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The sensitivity of soil respiration to soil temperature, moisture, and carbon supply at the global scale

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Abstract

Soil respiration (Rs) is a major pathway by which fixed carbon in the biosphere is returned to the atmosphere, yet there are limits to our ability to predict respiration rates using environmental drivers at the global scale. While temperature, moisture, carbon supply, and other site characteristics are known to regulate soil respiration rates at plot scales within certain biomes, quantitative frameworks for evaluating the relative importance of these factors across different biomes and at the global scale require tests of the relationships between field estimates and global climatic data. This study evaluates the factors driving Rs at the global scale by linking global datasets of soil moisture, soil temperature, primary productivity, and soil carbon estimates with observations of annual Rs from the Global Soil Respiration Database (SRDB). We find that calibrating models with parabolic soil moisture functions can improve predictive power over similar models with asymptotic functions of mean annual precipitation. Soil temperature is comparable with previously reported air temperature observations used in predicting Rs and is the dominant driver of Rs in global models; however, within certain biomes soil moisture and soil carbon emerge as dominant predictors of Rs. We identify regions where typical temperature-driven responses are further mediated by soil moisture, precipitation, and carbon supply and regions in which environmental controls on high Rs values are difficult to ascertain due to limited field data. Because soil moisture integrates temperature and precipitation dynamics, it can more directly constrain the heterotrophic component of Rs, but global-scale models tend to smooth its spatial heterogeneity by aggregating factors that increase moisture variability within and across biomes. We compare statistical and mechanistic models that provide independent estimates of global Rs ranging from 83 to 108 Pg yr^{-1}, but also highlight regions of uncertainty where more observations are required or environmental controls are hard to constrain.

Keywords: climate change, global carbon cycle, primary productivity, soil moisture, soil respiration, soil temperature

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Introduction

Global soils store over 1500 Pg of carbon (C), more than the atmosphere and terrestrial plant biomass combined (Scharlemann *et al.*, 2014). Each year, soil respiration pathways release 75–100 Pg C to the atmosphere as CO$_2$, outweighing fossil fuel emissions by an order of magnitude (Bond-Lamberty & Thomson, 2010a,b; Ballantyne *et al.*, 2015). Despite the importance of soil respiration (Rs) as an ecosystem carbon source, our understanding of global constraints to Rs and its sensitivity to changing climate conditions remains uncertain (Falkowski *et al.*, 2000; Emmett *et al.*, 2004; Seneviratne *et al.*, 2010; Wu *et al.*, 2011). Assessments of global- and biome-level net ecosystem exchange require applying climatic controls on Rs that are limited by scales of measurement (Jones *et al.*, 2003; Exbrayat *et al.*, 2013; Yang *et al.*, 2013; Xiao *et al.*, 2014). Because soils contain plant roots as well as microbial communities, soil respiration integrates both autotrophic and heterotrophic respiration processes, which are difficult to disentangle at both small and large spatial scales. Autotrophic respiration, however, is generally considered to be proportional to gross primary productivity (GPP), and total soil respiration measurements have been used to explore climatic controls on heterotrophic respiration (Rustad *et al.*, 2000; Raich *et al.*, 2002; Wieder *et al.*, 2013).

Quantitative models of Rs typically depend upon local-scale measurements of available energy, water, and carbon or upon global-scale observations informed by satellite measurements, using precipitation as a proxy for water availability and other broad assumptions. However, relatively few studies have assessed global variations in soil respiration with a large number of empirical measurements that can help bridge the gap between local, regional, and global scales (Rustad *et al.*, 2000; Seneviratne *et al.*, 2010; Hashimoto *et al.*, 2015; Sierra *et al.*, 2015). Specifically, soil moisture controls on

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respiration have not been evaluated from observations at the global scale.

In order for global land models to more accurately simulate the sensitivity of Rs to temperature, moisture, and productivity, biome-specific parameters may need to be developed in conjunction with estimates of NPP and soil carbon content. Many of the temperature and moisture scalars, thresholds, and optima in these models are assumed to be constant or change very little among biomes in the absence of more detailed information (Exbrayat *et al.*, 2013; Yang *et al.*, 2013; Yi *et al.* 2011). Site-specific and regional studies, however, suggest that the relative importance of factors like soil moisture or carbon content varies across different biomes due to soil properties (Davidson & Janssens, 2006; Moyano *et al.*, 2013), seasonality of precipitation (Chimner & Welker, 2005; Wei *et al.*, 2010; Wang *et al.*, 2013), vegetation characteristics, or other factors (Pacific *et al.*, 2009; Suseela *et al.*, 2012; Fissore *et al.*, 2013). Global land model simulations of terrestrial carbon fluxes that incorporate Rs components are commonly calibrated and validated against eddy covariance measurements of net ecosystem carbon exchange (Yang *et al.*, 2013), but to our knowledge these models have not yet been validated using remote-sensing data and field measurements of Rs.

The Global Soil Respiration Database (Bond-Lamberty & Thomson, 2010a,b) updates the collection of soil respiration studies originally analyzed by Raich & Schlesinger (1992) and contains 4387 observations of Rs from 1971 to the present. This database (SRDB version 2) reports location information and measurement data for about 3500 studies that report an annual integrated soil respiration flux. These measurements span a wide breadth of space and time, although most observations represent recent years and northern temperate latitudes. Recently these data have been used to show an apparent increase in soil respiration in response to warming surface temperatures and changes in precipitation (Bond-Lamberty & Thomson, 2010a,b; Hashimoto *et al.*, 2015), outline uncertainty in nonbiological influences of soil respiration (Rey, 2014), question the climate and vegetation controls on heterotrophic respiration functions implemented in earth-system models (Shao *et al.*, 2013), and assess precipitation and temperature sensitivity at different scales (Sierra *et al.*, 2015). We contribute to this growing body of work by linking Rs observations to independent estimates of soil moisture, precipitation, soil temperature, vegetation net and gross primary production (NPP, GPP), and soil carbon content from datasets designed for studies at regional and global scales. This study explores the extent to which soil respiration is controlled by these environmental factors at global and biome scales and incorporates these empirical constraints into statistical models built on mechanistic bases for predicting Rs. These analyses identify dominant factors regulating Rs in different biomes and highlight uncertainty around the relative importance of these environmental factors across biomes when incorporated into global predictions.

Materials and methods

Data assembly and integration

We linked soil moisture and temperature estimates from the global ERA-Interim re-analysis product (Berrisford *et al.*, 2011; Dee *et al.*, 2011) from the period 1979 to the present (0.5-degree resolution) to annual respiration values from the SRDB. We used soil temperature and soil moisture estimates for level 1 (surface, <20 cm) depths, and we collected daily mean estimates for each of these variables before aggregating them into annual statistics. Satellite data were queried for locations and years corresponding with annual Rs estimates from the SRDB. We collected annual GPP and NPP values in the same fashion from two sources: the satellite observation-based 1-km resolution MODIS (Moderate Resolution Imaging Spectroradiometer) MOD-17A2/3 (Collection 5) global product (Running *et al.*, 2004; Zhao *et al.* 2005), covering 2000–2012, and AVHRR (Advanced Very High Resolution Radiometer)-based Global Production Efficiency Model product, distributed by the University of Maryland’s Global Land Cover Facility and covering 1979–1999 (Prince & Small, 2003). Annual GPP figures for the years 2000–2012 were aggregated from 8-day values. We collected soil organic carbon estimates (both total soil column parameters and upper 20 cm topsoil carbon estimates) and other site variables, such as soil pH, from the Soilgrids 1 km product, distributed by the International Soil Reference and Information Centre (Hengl *et al.*, 2014). Land cover classification and vegetation characteristics were derived from MOD-17’s collection-5 plant functional types (Friedl *et al.*, 2010) as well as vegetation descriptions in the SRDB, and we partitioned the resultant dataset into nine global biomes characterized by similarities in climate and vegetation type (Fig. 1).

Gridded datasets were queried for locations and years corresponding with annual Rs estimates from the SRDB. For our analysis, we filtered the SRDB to eliminate those studies that are unlikely to represent typical soil respiration efflux at the mismatched spatial scale of the global grid-cell observations by eliminating manipulative studies and those flagged by the SRDB as problematic data or having a low number of measurements contributing to annual integrated Rs; these criteria and the stipulation that studies report annual calculations of Rs eliminated nearly 60% of the available SRDB record, which further reduced the number of measures in both arctic and tropical biomes. Furthermore, to control for topographic heterogeneity that may render local study site locations less suitable for representing regional conditions indicated from coarse footprint satellite and global climate observations, we applied a quarter-degree mask to a 1-km resolution digital elevation map (ASTER-GDEM) (Tachikawa *et al.*, 2011) around

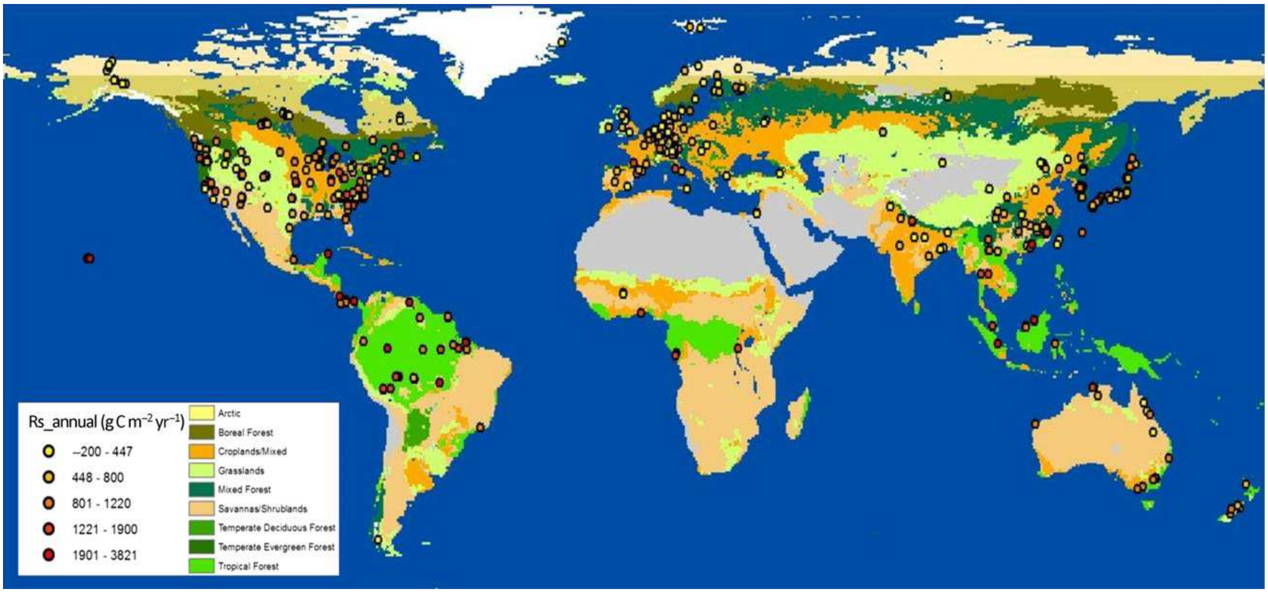

Fig. 1 Biomes and global Annual Soil Respiration observations of the study set. [Colour figure can be viewed at wileyonlinelibrary.com].

each *in situ* SRDB observation location and eliminated sites where the standard deviation of the regional topography exceeded 115 m. This process eliminated the most topographically heterogeneous 15% of the original SRDB dataset. Our final dataset contained 1740 annual Rs observations from 1979 to 2012 (Fig. 1), 1734 of which were spatially and temporally linked to soil moisture and temperature measurements, 1366 of which were linked to NPP measurements, and 1725 of which were linked to soil carbon estimates.

Statistical models

In order to explore the primary factors influencing spatial variability in Rs measurements, we performed a series of descriptive and predictive statistical analyses. First, univariate analyses allowed us to establish the primary variables significantly correlated with the Rs observations. Second, we calculated biome-scale mean Rs measurements and those of influential drivers. Third, we performed a principal components analysis (PCA) of the global dataset and independently for each biome to explore patterns by which several factors covaried and the relative strength with which they contributed to variability in Rs. We also produced regression trees to explore the hierarchical importance of these factors on Rs variability in each biome. Finally, we evaluated the performance of predictive models of Rs based upon the dataset. We compared the fit of a generalized additive model (GAM) to those of several commonly used model structures using a nonlinear least squares (NLS) procedure to fit the environmental variable coefficients. We addressed spatial and quantitative differences between these mechanistic models and the statistical models.

For each of the nine biomes, and for the global dataset as a whole, we tested for significant linear relationships between Rs and 9 independent variables. On a matrix of all variables, we calculated pairwise Pearson product–momentum correlations and partial correlation coefficients adjusting for all other variables. We also calculated the sample size, mean, and standard deviation for these variables for each biome (Table 1, Figs 2–4). Following Raich & Schlesinger (1992), we performed simple linear and nonlinear regression analyses for each environmental variable on biome-level Rs.

We analyzed both the global dataset and each biome individually using principal components analysis (PCA). We first calculated global PCAs of the independent variables most expected to influence Rs variability, from which we overlaid Rs values to assess where these values clumped relative to the loading values, and second, of data including Rs values as well as the significantly correlated independent variables.

Another means of explaining variation in the Rs values is through regression tree analysis (De'ath & Fabricius, 2000). This procedure splits the dataset by recursive partitioning of the variance in Rs. Each node of the regression tree model effectively ranks the independent environmental variables' explanatory power toward each subset of the Rs dataset. To avoid over-fitting, the regression trees were pruned using a reduced-error algorithm which terminates the recursive partitioning procedure when further splits no longer reduce cross-validation error.

We compared the performance of several regression model structures for predicting annual Rs in the dataset. Table 3 describes the model structure and performance of GAMs for the global dataset and for each biome individually, using the Pearson coefficient of determination (r^2), Akaike's information criterion (AIC), and root-mean-squared error (RMSE) to assess goodness of fit. These models assume a linear relationship between NPP and Rs as described in previous literature, as well as a linear fit of one or more additional soil characteristics (SOC or pH) depending upon the significance of that relationship in each data subset. Nonlinear temperature and moisture functions were calculated using a cubic-spline smoothing

Table 1 Summary of mean values for each biome

Biome	# Observations	Land area (# cells)	Mean soil respiration (g C m^{-2})	Mean soil temperature (°C)	Mean soil moisture (m^3 m^{-3})	Mean annual precipitation (mm)	Mean soil carbon (total) (tonnes ha^{-1})	Mean soil carbon (upper 20 cm) (tonnes ha^{-1})	Mean soil pH
Globe	1741		791.2 ± 496.7	12.2 ± 7.4	0.28 ± 0.06	1240.645 ± 815.5	386.65 ± 245.04	66.1 ± 39.64	5.8 ± 0.8
Arctic	29	5569	301.6 ± 266.9	−0.7 ± 8.9	0.23 ± 0.1	341.95 ± 290.18	580.62 ± 366	132.2 ± 33.7	5.67 ± 0.4
Boreal forests	184	2891	411.4 ± 217.6	2.3 ± 2.5	0.32 ± 0.02	531.63 ± 157.68	864.7 ± 231.5	144.4 ± 34.1	5.41 ± 0.39
Croplands/mixed	402	7457	798 ± 420.6	13.1 ± 6	0.28 ± 0.05	1036.1 ± 435.79	280.6 ± 126.1	46.8 ± 18.8	6.1 ± 0.63
Grasslands	163	7378	599.1 ± 439.3	9.8 ± 6.4	0.26 ± 0.04	766.23 ± 488.26	274.1 ± 179.1	46.5 ± 31.7	6.74 ± 0.74
Mixed forest	524	5212	780.2 ± 371	11.8 ± 4.5	0.30 ± 0.05	1395.28 ± 569.87	437.7 ± 156.3	70.4 ± 25.8	5.47 ± 0.6
Savannahs/shrublands	110	15036	992.4 ± 612.2	20.2 ± 5.4	0.25 ± 0.06	1130.81 ± 658.77	180.3 ± 101.8	29.7 ± 14.8	6.1 ± 1.05
Temperate deciduous forests	65	466	829.4 ± 337.4	9.3 ± 3.3	0.25 ± 0.05	1113.4 ± 330.5	308.3 ± 86.3	71.3 ± 18.3	5.53 ± 0.26
Temperate evergreen forests	123	313	773.3 ± 470.8	9.5 ± 2.8	0.28 ± 0.05	1243.6 ± 883.1	362.7 ± 117.9	66.5 ± 27.2	6 ± 0.91
Tropical forests	141	4674	1412.1 ± 684.2	24.7 ± 2.7	0.26 ± 0.09	2799.1 ± 1119.31	205.6 ± 86.8	42.9 ± 20.3	4.92 ± 0.57

Error bars = ±1 SD.

function. In our analysis, these general additive models serve as an empirical 'benchmark' predicting the observed data to the best degree for comparison with mechanistic models.

Mechanistic models

We fit two mechanistic model forms using a nonlinear least squares (NLS) fit procedure. Assuming an Arrhenius-style function to scale a hypothetical maximum respiration rate in response to temperature, and model parameters shaped as Michaelis–Menten functions to act as scalars of two other variables (following Raich *et al*., 2002; Chen *et al*., 2014), we evaluate the relative performance of models which converge on these coefficients for mean annual precipitation, mean soil moisture, total soil carbon, and topsoil carbon, and with or without an additional linear function of NPP. Although published work has described the ability of this model structure to predict variation in Rs with annual precipitation (Chen *et al*., 2010, 2014), the direct relationship with soil moisture at the global scale has not been previously tested. Because many studies have described a parabolic moisture function which dampens respiration rates at higher soil moisture levels, we repeated the above-described process to fit moisture coefficients within a model structure based on the Carnegie-Ames-Stanford Approach (CASA), a set of functions used to scale soil carbon decomposition in several major earth-system models (Potter *et al*., 1993; Melillo *et al*., 2000; Wang *et al*., 2010; Fung *et al*., 2015;). In addition to an exponential temperature function, the CASA model framework scales the response rate by a quadratic soil moisture function. These NLS regression models were validated using k-fold cross-validation on five testing and training datasets, each containing 20% of the original data. Additionally, we calculated total global Rs estimates for each of these models by multiplying the predicted Rs rate in each grid cell by its area and summing grid cells for global estimates. Error in these global estimates was calculated by propagating the site error and again multiplying by the area of the cells: $\mathrm{Rs}_{\mathrm{error}} = (\sqrt{n * \mathrm{RMSE}^2/n}) * \text{cell area}$. Importantly, these global estimates were calculated only where spatially delineated by the biomes in this study; wetland areas, which are known to contribute to global Rs but had too few Rs observations, were not considered in our global predictions and excluded from our spatial models.

Data processing and availability

To process the spatial and temporal components of the source data, we used both ArcGIS (distributed by ESRI) and NOAA's Weather and Climate Toolkit (www.ncdc.noaa.gov/wct). All statistical analyses were performed using RSTUDIO (Version 0.98.1091, rstudio.com). Principal components analysis was performed using the *devtools* and *ggbiplot* packages. Regression tree analysis was performed using the *rpart* and *plyr* packages. Statistical modeling was performed with the *gam*, *mgcv*, and *nls* packages. Raster analysis and modeling were performed using the *raster* and *rgdal* packages. Our dataset, supplemental information, and sample code are available in supporting documents online.

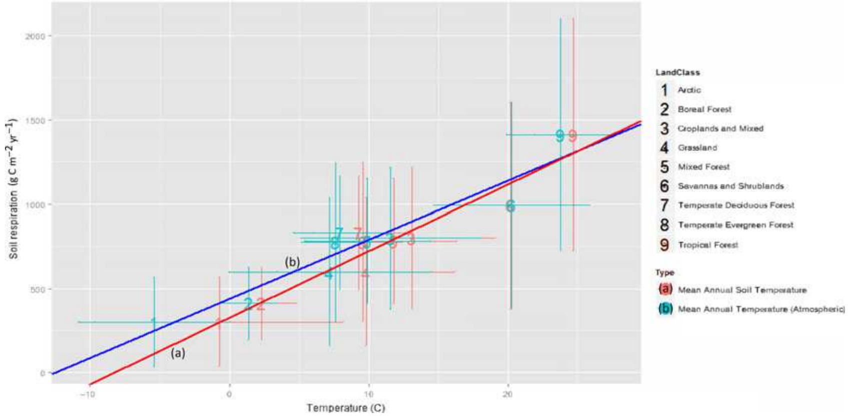

Fig. 2 Global Temperature Relationships. Biome mean soil respiration values and temperature variables. Error bars represent ±1 standard deviation in each plot. Color = temperature data source. Mean Annual Temperature is from SRDB_V2. Soil Temperature is from ERA-Interim. (a) Mean Annual Temperature (C), $y = 34.99x + 439.1$; $P < 0.01$; $R^2 = 0.89$; (b) Mean Soil Temperature (C), $y = 39.5x + 327.2$; $P < 0.01$; $R^2 = 0.91$. [Colour figure can be viewed at wileyonlinelibrary.com].

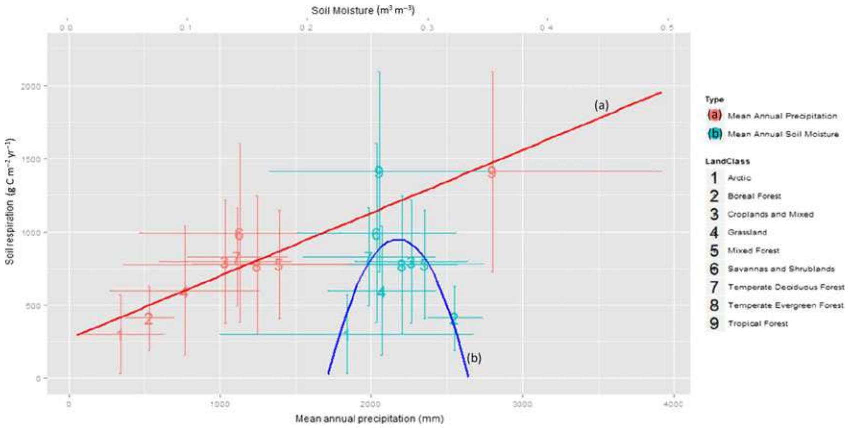

Fig. 3 Global Moisture Relationships. Biome mean soil respiration values and moisture variables. Error bars represent ±1 standard deviation in each plot. Color = moisture data source. Mean Annual Precipitation is from SRDB_V2. Soil Moisture is from ERA-Interim. (a) Mean Annual Precipitation (mm), $y = 270.33 + 0.43x$. $P < 0.05$; $R^2 = 0.88$; (b) Mean Soil Moisture (m^3 m^{-3}), $y = 150803.45x - 277187.14x^2 - 19562.43$; $P < 0.1$; $R^2 = 0.45$. [Colour figure can be viewed at wileyonlinelibrary.com].

Results

Consistent with previous studies (Raich *et al.*, 2002; Bond-Lamberty & Thomson, 2010a,b; Chen *et al.*, 2010), we find that temperature is the most important factor regulating global Rs. Mean annual soil temperature estimates derived from ERA-Interim re-analysis and MAT measurements from the SRDB are highly correlated (Table 2) and show similar controls on Rs (Fig. 2); we therefore address mean soil temperature for the remainder of the analysis. At the global scale, mean soil temperature shows a strong positive linear relationship with biome mean Rs (Fig. 2). In the regression tree analysis, mean soil temperature is the dominant factor explaining global Rs variability (Fig. 5). However, within biomes, the role of soil temperature is not always as dominant as some global land models have assumed (Chen & Tian, 2005). In biome-specific regression tree analyses, soil temperature is a secondary or tertiary factor in temperate evergreen forests, temperate deciduous forests, and boreal forests (supplemental information). The biplot shown in Fig. 6 reports the eigenvectors and proportion of variance explained by the first two principal components in the PCA. The variables included in each analysis are plotted as vectors representative of the strength and direction to which they load each component. Soil temperature and soil carbon content are the strongest loaders of the first

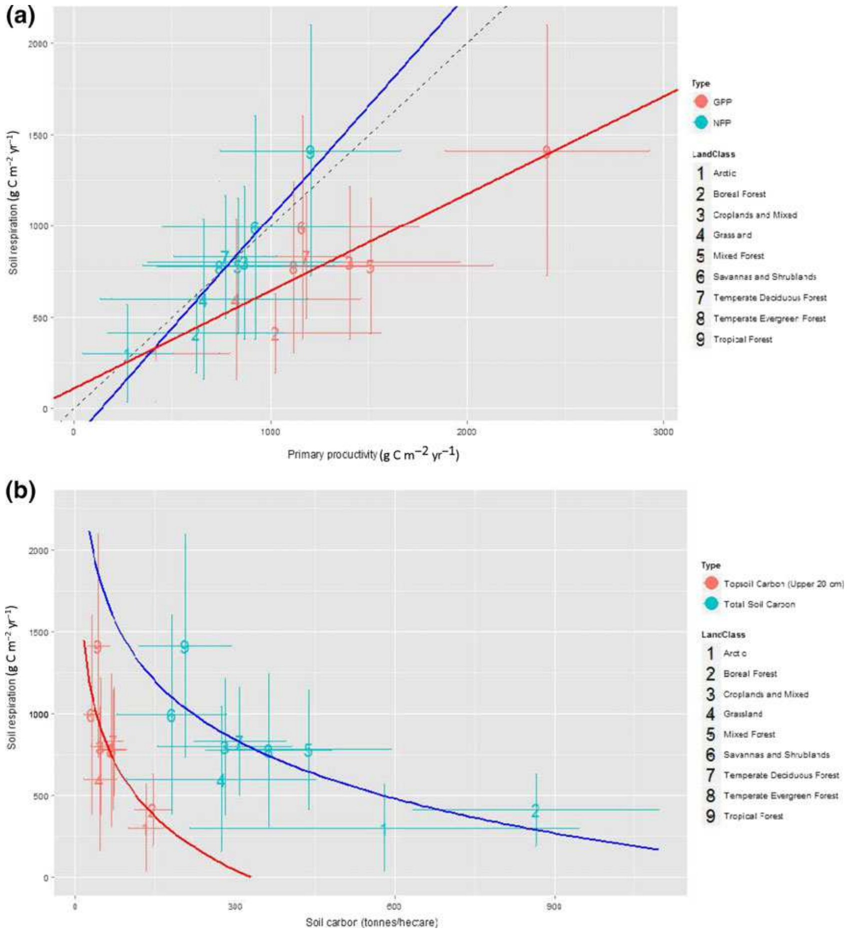

Fig. 4 Global Carbon Supply Relationships. Biome mean soil respiration values and carbon supply variables. Error bars represent ±1 standard deviation in each plot. (a) BLUE: Net Primary Productivity (g C m^{-2} yr^{-1}), $y = 1.22x - 170.5$. $P < 0.05$; $R^2 = 0.9$; RED: Gross Primary Productivity (g C m^{-2} yr^{-1}), $y = 0.532x + 112.68$. $P < 0.05$; $R^2 = 0.9$. Dashed line = 1 : 1. (b) BLUE: Total Soil Carbon (tonnes ha^{-1}), $y = 7.382 - 0.002{*}\log(x)$. $P < 0.05$; $R^2 = 0.34$; RED: Topsoil Carbon (tonnes ha^{-1}), $y = 2702.7 - 465.8{*}\log(x)$. $P < 0.05$; $R^2 = 0.49$. [Colour figure can be viewed at wileyonlinelibrary.com].

principal component (−0.61 and 0.62, respectively, Fig. 6), each explaining over half the variability in the Rs data but in opposite directions, and appear to be the strongest drivers of Rs differences between biomes.

Our analysis indicates significant soil moisture controls on global Rs. Soil moisture from ERA-Interim displays a much different relationship to Rs than mean annual precipitation. Mean annual precipitation (MAP) shows a strong positive and linear relationship with Rs at the global scale (Fig. 3), as has been shown in previous studies (Raich & Schlesinger, 1992; Davidson *et al.*, 2012), but the relationship with mean annual soil moisture is much more variable. The highest Rs values occur around 27% volumetric water content (Fig. 3), but Rs values are variable throughout the soil moisture range. Arctic and tropical soils show the greatest coefficient of variation in mean annual soil moisture. In tests for linear correlation with other variables, soil moisture shows the strongest relationship with soil carbon content when accounting for the influence of other variables (Pearson correlation = 0.53).

Within individual biomes, soil moisture is the dominant predictor in the regression tree analysis only in temperate evergreen and temperate deciduous forests (Supporting Information). In mixed forests, savannas and shrublands, and boreal forests, it is a dominant secondary or tertiary predictor of Rs after accounting for high soil temperatures. In the global PCA, soil moisture largely explains the residual variability in PC2 (loading = 0.64, Fig. 6). Importantly, it appears to describe more Rs variability within individual biomes, such as in arctic or tropical forest with high moisture variation, than across biomes. Soil moisture can help to further explain or more accurately predict Rs variability in these instances where temperature or precipitation is less variable within a biome's dataset.

Table 2 Generalized Additive Model statistics for each dataset

Biome	# Observations	Model parameters	*P*-value	r^2	RMSE	AIC
Globe	1741	Rs_annual = te(STMean, SMMean) + 0.17*NPP − 177.18*pH − 3.12*Soil_C	<0.0001	0.31	410.93	3739.6
Arctic	29	Rs_annual = te(STMean, SMMean)	<0.05	0.16	232.54	278.18
Boreal forests	184	Rs_annual = te(STMean, SMMean) + 1.06*NPP	<0.0001	0.55	141.97	299.83
Croplands/mixed	402	Rs_annual = te(STMean, SMMean)	<0.05	0.1	393.9	1026.69
Grasslands	163	Rs_annual = te(STMean, SMMean)	<0.001	0.34	346.44	427.93
Mixed forest	524	Rs_annual = te(STMean, SMMean) + 0.1*NPP + 4.33Soil_C	<0.0001	0.45	242.53	1208.49
Savannahs/shrublands	110	Rs_annual = te(STMean, SMMean)	<0.001	0.39	502.43	327.48
Temperate deciduous forests	65	Rs_annual = te(STMean, SMMean)	<0.05	0.12	297.15	376.4
Temperate evergreen forests	123	Rs_annual = te(STMean, SMMean)	<0.01	0.29	356.97	342.24
Tropical forests	141	Rs_annual = te(STMean, SMMean)	<0.05	0.13	573.01	410.55

STMean, mean soil temperature; SMMean, mean soil moisture; Soil_C, total soil carbon; te, 'Tecumseh' smoothing algorithm (cubic-spline regression); RMSE, root-mean-squared error (g C m^{-2} yr^{-1}); AIC, Akaike's information criterion.

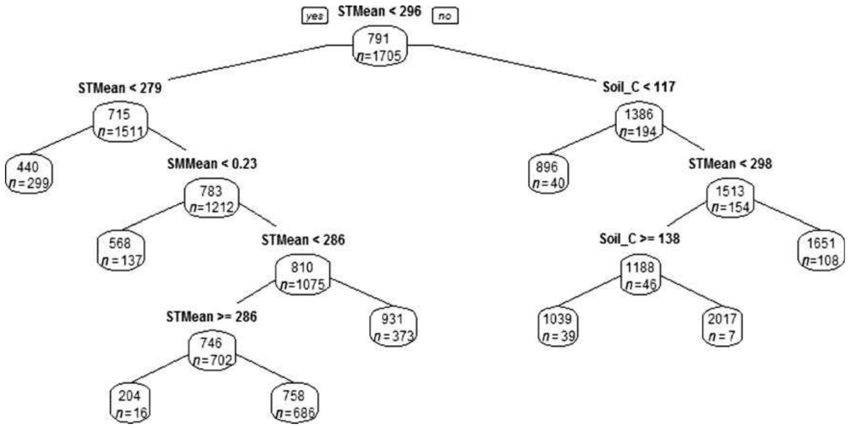

Fig. 5 Regression tree for the global dataset. Predictor coefficients and number of observations reported at each node. STMean, mean annual soil temperature (C); SMMean, mean annual soil moisture (m^3 m^{-3}); Soil_C, total soil carbon (tonnes ha^{-1}). NPP (g C m^{-2} yr^{-1}) also included as independent variable in model calibration.

Our use of GPP and NPP modeled from satellite observations further corroborates the early relationship described by Raich and Schlesinger. At the global scale, NPP is a strong positive and linear predictor of Rs (Fig. 4a), with a slope of 1.22. NPP also shows a significant positive Rs control within most biomes, except in forested biomes where NPP values are the least variable relative to those of Rs. NPP emerges as an important predictor of within-biome Rs only in croplands and grasslands, where it remains secondary to soil temperature. NPP plays a similar role as soil moisture in the PCA, where it loads the second principal component the most strongly (0.71, Fig. 6) and the direction of its vector parallels cropland and grassland data specifically.

Soil carbon estimates show a strong negative and nonlinear relationship with Rs at the global scale (Fig. 4b). Arctic and boreal biomes, with the highest soil carbon estimates, have the lowest Rs values; this difference skews the global soil respiration–soil carbon relationship and may limit our ability to construct empirical models of Rs based on soil carbon availability at the global scale. Grasslands, savannas and shrublands, and arctic biomes show the highest coefficients of variation in soil carbon. In the regression tree analysis, topsoil carbon is the strongest predictor of Rs variability in temperate evergreen and boreal forests. Soil carbon loads the first principal component in the PCA with equal strength to soil temperature, but in the opposite direction, negatively for higher Rs values (Fig. 6), suggesting that total soil carbon reflects the carbon remaining in soils as the result of temperature-mediated respiration rates.

In Fig. 7, we show the results of individual biome models derived using global gridded ERA-Interim climate data for 2014, and including the resulting RMSE for each model. Figure 8 displays three global maps of predicted Rs using gridded climate data from 2014. At the scale of annual Rs measurements and coarse global climatic measurements, each of our statistical or mechanistic modeling efforts captured between 29% and 65% of the variability in SRDB observed Rs. This is suggestive not only of the limitations of the driving datasets and resulting empirical models in accurately predicting global Rs spatial patterns, but also of the difficulty in corroborating the mechanistic relationships we model with observations and climate estimates made at broadscales. The GAMs developed in this analysis performed best for boreal forests ($r^2 = 0.55$) and mixed forests ($r^2 = 0.55$), which were the only biomes in which additional linear NPP coefficients were statistically significant and improved the model fit (Table 2). The differences between these biome-parameterized models and the global model are most evident when compared spatially (Fig. 8). Given the results in Figs 7a and 8a, the relative contribution of NPP to modeled Rs is likely the strongest driver of the large differences in predicted Rs in the tropics. Due largely to sparse site observations in this region, the resulting moisture–temperature functional relationship with Rs has the greatest degree of error in the tropics (RMSE = 573.01) relative to other biomes.

In statistical models, the CASA framework and parabolic moisture function explain more Rs variability than the Michaelis–Menten mechanistic framework when utilizing either soil moisture or MAP, which has been shown to be an effective predictor of global Rs in other studies (Table 3a, b) (Bond-Lamberty & Thomson, 2010a,b); the soil moisture optimum in the strongest of these (Table 3b-3; $r^2 = 0.65$) is around 38% volumetric water content. Each of the model structures used in the NLS process was able to converge on global functions relating soil moisture, temperature, and NPP, but insufficient variability in the data within individual biomes prevented statistically significant models from converging at the biome scale. Using the Michaelis–Menten structure, mean annual precipitation performed only slightly better than mean soil moisture in each model (Table 3a). NPP as an additional variable improved the fit of each model, as did soil pH although it added little explanatory power ($r^2 = 0.29$, 0.3, respectively, Table 3a). Use of the CASA model structure improved explan atory power both with and without the inclusion of a linear NPP function (Table 3b). The total soil carbon model with CASA structure explains nearly half of the Rs variability in cross-validation, but the spatial analysis shows that it greatly overestimates Rs specifically in some tropical areas with relatively high NPP and a lack of Rs observations (Fig. 8). The topsoil carbon model improved the explained spatial variability even without the inclusion of an NPP component, yet with a greater degree of RMSE uncertainty (Table 3b). Total annual global Rs was 93.9 ± 25.11 Pg C yr^{-1} in the global GAM. The global Michaelis–Menten model with precipitation produced an Rs rate of 80.3 ± 24.6 Pg C yr^{-1} globally, and the CASA-framework model with soil

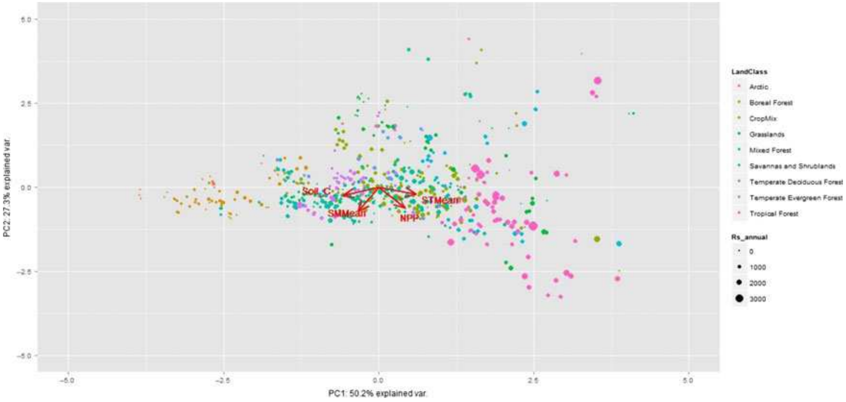

Fig. 6 Principal components analysis biplot of variability in independent variables. Red vectors represent principal component loadings of each variable. Point size = Annual Soil Respiration (g C m^{-2} yr^{-1}): [Colour figure can be viewed at wileyonlinelibrary.com].

-		*PC1*	*PC2*	*PC3*	*PC4*
-	*STMean*	*-0.6068083*	*0.2222568 -*	*0.3864441*	*-0.6580627*
-	*SMMean*	*0.3784518*	*0.6420554*	*-0.6241701*	*0.2344158*
-	*SatNPP*	*-0.3254588*	*0.7067730*	*0.5997726*	*0.1866048*
-	*Soil_C*	*0.6185746*	*0.1970752*	*0.3183482*	*-0.6907831*

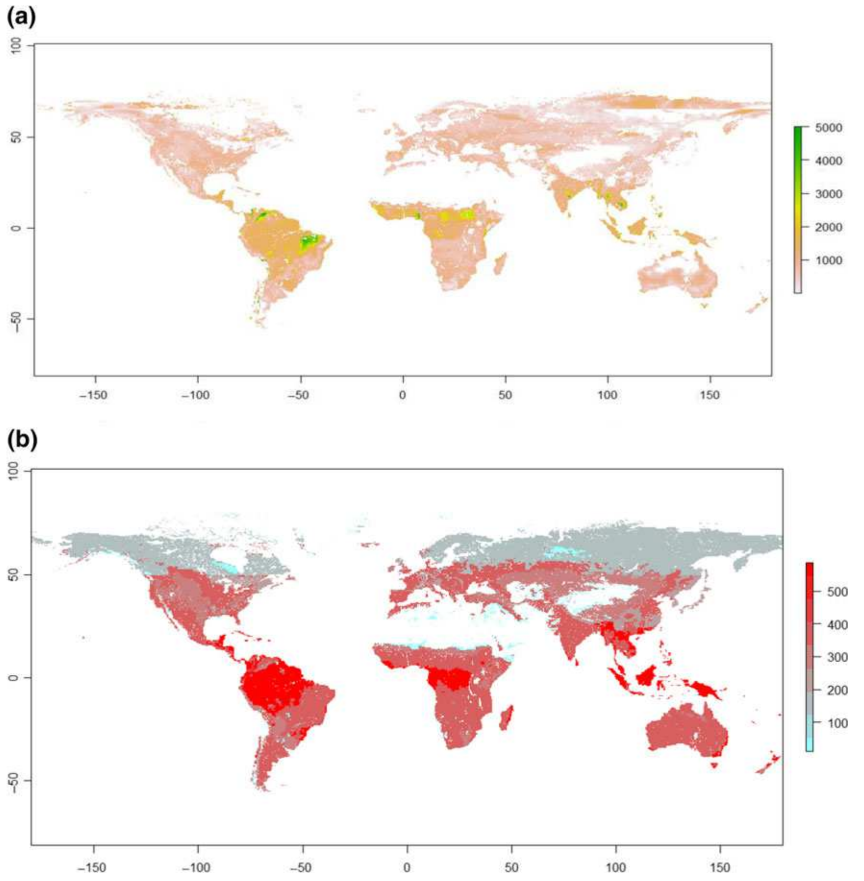

Fig. 7 The predicted results of Rs_annual in 2014 using biome-specific GAM models. (a) Predicted Rs_annual, (g C m^{-2} yr^{-1}) (b) RMSE of model for each biome (g C m^{-2} yr^{-1}). [Colour figure can be viewed at wileyonlinelibrary.com].

moisture and a linear NPP function produced a global Rs rate of 108.6 ± 69.6 Pg C yr^{-1}. Differences in the resulting model Rs totals and associated error ranges reflect the compounded error and uncertainty in certain regions (e.g. the highly productive tropics), which is evident in the spatial differences seen in Fig. 8.

Discussion

Researchers have identified the need for a comprehensive understanding of the primary environmental factors controlling soil respiration rates around the globe (Cox *et al*., 2000; Cramer *et al*., 2001; Trumbore, 2006; Todd-Brown *et al*., 2013). Benchmarking semi-empirical models of Rs against available observations has been shown to help constrain global climatic functions estimating the total Rs flux (Hashimoto *et al*., 2015). At the broad spatial and temporal scales explored in this study, we address important and unfortunate limits to scaling up predictions of Rs as a function of climatic and environmental factors with known mechanistic relationships at finer temporal and spatial scales.

The results of this study are consistent with previous studies reporting positive global relationships between mean annual Rs and mean atmospheric temperature and precipitation (Raich *et al*., 2002; Chen *et al*., 2014); however, our analysis clearly illustrates the importance of soil moisture in regulating Rs variability in specific biomes and the relative utility of these data at the global scale. Global-scale correlation between temperature, precipitation, and primary productivity has shown how environmental drivers regulate total Rs, but these relationships ‘given available data’ are insufficient to calibrate models that acknowledge differences within biomes. Earlier research has shown global Rs estimates to be approximately 24% greater than NPP (Raich & Schlesinger, 1992). Our analysis, with over 1000 additional observations including satellite-derived NPP, corroborates this finding (22%, Fig. 4a). The additional variability that results from heterotrophic respiration is explained in part by the soil carbon and soil moisture estimates.

This investigation highlights two important considerations regarding our ability to accurately assess soil

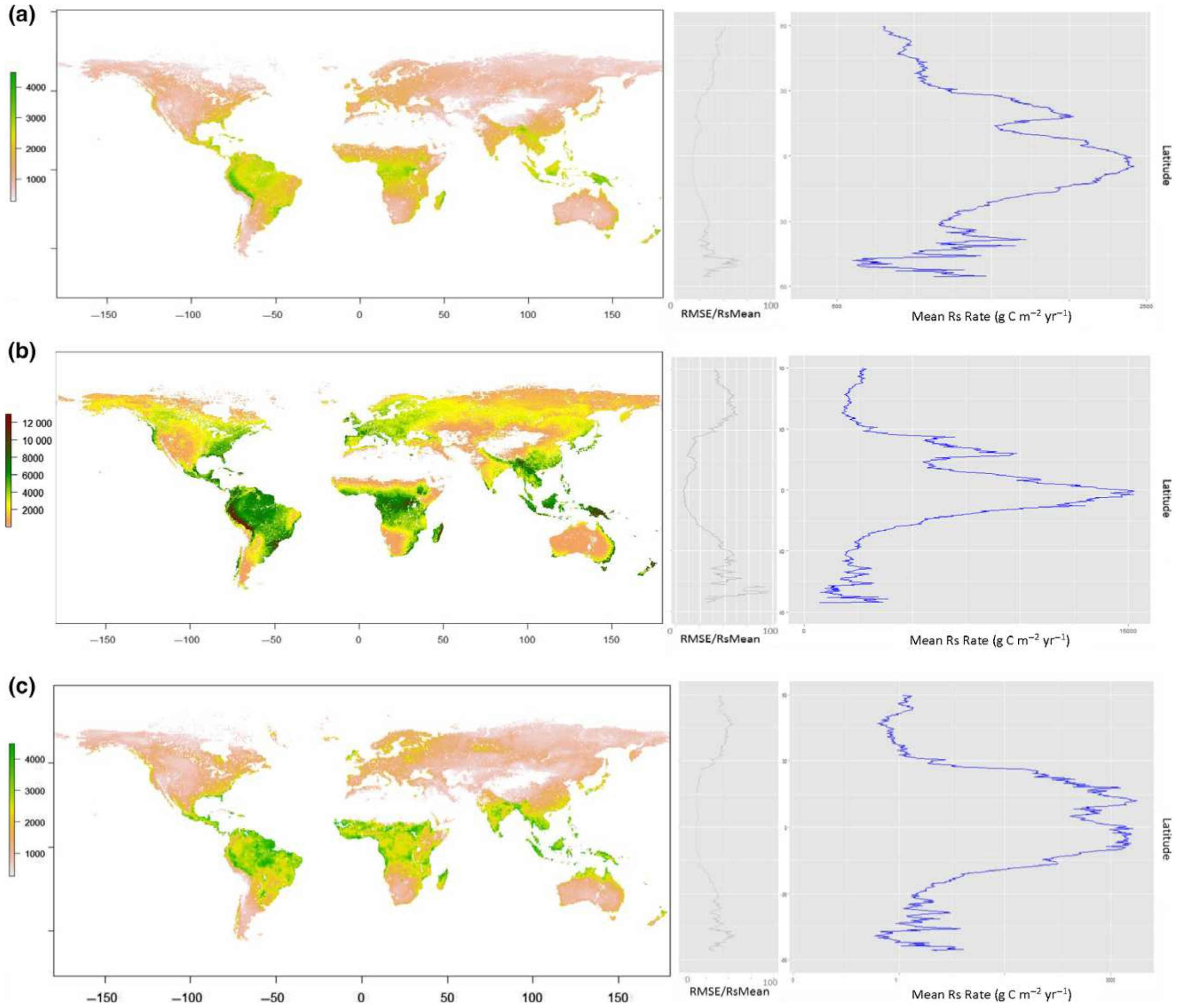

Fig. 8 The predicted results of Rs_annual in 2014 using global models. Left: predicted total annual Rs (g C m^{-2} yr^{-1}). Center: RMSE/Rs_annual represents the model error as a percent of predicted flux. Right: Mean annual Rs rate by latitude (g C m^{-2} yr^{-1}). (a) Global generalized additive model (Table 3) RMSE; 410.93 g C m^{-2} yr^{-1}; R^2 = 0.31. (b) Global NLS model with total soil carbon, CASA structure, and NPP coefficient (Table 3b-3). RMSE = 1140.22 g C m^{-2} yr^{-1}; R^2 = 0.41. (c) Global NLS model with total soil carbon, CASA structure, and no NPP coefficient (Table 3b-1). RMSE = 576.243 g C m^{-2} yr^{-1}; R^2 = 0.65. [Colour figure can be viewed at wileyonlinelibrary.com].

respiration at these scales. Firstly, when individual biome datasets are considered independently, they show contrasting relative degrees of importance among factors known to regulate soil respiration. Rs variability within biomes differs significantly according to the variability of some drivers. For example, NPP is a poor predictor of Rs variability globally and within forested biomes (tropical, temperate, and boreal), likely due to the low spatial variability exhibited by estimated NPP, which is unable to account for the observed Rs variability within these biomes. Soil moisture, however, is much more variable in temperate and boreal forests and indeed appears to be more important in regulating Rs within these biomes. Secondly, in most biomes there are insufficient data in this scaled-up approach to refine the fine-scaled details and incorporate such factors into biome-specific mechanistic models. Therefore, global models incorporating temperature, moisture, and carbon supply relationships averaged over large areas inherently miss the underlying spatial differences that these factors have at finer scales. This is highlighted, for example, by a disproportionate influence of NPP in the highest-productivity tropics (where we had little Rs data) influencing likely overestimates of global Rs

Table 3 Model Summaries for Nonlinear Least Squares fit procedure using (a) Arrhenius temperature function and Michaelis–Menten soil moisture, precipitation, and carbon parameters. (b) CASA model framework. Procedure calibrated only 1st Soil Moisture function numerator, regulating optimum of parabolic curve

	# Observations	Model parameters	*P*-value	r^2	RMSE	AIC
(a)						
1	1366	Rs_annual = $446.8e^{0.053\text{STMean}}$ (SMMean/ (SMMean − 0.006))(SoilC/SoilC + 71.1)) + 0.16NPP	<0.0001	0.3	411.9	14712.93
2	1725	Rs_annual = $104.2e^{0.025\text{STMean}}$ (SMMean/ (SMMean − 0.003))(SoilC/SoilC + 10.01)) − 96.6pH	<0.0001	0.29	412.27	14714.71
3	1366	Rs_annual = $447.3e^{0.054\text{STMean}}$ (MAP/(MAP − 14.9)) (SoilC/SoilC + 83.59)) + 0.11NPP	<0.0001	0.31	403.82	11913.62
4	1725	Rs_annual = $808.8e^{0.033\text{STMean}}$ (MAP/(MAP − 11.4)) (SoilC/SoilC + 27.42)) − 60pH	<0.0001	0.3	404.6753	11917
(b)						
1	1366	Rs_annual = Topsoil_C*1.94*$(1.72^{0.189\text{STMean})}$ $((\text{SMMean} - 0.748)/(0.55 - 0.748))^{6.6481}$ $((\text{SMMean} + 0.007)/(0.55 - 0.007))^{3.22}$ + 0.495NPP	<0.0001	0.49	438.981	18513.4
2	1725	Rs_annual = Topsoil_C*24*$(1.72^{0.11\text{STMean})}$ $((\text{SMMean} - 1.1)/(0.55 - 1.1))^{6.6481}$ $((\text{SMMean} + 0.007)/(0.55 - 0.007))^{3.22}$	<0.0001	0.37	564.4527	19131.34
3	1366	Rs_annual = Soil_C*68*$(1.72^{0.22\text{STMean})}$ $((\text{SMMean} - 2.2)/(0.55 - 2.2))^{6.6481}$ $((\text{SMMean} + 0.007)/(0.55 - 0.007))^{3.22}$ + 1.36NPP	<0.0001	0.41	1140.223	20867.26
4	1725	Rs_annual = Soil_C*64*$(1.72^{0.21\text{STMean})}$ $((\text{SMMean} - 2.1)/(0.55 - 2.1))^{6.6481}$ $((\text{SMMean} + 0.007)/(0.55 - 0.007))^{3.22}$	<0.0001	0.65	576.243	19182.32

STMean, mean soil temperature (C); SMMean, mean soil moisture (m^3 m^{-3}); Soil C, soil carbon (tonnes ha^{-1}); AP, mean annual precipitation (mm); Topsoil C, soil carbon in upper 20 cm (tonnes ha^{-1}); RMSE, root-mean-squared error (g C m^{-2} yr^{-1}); AIC, Akaike's information criterion. Annual global soil respiration = Σ(cell rate*cell area); Error = $(\sqrt{n * \text{RMSE}^2/n}) *$ cell area.

a: (1) Global model using soil moisture and an additional linear NPP parameter; (2) global model using soil moisture and an additional linear pH parameter; (3) global model using precipitation and an additional linear NPP parameter; (4) global model using precipitation and an additional linear pH parameter. b: (1) Global model using topsoil carbon and an additional linear NPP parameter; (2) global model using topsoil carbon and no additional linear NPP parameter; (3) global model using total soil carbon and an additional linear NPP parameter; (4) global model using total soil carbon and no additional linear pH parameter.

(Fig. 8b). The rates of error in predicting annual Rs in global models are disproportionately large, relative to total Rs rates, for arctic and boreal regions where total Rs is low (Fig. 8). These complications highlight limits toward the accuracy of global mechanistic model structures and the need for larger observational datasets that provide a more accurate reconstruction of the underlying variability necessary to allow biome-scale model structures to be better calibrated.

At the global scale, the highest annual Rs rates seem to occur where mean annual volumetric soil water content approaches ~27% (Fig. 3), which could corroborate the functions of recently constructed models (Falloon *et al.*, 2011; Davidson *et al.*, 2012; Yi *et al.* 2011), but the high degrees of spatial variation and difference in temporal scale that our models illustrate globally demonstrate the limits of a focused understanding. Our NLS procedure which incorporated a parabolic moisture function as used in several earth-system models (Melillo *et al.*, 2000; Exbrayat *et al.*, 2013) performed remarkably better than models which relied upon precipitation as seen in previous studies (Table 3a, b) (Chen *et al.*, 2010, 2014).

Soil moisture appears to explain more Rs variability in all forested biomes. This could be due in part to a relative lack of spatial variability in temperature and NPP within these ecosystems and in part to the mediating influence of snowpack and thaw dynamics on soil moisture variability (Brooks *et al.*, 2005, 2011; Monson *et al.*, 2006a,b; Öquist *et al.*, 2009), especially in the boreal forests (Dunn *et al.*, 2007; Du *et al.*, 2013). Because of the strong correlation between precipitation and NPP, soil moisture may help to better explain climatic variability which drives the heterotrophic component of soil respiration, as it integrates the effects of precipitation and temperature on soil conditions. The Rs response to soil moisture may attenuate expected Q10 responses to warming, and soil moisture may become a more important variable where increasing temperatures coincide with reductions in precipitation changes in its character.

The climatic influence on soil respiration is most evident when considering the negative relationship between soil carbon stocks and Rs at the global scale. That biomes with the highest mean soil carbon content show the lowest mean Rs values indicates that respiration can be less limited by carbon supply than by the interactive effects of soil moisture and temperature. Climate is the primary factor regulating the release or retention of significant soil carbon in regions like the arctic and boreal forests (Brooks *et al.*, 2005; Hartley *et al.*, 2008; Du *et al.*, 2013). There is significant uncertainty regarding climate change's potential to drive the mobilization and release of large amounts of soil organic carbon found in high northern latitudes (Elberling *et al.*, 2008; Schuur *et al.*, 2008), and changing precipitation and snow dynamics are likely to affect soil moisture conditions and respiration rates (Lee *et al.*, 2004; Euskirchen *et al.*, 2007; Yi *et al.* 2011). Relatively low NPP rates in these colder biomes amplify the importance of climatic factors in driving the decomposition of large soil organic carbon pools derived from past, rather than current, productivity, especially when considering that error in global models is a greater percentage of total Rs estimates at high latitudes.

Other important factors relevant to the relationship between precipitation, soil moisture, and carbon supply are difficult to disentangle at these broad scales. Soil texture is an important factor in determining the effect of varying levels of soil moisture as well as the quality of the soil carbon content in various locations, a factor emphasized by other researchers but not explicitly evaluated at the global scale in our study (Davidson *et al.*, 2000). Precipitation dynamics, as they relate to temperature, may be better addressed using data representing actual evapotranspiration or the ratio of actual to potential evapotranspiration. Each of these calculations, however, requires an increase in the detail, magnitude, and consistency of data across a very large number of studies that rendered them inadequate measures for a study at this scale. Similarly, strategies used to model primary productivity at scales suitable for this analysis require the acceptance of certain model assumptions and lack of mechanistic detail. Models of NPP, for example, do not include rates of root respiration, and this unaccounted component of autotrophic respiration could help explain differences between total Rs estimates and mean NPP or GPP rates across biomes.

In forested biomes, high rates of NPP and high Rs relative to model error may overwhelm the temperature and moisture influences on Rs uncertainty (Janssens *et al.*, 2001). Overestimates of Rs in our statistical models are underscored by relatively large uncertainty in the tropics, especially in regions with the highest NPP (Figs 7 and 8). Prior research has shown local soil moisture characteristics to affect Rs variability within tropical forests and has stressed the need to measure both soil moisture and soil properties at varying depths (Davidson *et al.*, 2000). Furthermore, primary productivity in tropical forests is exceedingly difficult to estimate (Cleveland *et al.*, 2015). Seasonal precipitation dynamics in tropical ecosystems also likely contribute to the high soil moisture variability shown in this study, but at annual timescales this is not captured and temperature still emerges as the dominant Rs control despite the control of moisture in some site-scale studies (Hashimoto *et al.*, 2004).

The general additive model used in this study describes an overfit statistical relationship between the satellite-derived variables and the observations in the SRDB, but it provides an empirically driven benchmark against which to compare fitted models with mechanistic bases. While the results of the models with Michaelis–Menten moisture or precipitation parameters corroborate prior research which is mainly focused on temperate ecosystems, our research clarifies the inherent errors associated with applying such analyses at global scales and highlights the spatial nature of these differences. Models with a quadratic soil moisture function modeled after CASA improve explained variance but often at the cost of increased RMSE. The addition of a fitted NPP coefficient in the total soil carbon model, for example, leads to significant overprediction of Rs in areas of high NPP when compared to the GAM (Fig. 8). These model results help to illustrate that even small changes in environmental scalars can have notable impacts on global estimations of soil carbon efflux, as has been shown in comparisons of major ESMs (Exbrayat *et al.*, 2013).

Relatively fewer measurements in some ecosystems, such as in tropical and temperate deciduous forests, make it difficult to assess climatic relationships and calibrate models using the empirical record at this scale. In Fig. 7 and Table 2, smooth functions of soil moisture and temperature were fit for each biome; relative differences in the performance of these models and in the Rs estimates made in Fig. 8 show that without enough data to explain variability within biomes as a function of NPP, for example, error in Rs estimates can vary significantly. Additionally, a global-scale analysis of soil respiration variability relies upon annual Rs measurements and the scale or location mismatch between these point data and gridded variables. It is more important to compare differences in the ranges of observed and estimated values at these scales than to make point-by-point comparisons (Shao *et al.*, 2013), but our analysis demonstrates the utility in benchmarking estimates against global soil respiration observations when calibrating model scalars to make spatially explicit global predictions (Reichstein & Beer, 2008). The influence of climatic variables on Rs calculated at finer scales in earth-system models must manifest even in annual observations at large scales. The relative differences in the outputs of these models suggest the importance of considering soil moisture influences on respiration and where areas of uncertainty in our global understanding of soil respiration necessitate further broadscale research.

This study illustrates the importance of soil moisture as a metric predicting Rs with other climatic and environmental variables that have been investigated as factors driving soil respiration rates at the global scale. By combining observations from the empirical record with satellite-derived measurements of soil moisture, temperature, and NPP, we are able to interpret the relationship between these factors and Rs across spatial scales and explore areas of uncertainty and areas where the relative dominance of one or more of these variables calls for further research. In general, we note that a limited number of observations in tropical regions with the highest predicted Rs rates and in arctic regions with the highest estimated soil carbon stocks are one obstacle to better constraining global-scale estimates of Rs. Without proper correction of the effects of spatial sampling, the heterogeneous distribution of the measurements may also bias global respiration estimates toward the rates of the most sampled biomes. We also note that much of the uncertainty in global-scale Rs modeling derives from the integration of instantaneous effects and seasonal dynamics of these variables at annual timescales. A bridge between the necessity for a large number of global observations and the need to incorporate smaller-scale temporal dynamics will require more studies such as this which integrate remote-sensing measurements and field observations to gain new insight into terrestrial ecosystem carbon dynamics at the global scale.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Supplementary Material.