# Climate and vegetation collectively drive soil respiration in montane forest-grassland landscapes of the southern Western Ghats, India

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## Abstract

$CO_2$ release rates from soils via soil respiration play an important role in the carbon budget of terrestrial ecosystems. Though the roles of soil temperature and moisture on soil respiration are well recognised, less is known about how their effects vary across different land-cover types. This study looked at the interactive effects of land-cover change and microclimate on temporal patterns of soil respiration in a montane forest-grassland-plantation mosaic in a highly diverse but climatically sensitive ecosystem in the tropical Western Ghats of India. Across all vegetation types, soil respiration rates were highest during south-west monsoon (June–October), when root growth, litter decomposition and microbial activity are relatively high and were lowest during the summer. Among vegetation types, soil respiration rates were higher in grasslands compared to non-native pine plantations, whereas that of forest and invasive wattle (*Acacia mearnsii*) plantations were intermediate between grasslands and pine plantations. The decline in respiration rates following conversion from grasslands to pine plantations could be due to relatively lower microbial activity, soil temperatures and, subsequently, slower litter decomposition. In addition, the sensitivity of soil respiration to changes in temperature and moisture differed between different vegetation types. Across all vegetation types, respiration was largely insensitive to changes in soil temperature when moisture levels were low. However, when soil moisture levels were high, respiration increased with temperature in grassland and wattle patches, decreased in the case of pine plantations and remained largely unchanged in shola forests. Our results suggest that changes in aboveground vegetation type can significantly affect soil C cycling even in the absence of any underlying differences in soil type.

## Introduction

Vegetation and soils are important components of the global terrestrial carbon pool, together accounting for ~2060 Pg of carbon, with about three-quarters of this being stored in soils (Scharlemann *et al.* 2014, Schlesinger & Andrews 2000). Soils are also primary mediators of global land-atmosphere carbon fluxes, with soil respiration, which results from root respiration and microbial decomposition of organic matter, releasing 75–100 Pg/year back to the atmosphere (Bond-Lamberty & Thomson 2010, Raich & Schlesinger 1992). Like most biochemical processes, rates of soil respiration are largely governed by temperature and moisture availability which play major roles in regulating both plant growth and soil microbial activity. Soil respiration rates are typically highest in the tropics where plant growth is luxuriant and conditions for decomposition are optimal and lowest in cold and dry biomes where microbial activity is limited by low temperatures and moisture availability, respectively (Raich & Schlesinger 1992). The tropics currently contribute ~67% of the global soil $CO_2$ efflux (Bond-Lamberty & Thomson 2010, Hashimoto *et al.* 2015, Schlesinger & Andrews 2000). Future changes in temperature and precipitation regimes in tropical regions are likely to affect soil respiration rates with potentially significant effects on the global C-cycle and atmospheric $CO_2$ levels (Schlesinger & Andrews 2000).

Besides climatic variables, changes in land use and land cover also influence global terrestrial-atmosphere $CO_2$ fluxes. Since the 1990s, ~1.14 Pg of C are estimated to have been released back into the atmosphere annually, largely as a result of the conversion of intact forests to secondary forests, pastures and croplands (Ciais *et al.* 2013, DeFries *et al.* 1999, Houghton *et al.* 2012, Pan *et al.* 2011). Land-cover changes, besides having significant negative impacts on biodiversity, can also alter ecosystem processes by changing the quantity and quality of carbon inputs to soils, changing soil temperature and moisture regimes and by altering hydrological cycles (Delgado-Balbuena *et al.* 2013, Parr *et al.* 2014, Raich & Schlesinger 1992, Veldman 2015). However, the

**Figure 1.** Temperature and precipitation regimes in the study area. (a) Mean minimum and mean maximum monthly temperatures in the study region. (b) Mean monthly precipitation received in the study region. (Error bars in both figures represent standard errors of the mean; source: Indian Meteorological Department (IMD) data for Ooty from 1969 to 2005).
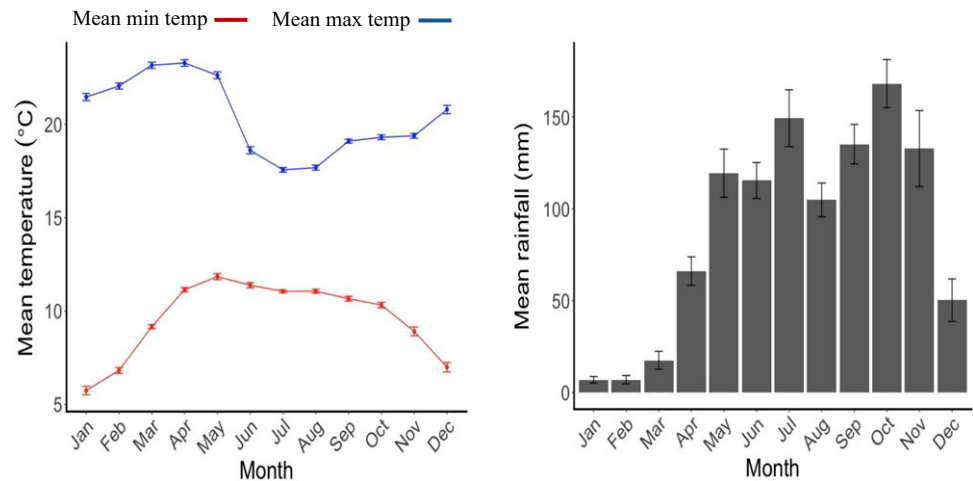
impact of such land-cover changes on ecosystem processes, particularly in tropical regions, has not received sufficient attention. More accurate quantification of the effects of land-cover changes on carbon fluxes to the atmosphere is needed for better implementing policies such as REDD + (Reducing Emissions from Deforestation and Degradation), especially in the tropics which account for a substantial proportion of the emissions due to land-cover changes (Le Quere 2009).

In this study, we quantified soil $CO_2$ effluxes over three years across different land-cover types in the climatically sensitive tropical montane forest-grassland mosaics of the Western Ghats biodiversity hotspot in India. These mosaics have undergone extensive land-cover changes since the mid-nineteenth century, primarily through the establishment of non-native plantations in grasslands, especially of acacia (*Acacia* spp.), eucalyptus (*Eucalyptus* spp.), pine (*Pinus* spp.) and tea (*Camellia sinensis*) (Joshi *et al.* 2018, Sukumar *et al.*1995). Specifically, we looked at how land-cover changes influenced both total and temporal patterns of soil respiration and how such changes were mediated by alterations to moisture and temperature regimes.

## Methods

### Study area

Our study was conducted in the high elevation forest-grasslands mosaics of the upper Nilgiri landscape (11.27° N 76.55° E, elevation: ~2300 m) in the southern Western Ghats, India (Figure S1). The upper reaches (1200–2650 m) of India's Western Ghats biodiversity hotspot (8–21°N, 73–78°E) are characterised by stunted evergreen tree forest patches, locally known as sholas, embedded within grasslands, with abrupt transitions between them (Figure S1).

These bi-phasic mosaics are Pleistocene relics that have existed for more than 20,000 years (Sukumar *et al.* 1993,1995) and support a diverse array of plant and animal species, many of which are endemic (see Karunakaran *et al.* 1998, Mohandass & Davidar 2009, Robin & Sukumar 2002, Schaller 1970, Thomas & Palmer 2007). Over 80 species of trees, lianas and shrubs have been documented from the shola forests in the region (Mohandass & Davidar 2009). Rubiaceae, Lauraceae and Myrtaceae are the dominant families in these forests and comprise ~ 60% of the total stem density (Mohandass & Davidar 2009). Montane grasslands at the site support around 40 species of $C_4$ grasses (Joshi *et al.* in prep).

Large-scale plantations of alien tree species, chiefly eucalyptus (*Eucalyptus globulus*), pine (*Pinus patula*) and wattle (*Acacia mearnsii*), were established in grasslands of this landscape in the latter half of the nineteenth century (Joshi *et al.* 2018, Prabhakar 1994, Sukumar *et al.* 1995). Among these, wattle eventually became invasive and now occupies large tracts of former grassland. The landscape is currently characterised by a mix of native and exotic vegetation. The prominent land-cover types include native shola forests (~452 km²), grasslands (~139 km²), plantations of eucalyptus and pine and invasive wattle patches (~277 km²) and commercial tea (~369 km²) (Arasumani *et al.* 2019). We selected four land-cover types for this study that were in close proximity to each other – native shola forests, grasslands, invasive wattle patches and pine plantations.

Average monthly temperatures in the study area range from a mean minimum of 5°C in January to a mean maximum of 24°C in April (Figure 1) (Caner *et al.* 2007). Nocturnal frosts are common in grasslands during the winter (November to March) when temperatures routinely drop down below 0°C, but they are rare occurrences within shola forests. Annual precipitation is spatially and temporally variable across the landscape, ranging from 2500 to 5000 mm, with most of the rainfall received between May and November from the south-west monsoon. (Figure 1). Soils of the area are derived from parent rocks which are gneiss, charnockites and schists (Caner *et al.* 2007). However, C and N contents of shola forest soils are significantly greater than that of adjoining grasslands. The C content of shola forest soils and grassland soils in the top 15 cm average 12.9 and 8.5%, respectively, while soil N values average 0.9 and 0.5%, respectively (Raghurama 2013).

### Study design

In October 2014, we identified three replicate sites in each of four different land-cover types: shola forests, grasslands, wattle patches and pine plantations for the study. Replicate sites within each land-cover type were separated by a minimum distance of 100 m. At each site, we established five soil respiration collars spaced at least 1 m apart from each other in randomly selected locations that were representative of the land-cover type. In all cases, collars were established on gentle south facing slopes and >10 m from habitat edges. Respiration collars were 10 cm long open-ended PVC pipes with an inner diameter of 10 cm, inserted 3 cm into the soil with 7 cm exposed above the soil surface. Collars remained permanently installed in soils throughout the study, with a few exceptions when

collars were lost (due to animal activity or burnt following a fire event) and had to be replaced. In such cases, collars were replaced immediately, and at least a week before the next measurement. In total, we had 60 respiration collars across the different land-cover categories.

Soil respiration was measured every 2 weeks on average at each of the 60 collars using an EGM-4 Environmental Gas Monitor (EGM-4, PP Systems, USA). All measurements were made between 10 am and 4 pm. All plant material, primarily leaf litter, within collars was carefully removed before respiration measurements were taken and placed back after the measurements. $CO_2$ efflux rates were calculated following the procedure outlined in Marthews *et al.* (2014) as follows:

$$R_{UC} = \frac{C_{10} - C_1}{t_{10} - t_1} \times \frac{P}{T_a + 273.15} \times \frac{V_d}{A} \times \frac{44.01 \times 0.36}{R_U} \quad (1)$$

$$R_C = R_{UC} \times \frac{V_d + V_{added}}{V_d} \quad (2)$$

Here, $R_{uc}$ is the soil $CO_2$ efflux calculated without correcting for the added volume of the respiration collar. $C_{10}$-$C_1$ represents the difference in $CO_2$ efflux between the last 10 readings of each measurement cycle (each cycle normally lasting 124 seconds with 4–5 seconds per reading), and $t_{10}$-$t_1$ is the time difference, in seconds, between these measurements. In cases where measurements had less than 10 readings, we used the first and last flux values for the calculations. $P$ represents the ambient atmospheric pressure averaged over the period of measurement, $T_a$ the atmospheric temperature in Kelvin, $V_d$ the volume within the soil respiration chamber, A the soil area over which $CO_2$ efflux was measured, and $R_u$ the Universal Gas Constant ($8.314$ J K$^{-1}$ mol$^{-1}$). Equation (2) was used to estimate $R_c$ – the $CO_2$ efflux corrected for the added volume of the respiration collar at the time of measurement. Further details of the methods and calculations of $CO_2$ efflux can be found in Marthews *et al.* (2014).

Alongside $CO_2$ efflux measurements, ambient atmospheric temperature, soil temperature and soil moisture were also quantified. Soil temperature and moisture were measured at 0–12 cm depth at three locations around each collar using a handheld long-stem thermometer (HI145-00 and HI145-01, Hanna Instruments, USA) and a FieldScout TDR 200 soil moisture metre (Spectrum Technologies, USA), respectively.

For our analyses, we excluded measurements (58 out of 3355) which showed a decline in $CO_2$ accumulation within collars over the time period of measurement and had a negative slope, that is, they were indicative of measurement errors in the field. All data were then averaged by site (i.e., across the five collars) for the analysis. We analysed the effects of land-cover type, soil temperature and soil moisture on soil respiration rates using a linear mixed-effects model framework with the interaction of land-cover type, soil temperature and soil moisture as fixed effects and site as a random effect. Soil respiration values were log-transformed before analyses to meet the assumptions of homogeneity and normality of residuals. We also calculated annual estimates of soil respiration (g $CO_2$ per m$^2$ per yr) for each land-cover type by scaling up the mean hourly $CO_2$ efflux rates (g $CO_2$ per m$^2$ per hr) estimated for each site for the corresponding year (average hourly efflux rates × 24 × 365).

The R package nlme with *lme* (Pinheiro *et al.* 2018) was used to conduct the mixed-effects model analysis. All analyses were conducted using R version 4.0.3 (R Core Team, 2020).
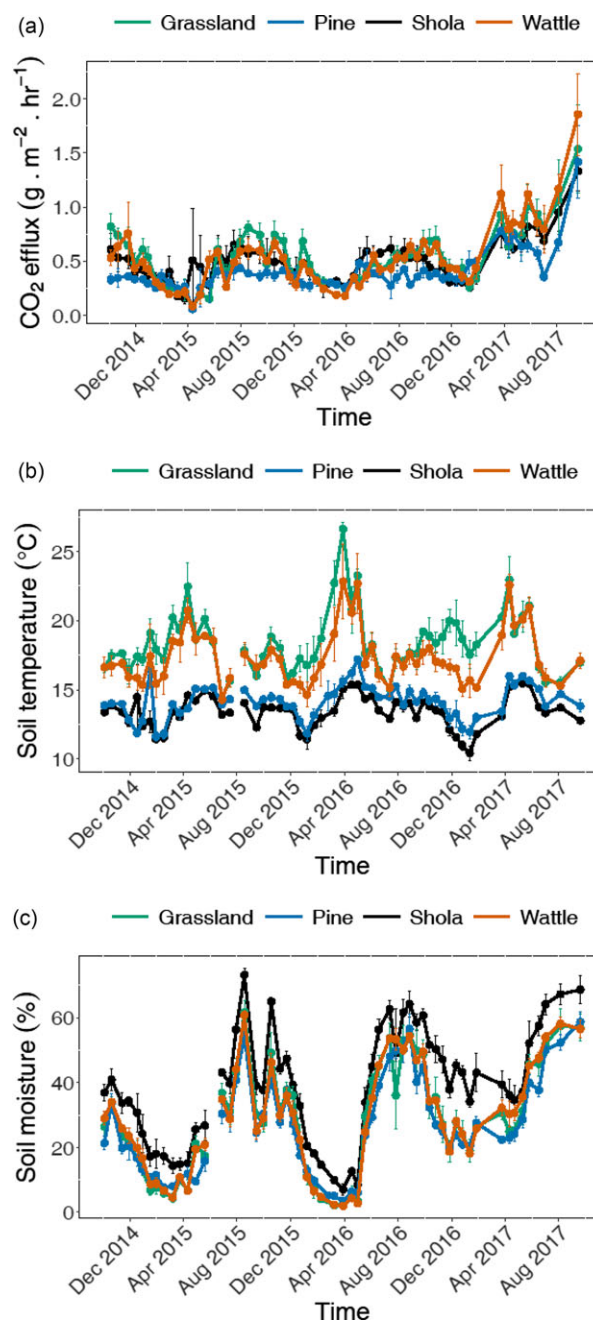


**Figure 2.** Patterns of change in (a) soil respiration, (b) soil temperatures 12 cm below the surface and (c) soil moisture in the top 12 cm over time ($n = 3$). Error bars represent standard errors of the mean (gaps in 2b and 2c are due to lack of measurements during the corresponding period because of instrument failure).

## Results

### Temporal dynamics of soil respiration across land-cover

Soil respiration rates across land-cover types varied both seasonally and annually and ranged from 0.02 to 2.94 g $CO_2$ per m$^2$ per hr across the study in the different land-cover types. Soil $CO_2$ efflux typically peaked during the south-west monsoon season (June–October) and declined through the winter (November–January) to lowest values in summer (February to May; Figure 2a). Highest instantaneous respiration rates were recorded in grasslands (average 0.54 g $CO_2$ per m$^2$ per hr across the study) and lowest rates from pine soils (average 0.41 g $CO_2$ per m$^2$ per hr[1], Table 1;

**Table 1.** Mean soil temperature, soil moisture and soil respiration across the land-cover categories. Range presented in brackets

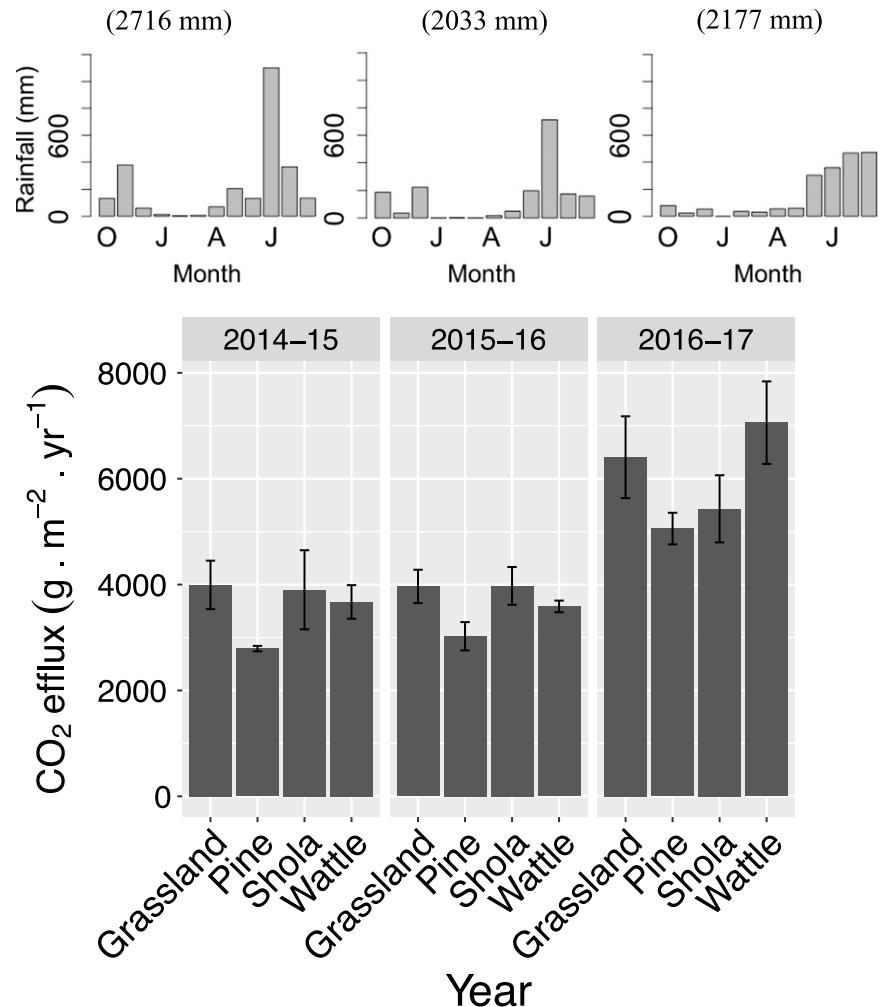| Land-cover category | Soil temperature at 12 cm depth (°C) | Soil moisture in the top 12 cm (%) | Soil respiration ($CO_2$g.m$^{-2}$.hr$^{-1}$) |
| --- | --- | --- | --- |
| Grassland | 18.30 (10.80–31.83) | 28.96 (1.37–70.70) | 0.53 (0.02–2.35) |
| Pine plantation | 14.11 (9.37–21.63) | 26.99 (1.73–70.33) | 0.41 (0.02–2.37) |
| Shola forest | 13.41 (9.09–19.60) | 40.26 (3.43–84.60) | 0.50 (0.02–2.94) |
| Wattle patches | 17.36 (10.85–29.02) | 29.29 (1.1–66.77) | 0.52 (0.02–2.48) |



**Figure 3.** Annual estimates of soil $CO_2$ effluxes across different land-cover types based on three years of monitoring. Bar graphs on the top show monthly precipitation (starting from October to September next year) measured at study sites during the corresponding year, with the total annual precipitation reported within brackets at the top.

Figure 2a). However, annual soil $CO_2$ effluxes did not differ significantly between land-cover categories (one-way ANOVAs, followed by pairwise comparisons using Tukey's Honestly Significant Difference (HSD) test, $P > 0.15$ for all pairwise comparisons for all three years). Across all land-cover categories, annual fluxes were greater in 2016–17 compared to the previous two years (Figure 3).

Seasonal soil $CO_2$ effluxes mirrored patterns in soil moisture. Over the course of the study, soil moisture levels ranged from 1% to 85% (volumetric water content), and not unexpectedly, peaked during the monsoon and were lowest in summer (Figure 2b). Soil moisture levels were higher in shola forests (average 40%) compared to other land-cover categories which did not differ from one another (average: 28%; Table 1). Soil temperature was similarly highly variable and ranged from 9.1 to 31.8°C over the course of the study. As expected, soil temperature also showed a

distinct seasonal pattern, being highest in summer (April) and lowest during the winter (December) (Figure 2c). Temperatures were consistently higher by 3–5°C, but also more variable, in grasslands and wattle patches compared to closed canopy shola forests and pine plantations (Table 1, Figure 2c).

### Interactive effects of land-cover type, soil temperature and moisture on soil respiration

The linear mixed model analysis revealed a marginally significant interactive effect of land-cover type, soil moisture and soil temperature on respiration, collectively explaining 60% of the variation in the data ($F = 2.30$, $df = 3$, $P = 0.07$; Table S1 and Table S2). To visualise this interaction, we modelled soil respiration as a function of temperature for equally spaced soil moisture levels across the different land-cover types (Figure 4). Soil moisture values were fixed at the
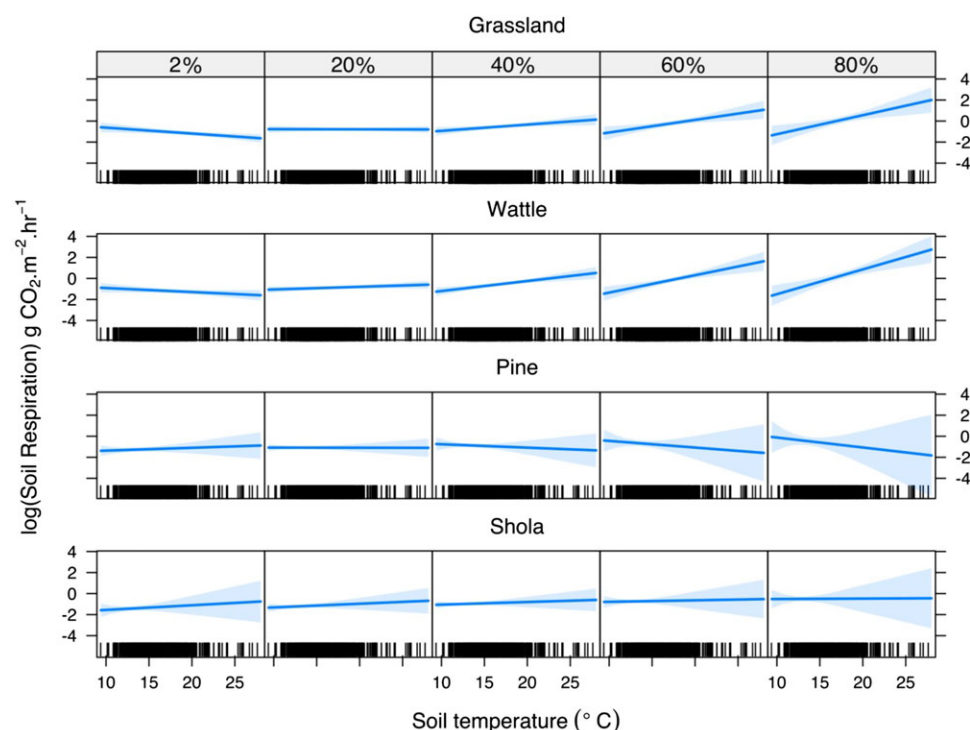
**Figure 4.** Effect plots depicting the interactive effect of soil moisture and soil temperature on soil $CO_2$ effluxes across the different land-cover types (each column represent soil moisture in %).

quantiles of measured instantaneous soil temperature measurements over the study (Figure 4). In both grassland and wattle patches, soil respiration was not affected by soil temperatures when moisture was low but increased with increasing soil temperature at high moisture levels (Figure 4). In pine plantations, respiration was similarly largely unaffected by temperature at low moisture levels but decreased with increasing temperatures when soil moisture was high (Figure 4). In contrast, soil respiration did not seem to be significantly impacted by changes in either soil temperature or moisture in shola forests (Figure 4).

## Discussion

Our results highlight that soil respiration in all focal land-cover categories was primarily governed by precipitation (Davidson *et al.* 2000, Fan *et al.* 2015, Sheng *et al.* 2010), peaking during the monsoon when root growth, microbial activity and litter decomposition are typically high (Singh & Gupta 1977) and dropping to their lowest levels during the summer. However, intra-annual patterns of precipitation distribution also potentially play a role in regulating total annual soil $CO_2$ effluxes in this system. In our study, the highest annual soil respiration levels were recorded during 2016–17 (Figure 3). These high levels were not attributable to greater total rainfall or higher temperatures during this year compared to earlier years. Although the reasons underlying these high respiration levels are unclear, one plausible explanation could be the more even distribution of precipitation recorded during 2016–17, which potentially lengthened the growing season, resulting in the greater overall fluxes recorded (Figure 3).

Across the different land-cover types, lowest mean instantaneous respiration rates were recorded in pine plantations (Table 1, Figure 2), which is consistent with previous large-scale syntheses that report ~10% lower respiration in coniferous stands compared

to adjacent broad-leaved forests (Raich & Tufekciogul 2000, Singh & Gupta 1977). The low rates of soil respiration recorded in pine plantations are potentially attributable to the poor quality and low nutrient content of pine needles and lower soil temperatures, resulting in slower litter decomposition rates and lower soil respiration rates in pine plantations (Balsar & Wixon 2009; Gao *et al.* 2018, Singh & Gupta 1977). Instantaneous soil respiration rates, however, did not differ much between grasslands, shola forests and wattle plantations (Table 1, Figure 2).

Although seasonal patterns of soil respiration were largely governed by soil moisture, instantaneous soil $CO_2$ efflux rates were additionally regulated by soil temperature in ways that differed across land-cover types. In most land-cover types, respiration was largely unaffected, or only marginally increased with soil temperature when moisture levels were low. Low water content is known to limit $CO_2$ production in soils, such that temperature effects are typically manifest only when there is sufficient water to allow root and microbial $CO_2$ production (Schlesinger & Andrews 2000). However, the nature of temperature–respiration relationships at high moisture levels differed between land-cover types (Figure 3). Respiration increased with temperature when moisture was high in both grassland and wattle patches, decreased in the case of pine plantations and remained largely unchanged in shola forests (Figure 3). The reasons underlying these differences are presently unclear but are potentially related to differences in microbial communities, which play significant roles in soil respiration in these systems (Tiruvaimozhi & Sankaran 2019), and their temperature optima in the different land-cover types. A contemporary study in the same grassland has shown that the contribution of microbes to soil respiration is significantly higher than that of roots and arbuscular mycorrhizal fungi (Tiruvaimozhi & Sankaran 2019). Overall, our results suggest that changes in vegetation type can affect soil C cycling not only by changing above and below-ground C stocks and altering microclimate but also by altering the temperature and moisture

sensitivity of soil respiration, potentially through changes in soil microbial communities, even in the absence of any underlying differences in soil type.

## Conclusions

Our results indicate that different vegetation types growing adjacent to one another under the same climatic and environmental conditions can have different soil respiration rates and different sensitivities of soil respiration to temperature and moisture. Soil respiration is a combination of both autotrophic (root) and heterotrophic activity (microbes and soil fauna) (Hanson *et al.* 2000) and is influenced by several factors, including substrate quality and quantity, microbial activity, composition and biomass, and soil temperature and moisture (Bowden *et al.* 2004 and references therein). All of these likely differ between land-cover types, but their relative contributions to the observed differences in soil respiration between land-cover types in our study remains unknown. Continued invasions and changes in land-cover, coupled with changes in temperatures and rainfall climatology, are likely to further alter soil respiration in this system in the future. Given the importance of soil respiration for net ecosystem C balance and global carbon budgets, a better understanding of the factors controlling soil respiration in different land-cover types is critical in order to predict the long-term responses of C-cycles in this ecosystem.

## References

**Arasumani M, Khan D, Vishnudas CK, Muthukumar M, Bunyan M and Robin VV** (2019) Invasion compounds an ecosystem-wide loss to afforestation in the tropical grasslands of the Shola Sky Islands. *Biological Conservation* **230**, 141–150.

**Balser TC and Wixon DL** (2009) Investigating biological control over soil carbon temperature sensitivity. *Global Change Biology*, **15**, 2935–2949.

**Bond-Lamberty B and Thomson A** (2010) Temperature-associated increases in the global soil respiration record. *Nature* **464**, 579.

**Bowden RD, Davidson E, Savage K, Arabia C and Steudler P** (2004) Chronic nitrogen additions reduce total soil respiration and microbial respiration in temperate forest soils at the Harvard Forest. *Forest Ecology and Management* **196**, 43–56.

**Caner L, Seen DL, Gunnell Y, Ramesh BR and Bourgeon G** (2007) Spatial heterogeneity of land cover response to climatic change in the Nilgiri highlands (southern India) since the last Glacial Maximum. *The Holocene* **17**, 195–205.

**Ciais P, Sabine C, Bala G, Bopp L, Brovkin V, Canadell J, Chhabra A, DeFries R, Galloway J, Heimann M and Jones C** (2013) *Carbon and other biogeochemical cycles*. In Stocker TF, Qin D, Plattner GK, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (eds), *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press.

**Davidson EA, Verchot LV, Cattanio JH, Ackerman IL and Carvalho JE** (2000) Effects of soil water content on soil respiration in forests and cattle pastures of eastern Amazonia. *Biogeochemistry* **48**, 53–69.

**DeFries RS, Field CB, Fung I, Collatz GJ and Bounoua L** (1999) Combining satellite data and biogeochemical models to estimate global effects of human-induced land cover change on carbon emissions and primary productivity. *Global Biogeochemical Cycles* **13**, 803–815.

**Delgado-Balbuena J, Arredondo JT, Loescher HW, Huber-Sannwald E, Chavez-Aguilar G, Luna-Luna M and Barretero-Hernandez R** (2013) Differences in plant cover and species composition of semiarid grassland communities of central Mexico and its effects on net ecosystem exchange. *Biogeosciences* **10**, 4673–4690.

**Fan LC, Yang MZ and Han WY** (2015) Soil respiration under different land uses in eastern China. *PloS One* **10**, e0124198.

**Gao W, Huang Z, Ye G, Yue X and Chen Z** (2018) Effects of forest cover types and environmental factors on soil respiration dynamics in a coastal sand dune of subtropical China. *Journal of Forestry Research* **1**, 1–11.

**Hanson RB, Ducklow HW and Field JG** (2000) *The Changing Ocean Carbon Cycle: a Midterm Synthesis of the Joint Global Ocean Flux Study*. Cambridge: Cambridge University Press.

**Hashimoto S, Carvalhais N, Ito A, Migliavacca M, Nishina K and Reichstein M** (2015) Global spatiotemporal distribution of soil respiration modeled using a global database. *Biogeosciences* **12**, 4121–4132.

**Houghton RA, House JI, Pongratz J, Van Der Werf GR, DeFries RS, Hansen MC, Quéré CL and Ramankutty N** (2012) Carbon emissions from land use and land-cover change. *Biogeosciences* **9**, 5125–5142.

**Joshi AA, Sankaran M and Ratnam J** (2018) 'Foresting' the grassland: historical management legacies in forest-grassland mosaics in southern India, and lessons for the conservation of tropical grassy biomes. *Biological Conservation* **224**, 144–152.

**Karunakaran PV, Uniyal VK and Rawat GS** (1998) *Ecology and Conservation of the Grasslands of Eravikulam National Park, Western Ghats*. Dehradun: Wildlife Inst. of India.

**Le Quéré C, Raupach MR, Canadell JG, Marland G, Bopp L, Ciais P, Conway TJ, Doney SC, Feely RA, Foster P and Friedlingstein P** (2009) Trends in the sources and sinks of carbon dioxide. *Nature Geoscience* **2**, 831.

**Marthews TR, Metcalfe D, Malhi Y, Phillips O, HuaracaHuasco W, Riutta T, Ruiz Jaén M, Girardin C, Urrutia R, Butt N, Cain R, OliverasMenor I and colleagues from the RAINFOR** and GEM networks (2014) Measuring Tropical Forest Carbon Allocation and Cycling: A *RAINFOR-GEM* Field Manual for Intensive Census Plots (v2.2). Manual. Global Ecosystems Monitoring network. Available at http://gem.tropicalforests.ox.ac.uk/ (accessed 25 January, 2013).

**Mohandass D and Davidar P** (2009) Floristic structure and diversity of a tropical montane evergreen forest (shola) of the Nilgiri Mountains, southern India. *Tropical Ecology* **50**, 219.

**Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, Kurz WA, Phillips OL, Shvidenko A, Lewis SL, Canadell JG and Ciais P** (2011) A large and persistent carbon sink in the world's forests. *Science* **333**, 988–993.

**Parr CL, Lehmann CE, Bond WJ, Hoffmann WA and Andersen AN** (2014) Tropical grassy biomes: misunderstood, neglected, and under threat. *Trends in Ecology & Evolution* **29**, 205–213.

**Pinheiro J, Bates D, DebRoy S, Sarkar D and R Core Team** (2018) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1–131. Available at https://CRAN.R-project.org/package=nlme (accessed 30 September, 2017).

**Prabhakar R** (1994) *Resource, Use, Culture And Ecological Change: A Case Study Of The Nilgiri Hills Of Southern India*. Bangalore, India: Centre for Ecological Sciences, Indian Institute of Science.

**Raghurama M** (2013) *Variation in the Sequestration of Carbon and Nitrogen in Soils with change in Vegetation and Depth: A study in the Nilgiri Mountains, India.* Pilani (Rajasthan): Birla Institute Of Technology and Science.

**Raich JW and Schlesinger WH** (1992) The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus B* **44**, 81–99.

**Raich JW and Tufekciogul A** (2000) Vegetation and soil respiration: correlations and controls. *Biogeochemistry* **48**, 71–90.

**Robin VV and Sukumar R** (2002) Status and habitat preference of white-bellied ShortwingBrachypteryx major in the Western Ghats (Kerala and Tamilnadu), India. *Bird Conservation International* **12**, 335–351.

**Schaller GB** (1970) Observations on Nilgiri tahr (*Hemitragus hylocrius* Ogilby, 1838). *Journal of the Bombay Natural History Society* **67**, 365–389.

**Scharlemann JP, Tanner EV, Hiederer R and Kapos V** (2014) Global soil carbon: understanding and managing the largest terrestrial carbon pool. *Carbon Management* **5**, 81–91.

**Schlesinger WH and Andrews JA** (2000) Soil respiration and the global carbon cycle. *Biogeochemistry* **48**, 7–20.

**Sheng HA, Yang Y, Yang Z, Chen G, Xie J, Guo J and Zou S** (2010) The dynamic response of soil respiration to land-use changes in subtropical China. *Global Change Biology* **16**, 1107–1121.

**Singh JS and Gupta SR** (1977) Plant decomposition and soil respiration in terrestrial ecosystems. *The Botanical Review* **43**, 449–528.

**Sukumar R, Ramesh R, Pant RK and Rajagopalan G** (1993) A δ13C record of late quaternary climate change from tropical peats in southern India. *Nature* **364**, 703.

**Sukumar R, Suresh HS and Ramesh R** (1995) Climate change and its impact on tropical montane ecosystems in southern India. *Journal of Biogeography* **1**, 533–536.

**Team RC** (2020) *R: A Language and Environment for Statistical Computing.* Vienna, Austria: R Foundation for Statistical Computing.

**Thomas S and Palmer M** (2007) The montane grasslands of the Western Ghats, India: community ecology and conservation. *Community Ecology* **8**, 67–73.

**Tiruvaimozhi YV & Sankaran M** (2019). Soil respiration in a tropical montane grassland ecosystem is largely heterotroph-driven and increases under simulated warming. *Agricultural and Forest Meteorology* **276**, 107619.

**Veldman JW, Overbeck GE, Negreiros D, Mahy G, Le Stradic S, Fernandes GW, Durigan G, Buisson E, Putz FE and Bond WJ** (2015) Tyranny of trees in grassy biomes. *Science* **347**, 484–485.