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

Atul Arvind Joshi[1, 2], Jayashree Ratnam[1], Harinandanan Paramjyothi[1, 3],Mahesh Sankaran[1, 4]

[1] National Centre for Biological Sciences (NCBS), Tata Institute of Fundamental Research, GKVK Campus, Bellary Road, Bangalore, Karnataka 560065, India

[2] Manipal Academy of Higher Education, Manipal, Karnataka 576104, India

[3] Research Institute for the Environment and Livelihoods, Charles Darwin University, Darwin NT 0909, Australia

[4] School of Biology, University of Leeds, Leeds LS2 9JT, UK

* Corresponding author

E-mail: atulj@ncbs.res.in

Author contribution:

Atul Arvind Joshi: Conceptualization, Methodology, Formal analysis, Investigation, Writing: Original draft

Jayashree Ratnam: Methodology, Writing: review and editing

Harinandanan Paramjyothi: Investigation

Mahesh Sankaran: Conceptualization, Methodology, Formal analysis, Funding acquisition, Supervision, Writing: review and editing

Abstract

Land-use conversion to non-native species plantations not only affects biodiversity but also alters important ecosystem functions including above- and below-ground carbon sequestration, and CO_2 release rates from soils via soil respiration. Though the role of soil temperature and moisture on soil respiration is well recognized, little is known about how their effects vary across different land-use types. This study looked at the effects of land-cover change on temporal patterns of soil respiration in a montane forest-grassland-plantation matrix, a highly diverse but climatically sensitive ecosystem in the tropical Western Ghats of India. Among native vegetation types, soil respiration rates were higher in grassland compared to forest patches. Invasion of grassland by an exotic tree species - wattle (*Acacia mearnsii*) reduced soil respiration rates to levels similar to that of forests. However, conversion of native grasslands to non-native pine (*Pinus patula*) plantations led to the largest declines in soil respiration rates. 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.

Keywords: Shola-grassland, climate change, soil carbon, land-use, plantations, invasion

Introduction

Terrestrial ecosystems, including vegetation and soils, are important components of the global carbon pool, together accounting for about ~2060 Pg of carbon, with about three

quarters of this being stored in soils [1,2]. 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, currently releasing ~75-100 Pg/year back to the atmosphere [3,4]. 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 as well as 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 [3]. The tropics currently contribute ~67% of the global soil CO_2 efflux [1,4,5]. Future changes in temperature and precipitation regimes in tropical regions are therefore likely to affect soil respiration rates with potentially significant effects on the global C-cycle and atmospheric CO_2 levels [1].

Besides climatic variables, changes in land use and land cover also influence global terrestrial-atmosphere CO_2 fluxes. Since the 1990's, ~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 [6-9]. Land-use 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 [3, 10-12]. However, the impact of such land-use changes on ecosystem processes, particularly in tropical regions, has received very little attention. More accurate quantification of the effects of land-use 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 the substantial proportion of the emissions due to land-use changes [13].

In this study, we quantified soil CO_2 effluxes over three years across different land-use types in the climatically sensitive tropical montane forest-grassland mosaics of the Western Ghats biodiversity hotspot in India. These mosaics have undergone extensive land-use 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*). Specifically, we looked at how land-cover changes influenced both total and temporal patterns in 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 (Fig1). The upper reaches (1200 m to 2650 m) of India's Western Ghats biodiversity hotspot (8° to 21°N, 73° to 78°E) are characterized by stunted evergreen tree forest patches, locally known as sholas, embedded within grasslands, with abrupt transitions between them (Fig 1). These bi-phasic mosaics are Pleistocene relics that have been in existence for more than 20,000 years [14,15], and support a diverse array of plant and animal species, many of which are endemic [See:16-20].

Large-scale plantations of alien tree species, chiefly of eucalyptus (*Eucalyptusglobulus*), pine (*Pinuspatula*) and wattle (*A. mearnsii*) were established in grasslands of this landscape in the latter half of the nineteenth century [21,22]. Among these, wattle eventually became invasive and now occupies large tracts of former grassland. The landscape is currently characterized

by a mix of native and exotic vegetation. The prominent land-cover types include native shola forests, grasslands, invasive wattle patches, and plantations of eucalyptus, pine and commercial tea. We selected four land-use types for this study that were in close proximity to each other - native shola forests, grasslands, invasive wattle patches and pine plantations.

Fig 1. Map showing the distribution of shola-grassland ecosystems across the Western Ghats biodiversity hot-spot, with the study area circled. (Reproduced with modification from Das et al. 2015 [23]).

Average annual temperatures in the study area range from a minimum of 5°C in January to a maximum of 24°C in April [24]. Nocturnal frosts are common in grasslands during the winter (November to March) when temperatures routinely drop down below 0°C. Annual precipitation is spatially and temporally variable across the landscape, ranging from 2500 to 5000mm, with most of the rainfall received between June and October from the south-west monsoon. Soils of the area are derived from parent rocks which are gneiss, charnockites and schists [24].

Study design

In October 2014, we identified three replicate sites in each of four different land-use types: shola forests, grasslands, wattle patchesand pine plantations for the study. Replicate sites within each land-use type were separated by a minimum distance of 100m. At each site, we established five soil respiration collars spaced at least 1m apart from each other. Respiration collars were 10cm long open-ended PVC pipes with an inner diameter of 10cm, inserted 3cm into the soil with 7cm exposed above the soil surface. Collars remained permanently installed in the soil 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

119 replaced immediately, and at least a week before the next measurement. In total, we had 60
120 respiration collars across the different land use categories.
121
122 Soil respiration was measured every 2 weeks at each of the 60 collars using an EGM-4
123 Environmental Gas Monitor (EGM-4, PP Systems, USA). All measurements were made
124 between 10 am and 4 pm. All plant material, primarily litter, within collars was carefully
125 removed before respiration measurements were taken. CO_2 efflux rates were calculated
126 following Marthews et al. 2014 [25]. Alongside CO_2 efflux measurements, ambient
127 atmospheric temperature, soil temperature and soil moisture were also quantified. Soil
128 temperature and soil moisture were measured at 0-12 cm depth at three locations around each
129 collar using a handheld long-stem thermometer (HI145-00 and HI145-01, Hanna Instruments,
130 USA) and soil moisture using a FieldScout TDR 200 soil moisture meter (Spectrum
131 Technologies, USA), respectively.
132
133 Given the possibility of measurement errors in CO_2 effluxes while using the EGM in the
134 field, only those CO_2 efflux measurements which satisfied a criterion of a positive slope with
135 when CO_2 accumulation was plotted against time, with $R^2 \geq 0.9$, were used in subsequent
136 analyses [26]. Further, we expected soil respiration values to be similar among the five
137 replicate collars within a site. In cases where CO_2 efflux of an individual respiration collar
138 was less than half or greater than twice the mean of the CO_2 efflux of the other four adjacent
139 respiration collars at a site, the measurement was removed from the dataset. All data were
140 then averaged by site for the analysis. Annual estimates of soil respiration ($g.m^{-2}.yr^{-1}$) for
141 each land-use type were obtained by scaling up the mean hourly CO_2 efflux rates ($g.m^{-2}.hr^{-1}$)
142 estimated for each site for the corresponding year.
143

144 We analysed the effects of land-use type, soil temperature and soil moisture on soil
145 respiration using a linear mixed effect model framework with the interaction of land-use type,
146 soil temperature and soil moisture as fixed effects and site as a random effect. Soil respiration
147 values were log transformed before analyses to meet the assumptions of homogeneity and
148 normality of residuals.
149
150 The R package nlme with *lme* [27] was used to conduct the mixed effect model analysis. All
151 analyses were conducted using R version 3.3.2 [28].

152 **Results**

153 *Temporal dynamics of soil respiration across land-uses*

154 Soil respiration rates across land-use types varied both seasonally and annually, and ranged
155 from 0.07 to 2.2 CO_2 $g.m^{-2}.hr^{-1}$ across the study in the different land use types. Soil CO_2
156 efflux typically peaked during the south-west monsoon season (June-October), and declined
157 through the winter (November - January) to lowest values in summer (February to May; Fig
158 2a). Highest respiration rates were recorded in grasslands (average 0.57 $g.m^{-2}.hr^{-1}$ across the
159 study) and lowest rates from pine soils (average 0.42 $g.m^{-2}.hr^{-1}$, Table 1; Fig 2a). Annual soil
160 CO_2 effluxes in all land-use types were higher in 2016-17 compared to the previous two years
161 (Fig 3). This increase appears to be associated with a more even distribution of precipitation
162 throughout the year rather than higher total rainfall amounts (Fig 3).
163 **Fig 2. Patterns of change in a) soil respiration, b) soil moisture 0-12cm below the surface**
164 **and c) soil temperature 0-12 cm below surface over time (n=12). (gaps in 2b and 2c are**
165 **due to no measurements during the correspondent period because of instrument**
166 **failure).**
167 **Fig 3. Annual estimates of soil CO_2 effluxes across different land-use types based on**

three years of monitoring. Bar graphs on top show monthly precipitation measured at study sites during the corresponding year. Total precipitation during the corresponding year are shown in brackets on top of bar graphs.

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

Land-use category	Soil temperature at 0-12cm depth (℃)	Soil moisture at 0-12cm depth (%)	Soil respiration ($CO_2 g.m^{-2}.hr^{-1}$)
Grassland	18.3 (10.8-31.8)	29.7 (1.4-70.7)	0.57 (0.14-2.2)
Pine plantation	14.1(10.1-21.6)	28.2 (1.7-70.3)	0.42 (0.10-2.2)
Shola forest	13.4 (9.2-19.6)	41.7 (3.4-84.6)	0.51 (0.07-1.73)
Wattle patches	17.4 (11.6-29.0)	29.7 (1.1-66.8)	0.52 (0.10-1.9)

Seasonal soil CO_2 effluxes mirrored patterns in soil moisture. Over the course of the study, soil moisture levels ranged from 1% to 85%, and not unexpectedly, peaked during the monsoon and were lowest in summer (Fig 2b). Soil moisture levels were higher in shola forests (average 42%) compared to other land-use categories which did not differ from one another (average: 29%; Table 1). Soil temperature was similarly highly variable and ranged from 9.2 to 31.8℃ 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) (Fig 2c). Temperatures were consistently higher, but also more variable in grasslands and wattle patches compared to closed canopy shola forests and pine plantations (Table 1, Fig 2c).

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

The linear mixed model analysis revealed a significant interactive effect of land-use type, soil moisture and soil temperature on respiration, collectively explaining 66% of the variation in the data ($F = 4.48$, $df = 3$, $P = 0.004$; Table S1). To visualize this interaction, we modelled soil respiration as a function of temperature for fixed soil moisture levels across the different land use types (Fig 4). Soil moisture values were fixed at the quantiles of measured instantaneous soil temperature measurements over the study (Fig 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 (Fig 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 (Fig 4). In contrast, soil respiration did not seem to be significantly impacted by changes in either soil temperature or moisture in shola forests (Fig 4).

Fig 4. Effect plots depicting the interactive effect of soil moisture and soil temperature across the different land-use types (Each column represent soil moisture in %).

Discussion

Our results indicate that land-use changes have substantially altered CO_2 fluxes in this ecosystem. Grasslands consistently had higher CO_2 effluxes when compared to native shola forests. However, conversion of natural grasslands to alien pine plantations and invasive wattle patches has lowered soil respiration rates. The direction and magnitude of effects on soil respiration due to these land-use changes appear to be collectively governed by the identity of the associated tree species as well as their impacts on local micro-climates. Reductions in soil C effluxes were highest following conversion of grasslands to pine plantations, and somewhat lower following invasion of grasslands by wattle. In addition, conversion of grassland to pine plantations also appears to have altered the sensitivity of soil respiration to changes in soil temperature and moisture.

211

212 Soil respiration in all focal land-use categories was primarily governed by precipitation [29-
213 31], peaking during the monsoon when root growth, microbial activity and litter
214 decomposition are typically high [32] and dropping to their lowest levels during the summer.
215 However, intra-annual patterns of precipitation distribution also appear to play an important
216 role in regulating total annual soil CO_2 effluxes in this system. The highest annual soil
217 respiration levels recorded during 2016-17 in our study (Fig 3) coincided with a more even
218 distribution of precipitation through the year, and a potential lengthening of the growing
219 season, rather than higher overall precipitation during the year.

220

221 Across the different land-use types, highest rates of soil respiration rates were recorded in
222 grasslands (Table 1, Fig 3), which is in accordance with previous global syntheses that have
223 reported ~20% higher respiration in grasslands than in comparable forest stands [33].
224 Respiration rates in shola forests were lower by comparison (Table 1, Fig 3). Invasion of
225 grasslands by wattle reduced soil respiration rates to levels similar to those of natural shola
226 forests while, conversion of grasslands to pine plantations was associated with the greatest
227 reductions in soil respiration (Table 1, Fig 3), consistent with previous large-scale syntheses
228 that report ~10% lower respiration in coniferous stands compared to adjacent broad-leaved
229 forests [32,33]. The low rates of soil respiration recorded in pine plantations is potentially
230 attributable to the poor quality and low nutrient content of pine needles, resulting in slower
231 litter decomposition rates and lower soil respiration rates in pine plantations [32].

232

233 Although seasonal patterns of soil respiration were largely governed by soil moisture,
234 instantaneous soil CO_2 efflux rates were additionally regulated by soil temperature in ways
235 that differed across land-use types. In most land-use types, respiration was largely unaffected,

236 or only marginally increased with soil temperature when moisture levels were low. Low
237 water content is known to limit CO_2 production in soils, such that temperature effects are
238 typically manifest only when there is sufficient water to allow root and microbial CO_2
239 production [29]. However, the nature of temperature-respiration relationships at high
240 moisture levels differed between land-use types (Fig 4). Respiration increased with
241 temperature when moisture was high in both grassland and wattle patches, decreased in the
242 case of pine plantations, and remained largely unchanged in shola forests (Fig 4). The
243 reasons underlying these differences are presently unclear, but are potentially related to
244 differences in the temperature optima of microbial communities in the different land-use
245 types. Given that pine plantations were originally grassland, these results suggest that
246 changes in vegetation type can affect soil C cycling not only by changing above and below-
247 ground C stocks, but also by altering the temperature and moisture sensitivity of respiration
248 even in the absence of any underlying differences in soil type.

249

250 **Conclusions**

251 Our results indicate that different vegetation types growing adjacent to one another under the
252 same climatic and environmental conditions can have different soil respiration rates and
253 different sensitivities of soil respiration to temperature and moisture [20]. Soil respiration is
254 a combination of both autotrophic (root) and heterotrophic activity (microbes, soil fauna)
255 [34], and is influenced by several factors including substrate quality and quantity, microbial
256 activity, composition and biomass, and soil temperature and moisture [35 and references
257 therein). All of these likely differ between land-use types, but their relative contributions to
258 the observed differences in soil respiration between land-use types in our study remains
259 unknown. What is clear, however, is that past changes in land use and invasions by exotic

species have significantly altered C cycling in this system. Continued invasions and changes in land-use, 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-use types is critical in order to predict the long-term responses of C-cycles in this ecosystem.

Acknowledgements

We thank Ministry of Earth Sciences, India (Grant Number: MoES/NERC/16/02/10 PC-11) and National Centre for Biological Sciences, Bangalore for financial support for conducting this study. We are grateful to Tamil Nadu Forest Department for permits. We thank Dr. Jagdish Krishnaswamy (ATREE) and Dr. Ravi Bhalla (FERAL) for sharing precipitation data, and Dr. Kavita Isvaran, Nachiket Kelkar, and Dr. Varun Varma for help with the analysis. We also thank Amol, Kavita, Manaswi, Selvakumar, Susilan, Yadugiri, the FERAL field team in the Nilgiris, residents of Emerald village and the frontline staff of the Nilgiri South Forest Division of Tamil Nadu Forest Department for all their help during field data collection.

References

1. Schlesinger WH, Andrews JA. Soil respiration and the global carbon cycle. Biogeochemistry. 2000 Jan 1;48(1):7-20.
2. Scharlemann JP, Tanner EV, Hiederer R, Kapos V. Global soil carbon: understanding and managing the largest terrestrial carbon pool. Carbon Management. 2014 Feb 1;5(1):81-91.

3. Raich JW, Schlesinger WH. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus B. 1992 Apr;44(2):81-99.
4. Bond-Lamberty B, Thomson A. Temperature-associated increases in the global soil respiration record. Nature. 2010 Mar;464(7288):579.
5. Hashimoto S, Carvalhais N, Ito A, Migliavacca M, Nishina K, Reichstein M. Global spatiotemporal distribution of soil respiration modeled using a global database. Biogeosciences. 2015;12:4121-32.
6. DeFries RS, Field CB, Fung I, Collatz GJ, Bounoua L. 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. 1999 Sep 1;13(3):803-15.
7. Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, Kurz WA, Phillips OL, Shvidenko A, Lewis SL, Canadell JG, Ciais P. A large and persistent carbon sink in the world's forests. Science. 2011 Jul 14:1201609.
8. Houghton RA, House JI, Pongratz J, Van Der Werf GR, DeFries RS, Hansen MC, Quéré CL, Ramankutty N. Carbon emissions from land use and land-cover change. Biogeosciences. 2012 Dec 13;9(12):5125-42.
9. Ciais P, Sabine C, Bala G, Bopp L, Brovkin V, Canadell J, Chhabra A, DeFries R, Galloway J, Heimann M, Jones C. 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.
10. Delgado-Balbuena J, Arredondo JT, Loescher HW, Huber-Sannwald E, Chavez-Aguilar G, Luna-Luna M, Barretero-Hernandez R. Differences in plant cover and

species composition of semiarid grassland communities of central Mexico and its effects on net ecosystem exchange. Biogeosciences. 2013 Jul 12;10(7):4673-90.

11. Parr CL, Lehmann CE, Bond WJ, Hoffmann WA, Andersen AN. Tropical grassy biomes: misunderstood, neglected, and under threat. Trends in ecology & evolution. 2014 Apr 1;29(4):205-13.
12. Veldman JW, Overbeck GE, Negreiros D, Mahy G, Le Stradic S, Fernandes GW, Durigan G, Buisson E, Putz FE, Bond WJ. Tyranny of trees in grassy biomes. Science. 2015 Jan 30;347(6221):484-5.
13. Le Quéré C, Raupach MR, Canadell JG, Marland G, Bopp L, Ciais P, Conway TJ, Doney SC, Feely RA, Foster P, Friedlingstein P. Trends in the sources and sinks of carbon dioxide. Nature geoscience. 2009 Dec;2(12):831.
14. Sukumar R, Ramesh R, Pant RK, Rajagopalan G. A δ13C record of late Quaternary climate change from tropical peats in southern India. Nature. 1993 Aug;364(6439):703.
15. Sukumar R, Suresh HS, Ramesh R. Climate change and its impact on tropical montane ecosystems in southern India. Journal of Biogeography. 1995 Mar 1:533-6.
16. Schaller GB. Observations on Nilgiri tahr (Hemitragus hylocrius Ogilby, 1838). Journal of the Bombay Natural History Society. 1970;67(3):365-89.
17. Karunakaran PV, Uniyal VK, Rawat GS. Ecology and conservation of the grasslands of Eravikulam National Park, Western Ghats. Wildlife Inst. of India; 1998.
18. Robin VV, Sukumar R. Status and habitat preference of White-bellied Shortwing Brachypteryx major in the Western Ghats (Kerala and Tamilnadu), India. Bird Conservation International. 2002 Dec;12(4):335-51.
19. Thomas S, Palmer M. The montane grasslands of the Western Ghats, India: community ecology and conservation. Community Ecology. 2007 Apr 23;8(1):67-73.

20. Mohandass D, Davidar P. Floristic structure and diversity of a tropical montane evergreen forest (shola) of the Nilgiri Mountains, southern India. Tropical Ecology. 2009 Dec 1;50(2):219.
21. Prabhakar R. Resource, Use, Culture And Ecological Change: A Case Study Of The Nilgiri Hills Of Southern India.
22. Joshi AA, Sankaran M, Ratnam J. 'Foresting'the grassland: Historical management legacies in forest-grassland mosaics in southern India, and lessons for the conservation of tropical grassy biomes. Biological Conservation. 2018 Aug 31;224:144-52.
23. Das A, Nagendra H, Anand M, Bunyan M. Topographic and bioclimatic determinants of the occurrence of forest and grassland in tropical montane forest-grassland mosaics of the Western Ghats, India. PloS one. 2015 Jun 29;10(6):e0130566.
24. Caner L, Seen DL, Gunnell Y, Ramesh BR, Bourgeon G. Spatial heterogeneity of land cover response to climatic change in the Nilgiri highlands (southern India) since the Last Glacial Maximum. The Holocene. 2007 Feb;17(2):195-205.
25. Marthews TR, Metcalfe D, Malhi Y, Phillips O, Huaraca Huasco W, Riutta T, Ruiz Jaén M, Girardin C, Urrutia R, Butt N, Cain R, Oliveras Menor I and colleagues from the RAINFOR and GEM networks. Measuring Tropical Forest Carbon Allocation and Cycling: A *RAINFOR-GEM* Field Manual for Intensive Census Plots (v2.2). Manual. 2012; Global Ecosystems Monitoring network, http://gem.tropicalforests.ox.ac.uk/.
26. Savage K, Davidson EA, Richardson AD. A conceptual and practical approach to data quality and analysis procedures for high-frequency soil respiration measurements. Functional Ecology. 2008 Dec 1;22(6):1000-7.
27. 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. 2018 Apr 7,

https://CRAN.R-project.org/package=nlme.

28. Team RC. R: A language and environment for statistical computing.R Foundation for Statistical Computing, Vienna, Austria. 2014.
29. Davidson EA, Verchot LV, Cattanio JH, Ackerman IL, Carvalho JE. Effects of soil water content on soil respiration in forests and cattle pastures of eastern Amazonia. Biogeochemistry. 2000 Jan 1;48(1):53-69.
30. Sheng HA, Yang Y, Yang Z, Chen G, Xie J, Guo J, Zou S. The dynamic response of soil respiration to land-use changes in subtropical China. Global Change Biology. 2010 Mar;16(3):1107-21.
31. Fan LC, Yang MZ, Han WY. Soil respiration under different land uses in eastern China. PloS one. 2015 Apr 13;10(4):e0124198.
32. Singh JS, Gupta SR. Plant decomposition and soil respiration in terrestrial ecosystems. The botanical review. 1977 Oct 1;43(4):449-528.
33. Raich JW, Tufekciogul A. Vegetation and soil respiration: correlations and controls. Biogeochemistry. 2000 Jan 1;48(1):71-90.
34. Hanson RB, Ducklow HW, Field JG, editors. The changing ocean carbon cycle: a midterm synthesis of the Joint Global Ocean Flux Study. Cambridge University Press; 2000 Jan 13.
35. Bowden RD, Davidson E, Savage K, Arabia C, Steudler P. Chronic nitrogen additions reduce total soil respiration and microbial respiration in temperate forest soils at the Harvard Forest. Forest Ecology and Management. 2004 Jul 12;196(1):43-56.

Supporting information caption

S1 Table. Linear mixed effect (LME) model of the interactive effect of land-use types, soil moisture and soil temperature on the soil respiration.