, 2010; Lu et al., 2013; Wang et al., 2014). The observed increases in respiration under warmer conditions can be driven by several mechanisms. First, greater soil  $\text{CO}_2$  efflux can result from greater microbial metabolism under warmed conditions, given that heterotrophs contribute the majority of the respiration in this system (Schindlbacher et al., 2011; Luo et al., 2014). Previous studies have also shown that autotroph and heterotroph respiration responses to changing temperature regimes can be very different, with heterotrophs, rather than autotrophs, reported to be more sensitive to increasing temperatures (Wei et al., 2010; Li et al., 2013; Wang et al., 2014). Heterotroph contributions to soil respiration, globally, have increased from 54% to 63% from

1990 to 2014, potentially in response to changing climate (Bond-Lamberty et al., 2018). Second, higher levels of labile C under warmed conditions can drive shifts to a more 'rapid' nutrient and C cycling system, leading to greater soil respiration (Metcalf et al., 2011; Luo et al., 2014).

Soil respiration responses to warming can also be mediated by microbial community shifts, and soils with different microbial community compositions have been demonstrated to respond differently to temperature increases (Auffret et al., 2016). For instance, warming has been shown to promote certain bacterial phyla over fungal phyla (Luo et al., 2014), and increased bacteria:fungi ratios are associated with faster C and nutrient cycling (Wardle et al., 2004). Fungal communities, too, have been demonstrated to shift under warming to favour taxa that are better decomposers of recalcitrant C (Treseder et al., 2016), which would then amplify  $\text{CO}_2$  efflux from these soils. However, at present, it is not clear which of these mechanisms may be driving warming-mediated increases in soil respiration in our study system.

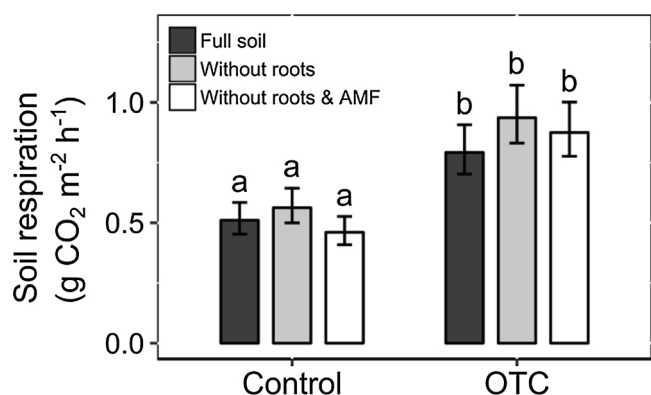
**Table 1**

Summary of LMM results of soil respiration responses to warming treatment, partitioning treatments, and instantaneous soil temperature and instantaneous soil moisture.

SI No.	Predictors	Effect	Wald chi-square	df	P
1.	Warming and partitioning treatments	Warming	44.7641	1	< 0.001
		Partitioning treatment	2.5216	2	0.28
		Warming × Partitioning treatment	1.1280	2	0.57
2.	Instantaneous soil moisture and soil temperature, and warming	Soil moisture	57.8397	1	< 0.001
		Soil temperature	0.0005	1	0.98
		Warming	9.7556	1	0.002
		Soil temperature × Soil moisture	12.7965	1	< 0.001
		Soil temperature × Warming	0.1610	1	0.69
		Soil moisture × Warming	2.8782	1	0.09
		Soil temperature × Soil moisture × Warming	2.0987	1	0.15
3.	Instantaneous soil moisture and warming	Soil moisture	57.1421	1	< 0.001
		Warming	9.1714	1	0.002
		Soil moisture × Warming	5.1778	1	0.023

Values in section 2 are from the 'full model', an LMM with soil moisture, soil temperature, warming treatment and interactions as fixed effects.

Values in this section 3 are from the 'best model' (see Table 2), an LMM with soil moisture, warming treatment and their interactions as fixed effects.



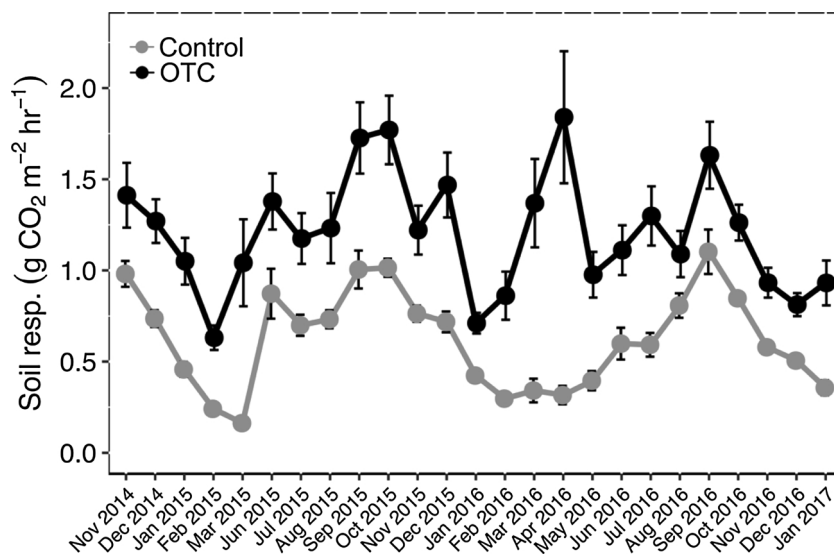
**Fig. 3.** Average soil respiration in control and warmed conditions in the three partitioning treatments. 'Full soil' treatment is represented by dark grey bars, 'soil without roots' by light grey bars, and 'soil without roots and AMF' by white bars. Means and error bars (1SE around the mean) obtained from the mixed effects model used for analysis. Different letters indicate statistically significant differences among treatments ( $P < 0.01$  or lesser).

**Table 2**

Model comparisons of LMMs to assess instantaneous soil moisture and/or temperature and warming treatment effects on soil respiration. Marginal and conditional  $R^2$  values give an indication of the variation explained by the fixed effects only and the fixed and random effects together, respectively, in mixed effects models.

Model (fixed effects)	AIC	$\Delta$ AIC	$R^2_{\text{marginal}}$	$R^2_{\text{conditional}}$
Inst. soil moisture × Inst. soil temperature × Warming	1455.884	28.524	0.16	0.30
Inst. soil temperature × Warming	1478.419	51.059	0.06	0.22
Inst. soil moisture × Warming	1427.360	0	0.15	0.28

Instantaneous soil temperature was found to be a weak predictor of soil respiration in this system. Respiration responses to the warming treatment, however, suggest a positive effect of shallow-soil temperature on respiration over longer timescales. Soil respiration was positively related to instantaneous soil moisture in these markedly seasonal montane grasslands, with clear wet and dry seasons. Moisture effects on (especially heterotrophic) soil respiration have been widely reported. Moisture affects respiration via its influence on several physiological, biochemical and ecological factors such as decomposer substrate availability, nutrient and dissolved organic matter mobility,



**Fig. 4.** Average soil respiration in control and OTC plots averaged per month, across partitioning treatments. Dots in grey represent control plots and those in black represent OTCs. Error bars represent 1SE around the mean.

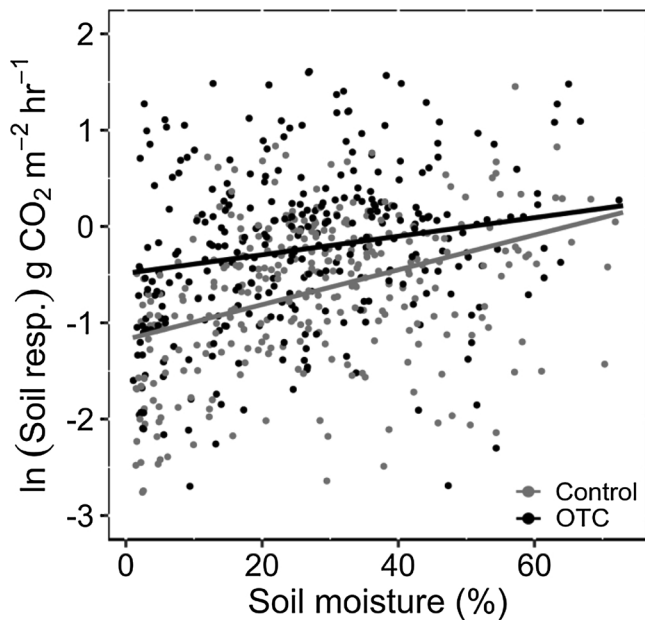


Fig. 5. Soil respiration under control and warmed conditions in the 'full soil' treatment are positively related to average soil moisture. Control:  $\ln(\text{CO}_2 \text{ efflux}) = -1.17 + (0.02 \times \text{soil moisture})$ ; OTC:  $\ln(\text{CO}_2 \text{ efflux}) = -0.49 + (0.01 \times \text{soil moisture})$ . Both slopes are significantly different from 0 ( $P < 0.001$  in both cases). Slopes were obtained from linear mixed effects model analysis. Data for control plots are represented in grey and OTCs in black.

osmoregulation and changes in microbial community composition (Orchard and Cook, 1983; Scott-Denton et al., 2006; Wei et al., 2010; Yan et al., 2009; Moyano et al., 2013). Further, experiments in temperate ecosystems have demonstrated that while soil respiration minima correspond to low temperature conditions, peaks coincide with the 'growing season', often responding to moisture rather than temperature maxima (Heinemeyer et al., 2012; Hoover et al., 2016; Liu et al., 2016).

While soil respiration peaked in the wet season in this study system, warming amplified soil respiration during the dry season. Warming-mediated amplification of respiration during the drier months can be because some of the driest months in these montane grasslands are also the coldest, during which soil microbes under warmed conditions will likely have greater metabolism leading to the higher levels of respiration. Overall, we see the highest respiration levels under wetter and warmer conditions. Indeed, soil temperature and moisture have been shown to have combined effects on soil respiration in several ecosystems (Hursh et al., 2017). Further, a modelling study analysing global soil respiration responses to environmental factors also suggests that the regions with high soil respiration, globally, are associated with both high temperature and precipitation (Hashimoto et al., 2015).

On the whole, the present study indicates that warming is likely to substantially increase soil respiration levels in this tropical montane grassland ecosystem, with effects more pronounced under drier conditions. While the mechanisms behind soil respiration responses to warming in our study system are as yet unclear, our results suggest that decomposers play a major role in regulating observed soil  $\text{CO}_2$  efflux responses to warming. In the longer term, acclimation over time of roots, AMF and other soil components to altered temperature regimes, or depletion of resources such as water or labile carbon, might alter  $\text{CO}_2$  efflux responses to warmer temperatures (Atkin et al., 2000; Luo et al., 2001; Melillo et al., 2002; Kirschbaum, 2004; Heinemeyer et al., 2006; Auffret et al., 2016; Romero-Olivares et al., 2017). Soil respiration can also be affected in the long term by warming-mediated alteration of factors such as vegetation composition and structure (Cartmill, 2011; Metcalfe et al., 2011; Rudgers et al., 2014; Mayer et al., 2017), length of

growing season (Rustad et al., 2001), AMF species pool (Kim et al., 2015) and decomposer community composition (Zogg et al., 1997; DeAngelis et al., 2015). Other global change factors, such as increased atmospheric nutrient deposition, can also influence warming effects on plants and microbes (Olsson et al., 2005). Future longer term studies that also estimate warming-induced changes in other parameters such as vegetation growth, foliar respiration, soil microbial biomass and other components of soil C are needed to assess the net contribution of these ecosystems as sources or sinks of carbon. Further, finer-scale temporal measurements of soil temperature, moisture and soil respiration can lead to quantification of parameters such as temperature sensitivity of soil respiration, and thereby, better characterization of carbon fluxes in this ecosystem.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agrformet.2019.107619>.

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