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THE SENSITIVITY OF SOIL RESPIRATION TO SOIL TEMPERATURE, MOISTURE, AND CARBON SUPPLY AT THE GLOBAL SCALE

By
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Abstract

THE SENSITIVITY OF SOIL RESPIRATION TO SOIL TEMPERATURE, MOISTURE, AND CARBON SUPPLY AT THE GLOBAL SCALE

Chairperson: Dr. Ashley Ballantyne

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Soil respiration is one of the most important terms in the global carbon budget, yet we know very little about how important environmental factors control this process at the global scale. Soils contain more carbon than terrestrial biomass and the atmosphere combined and contribute ten times more carbon dioxide to the atmosphere each year than the burning of fossil fuels. This study provides new insight on the factors driving soil respiration at the global scale by assimilating satellite observations of soil moisture, temperature, and net primary productivity with the Global Soil Respiration Database (SRDB).While temperature, moisture, carbon supply and other site characteristics are known to regulate soil respiration rates at the plot scale within certain biomes, there is no quantitative framework for evaluating the relative importance of these factors across different biomes and at the global scale. We link a subset of observations in the SRDB to soil moisture, soil temperature, net primary productivity (NPP), and soil carbon from global datasets in order to explore the relative strengths of these environmental regulators on soil respiration. We find that calibrating models with parabolic soil moisture functions can improve predictive power over similar models with asymptotic functions of mean annual precipitation. At the global scale, soil temperature is the dominant factor regulating soil respiration; however, soil moisture emerges as the dominant factor regulating soil respiration in temperate and boreal forested ecosystems, and NPP emerges as the dominant factor regulating soil respiration in croplands and grasslands dominated ecosystems. We compare the ways in which these statistical relationships predict global soil respiration values in generalized additive models and several calibrated models with mechanistic structures, which estimate total respiration fluxes ranging from 83 to 108 Pg/yr.

Acknowledgements

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Table of Contents

Contents

Introduction

Soils contain more carbon than the atmosphere and terrestrial plant biomass combined, and CO_2 respired from soils outweighs fossil fuel emissions by an order of magnitude (Carvalhais et al. 2014, Ballantyne et al 2015, Bond-Lamberty and Thompson 2010), yet our understanding of soil respiration and its response to global climate change remains uncertain (Falloon et al. 2011, Seneviratne et al. 2010, Emmet et al 2004). Assessments of global and biome-scale net ecosystem exchange require an application of climatic controls on respiration which is limited by scales of measurement (Yang et al. 2013; Xiao et al. 2014, Exbrayat et al. 2013). Because soils contain plant roots as well as microbial communities, soil respiration is integrates both autotrophic and heterotrophic respiration processes, which are difficult to disentangle at large spatial scales. Autotrophic respiration, however, is generally considered to be proportional to gross primary productivity, and total soil respiration measurements have been used to explore climatic controls on heterotrophic respiration (Wieder, Bonan, and Allison 2013; Rustad, Huntington, and Boone 2000; Raich, J.; Potter, C.; Bhagawati 2002).

Quantitative models of soil respiration (Rs) are typically constrained by local-scale measurements or by global-scale observations informed by satellite measurements and broad assumptions. 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, Huntington, and Boone 2000; Seneviratne et al. 2010; Sierra et al. 2015). Soil moisture controls on respiration have not been evaluated from observations at the global scale.

Raich and Schlesinger (1992) published one of the first global analyses of soil respiration, describing positive and linear controls on mean soil respiration rates in different biomes by mean annual temperature (MAT), mean annual precipitation (MAP), and net primary productivity (NPP). They also estimated global soil carbon efflux and turnover times based upon soil carbon storage estimates calculated for global biomes. However, this early research relied upon Rs estimates from less than 200 study sites worldwide. While some ecosystems still have seen relatively fewer observations than, for example, temperate forests in the northern hemisphere (Bond-Lamberty and Thompson, 2010) today a much greater breadth of soil respiration research across a wide array of biomes allows for more comprehensive analysis of environmental controls on Rs.

Researchers have established 1st-order controls on soil respiration rates by temperature at the plot scale. Typically, Arrhenius kinetics expressed as Q10 relationships have been applied to explain the non-linear sensitivity of respiration rates to temperature and have also been adopted by earth-system models (Chen and Yian 2005; Cox. Et al. 2000, Cramer et al 2001, Exbrayat et. al 2013). At the plot scale, several studies have explored the interactive effects of temperature controls with transient moisture conditions and soil characteristics (Davidson et al 2012, Grogan 2012, Haven 2004). Studies exploring local soil moisture controls on respiration have typically described the respiration response to moisture as parabolic, with optimum rates of respiration around 60% water holding capacity or roughly 25% volumetric water content (Moyano, Manzoni, and Chenu 2013). However, responses at high moisture levels are less understood, and some ecosystems maintain respiration rates even at more saturated conditions (Dunn et al. 2007; Falloon et al. 2011).

There is uncertainty about the global interaction of the temperature response with soil moisture (Rey 2014; Moyano, Manzoni, and Chenu 2013; F. E. Moyano et al. 2012), primary productivity (Raich, J.W.; Schlesinger 1992), or microbial community responses (Wieder, Bonan, and Allison 2013; Monson et al. 2006). Often respiration has been modeled as asymptotic above certain moisture levels; this could be due to the interactive influences of temperature and moisture, whereby above levels of adequate soil moisture, temperature may become the driving factor limiting respiration rates (Lellei-Kovacs et. al, 2011). Some models have shown that we may often overestimate the effects of increasing temperatures while underestimating the moisture levels at which soil carbon decomposition increases (Ise and Moorcroft, 2006). Global analyses of soil respiration have underscored uncertainty regarding how soil moisture dynamics will affect climate change feedbacks (Ryan et. al. 2005, Rustad et. al., 2000).

In order for global land models to accurately simulate the sensitivity of soil respiration to temperature, moisture, and productivity, biome-specific parameters may need to be optimized in conjunction with estimates of NPP and soil carbon content. Many of the scalars, thresholds, and optimal moisture and temperature levels in these models are assumed to be constant across biome types in the absence of more detailed biome-level information. (Exbrayat et al. 2013; Yang et al. 2013; Kimball et al 2012). Site-specific and regional studies, however suggest that the relative importance of factors like soil moisture or carbon content varies in different biomes due to soil properties (Davidson and Janssens 2006; Moyano, Manzoni, and Chenu 2013), seasonality of precipitation (Wei, Weile, and Shaopeng 2010; Wang et al. 2013), vegetation characteristics or other factors (Fissore, Giardina, and Kolka 2013; Pacific et al. 2011; Suseela et al. 2012). Most models of net ecosystem exchange which incorporate soil respiration components are validated against eddy covariance tower measurements of total gas exchange (Yang et al. 2013), but have not been validated directly between remote sensing data and field measurements of soil respiration.

The Global Soil Respiration Database (SRDB), distributed by Oak Ridge National Laboratory (Bond-Lamberty and Thomson 2010), updates Raich and Schlesinger's collection of soil respiration studies and contains 4387 observations detailing field measurements of Rs from 1971 to the present. This database reports location information and measurement data for a host of factors which vary by study source; importantly, about 3500 of these studies report a figure of annual integrated soil respiration measurements. These measurements span a wide breadth of space and time, though increasing in number for more recent years and for more temperate latitudes in the Northern Hemisphere. Recently these data have been used to show an apparent increase in soil respiration as a result of warming surface temperatures (Bond Lamberty and Thompson 2010), outline uncertainty in non-biological influences of soil respiration (Rey 2014), question the climate and vegetation controls on heterotrophic respiration in earth-system models (Shao et. al 2014) and assess precipitation and temperature sensitivity at different scales (Sierra et al 2015). We contribute to this growing body of work by linking these annual soil respiration estimates to independent measurements of soil moisture, soil temperature, NPP, and soil carbon content from sources collected at global scales. This study explores the extent to which soil respiration is controlled by these factors at global and biome scales and incorporates these empirical constraints into statistical models with mechanistic bases.

Specific Research Questions

1. What are the primary factors driving spatial variation in soil respiration at the global scale?
2. To what extent can soil moisture explain variability in soil respiration rates in addition to climatic drivers that have been described at the global scale?
3. How do soil temperature, soil moisture, soil carbon and NPP explain historical Rs variability at the global scale and differently among biomes?

Methods

a) Data Assimilation

We linked satellite estimates of soil moisture and temperature from the ERA-Interim reanalysis product to annual respiration values from the SRDB. ERA-Interim is distributed by the European Center for Mid-Range Weather Forecasting and covers the period from 1979 to the present (Dee et al 2011). Satellite data were queried for locations and years corresponding with annual Rs estimates from the SRDB. We collected annual NPP values in the same fashion from two sources: MOD-17, distributed by the Numerical Terradynamic Simulation Group (Running et al. 2004), covered the period from 2000-2012, and the AVHRR-Global Production Efficiency Model, distributed by the Global Land Cover Facility, covered 1979-1999 (Prince and Small 2003). We collected soil carbon estimates and other site variables from the Soilgrids1km 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 as well as the SRDB, and we partitioned the resultant dataset into nine biomes characterized by similarities in climate and vegetation type.

For our analysis, we filtered the resultant dataset in order to eliminate those studies which would be unlikely to represent typical soil respiration efflux at the mismatched spatial scale of these grid-cell observations. We eliminated manipulative studies and those flagged by the SRDB as low-quality or having a low number of measurements contributing to annual integrated Rs or data problems; these two criteria and the stipulation that studies report annual calculations of Rs cut the total SRDB by nearly 60%, which further reduced the number of measures in both arctic and tropical biomes. Further, around each observation we applied a quarter-degree mask to a digital elevation map (NASA's ASTER-GDEM) and filtered from our dataset locations with highly heterogeneous topography at these scales. We repeated our pairwise correlation analysis on several thresholds of this filter, and ultimately culled an additional 15% of the original dataset with the widest standard deviations in elevation values (>115m). Our final data set contained 1740 annual Rs observations from 1979-2012 (Figure 1); 1734 of these had spatially and temporally concurrent soil moisture and temperature measurements from our linked data, 1366 NPP measurements, and 1725 soil carbon estimates.

b) Statistical Analyses

In order to explore the primary factors influencing spatial variability in Rs measurements we performed a series of statistical analyses from descriptive to predictive. First, univariate analyses allowed us to establish the primary variables significantly correlated with Rs observations. Second, we calculated biome-scale mean Rs measurements and those of influential drivers. Third, we performed a principal components analysis for the global dataset and independently for each biome to explore patterns by which several factors co-varied and the relative strength with which they contribute to variability in the measurements. 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 compare the fit of a generalized additive model with a smoothed function fitting soil temperature and moisture controls to that of several commonly used model structures in which we use a non-linear least squares procedure to fit the coefficients of functions which scale Rs by its driving variables.

c) Variable correlation

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 aggregate information on each of these variables by biome, and report the sample size, mean, standard deviation, and coefficient of variation for these variables in each biome in table 1 and figures 3-5. Following Raich and Schlessinger (1992), we perform simple regression analyses for each variable on Rs aggregated by biome.

d) Multivariate Analyses

Similarly, we analyzed the global dataset and each biome individually using principal components analysis. The bi-plots reported in appendix D and figure 6 report the eigenvectors and proportion of variance explained by the first two principal components. The variables included in each analysis are plotted as vectors representative of the strength and direction to which they load each component. We calculated global PCAs first of the independent variables most expected to influence Rs variability, upon 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 visualized in regression tree analyses. This procedure subsets the dataset by maximum variance according to recursive partitioning. Each node of the regression tree models effectively ranks the independent variables' explanatory power towards each subset of the dataset. To avoid over-fitting, trees were pruned using a reduced-error algorithm which terminates the recursive partitioning procedure when further splits no longer reduce cross-validation error.

e) Predictive Models

We compare the performance of several regression model structures predicting annual Rs in the dataset. Table 3 describes the model structure and performance of generalized additive models for the global dataset and for each biome individually, using calculations of r^2, Akaike's Information criterion (AIC), and root mean square error (RMSE) to assess goodness of fit. These models assume a linear function 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. Non-linear temperature and moisture functions were calculated using a cubic-spline smoothing function. In our analysis, these general additive models serve as a statistical "benchmark" predicting the observed data to the best degree for comparison with mechanistically-constrained models, despite the potential for their functions to be over-fit. In figure 8, we show the results of running each biome's individual model on gridded data for the year 2014 as well as the RMSE for each model.

We fit two mechanistic model forms using a non-linear least squares (NLS) fit procedure. Assuming an Arrhenius-style function to scale a hypothetical maximum respiration rate, and model parameters shaped as Michaelis-Menten functions to act as scalars of two other variables (following Chen et al 2014, Raich et al 2002), 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 mean annual precipitation, the relationship with moisture has not been previously tested. Because many studies have described a parabolic moisture function which dampens respiration rates at higher moisture levels, we repeat the above-described process to fit moisture coefficients within a model structure based on that used in the Carnegie-Ames-Stanford Approach (CASA), a set of functions used to scale soil carbon decomposition in several major earth system models (Wang et al 2010, Fung et al 2005, Melillo et al 2000). In addition to an exponential temperature function, the CASA model framework scales the response rate by a quadratic moisture function. These non-linear least squares regression models were validated using k-fold cross-validation on five testing and training datasets, each containing 20% of the original data. Figure 9 displays three global maps of predicted Rs using gridded data from the year 2014. These maps report the results of the global GAM model, the NLS model with mean annual precipitation and a linear NPP function, and the CASA-styled model with optimized soil moisture and temperature parameters and a linear NPP function. 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 totaling the global estimates. Error in these global estimates was calculated by propagating the site error and again multiplying by the area of the cells: $Rs_{error} = (\sqrt{n * RMSE^2}/n) * cell\ area$. Importantly, these global estimates are calculated only upon spaces delineated by the biomes in this study; wetland areas, which are known contribute to global Rs but had too few observations in the SRDB, are masked out of these global maps.

Results

a) Soil Temperature Controls on Soil Respiration

Consistent with previous results we find that temperature is the most important factor regulating global Rs. Within biomes, however, its role is not always as dominant. Mean Soil Temperature from the ERA-Interim product and MAT from the SRDB are highly correlated (Table 2) and show similar controls on Rs (Figure 3); we therefore address soil temperature throughout this analysis. At the global scale, mean annual soil temperature shows a strong positive linear relationship with biome mean Rs (Figure 3b), and soil temperature values are the most variable within the Arctic dataset. In regression tree analysis, temperature is the dominant factor explaining global Rs (Figure 7), and dominant in all biome datasets except for temperate evergreen forests, temperate deciduous forests, and boreal forests (Appendix C). Soil temperature is the strongest loader of the first principal component in the PCA (-0.61, Figure 6), which explains just over half the variability in the data, and it appears to be the strongest driver of differences between biomes.

b) Soil Moisture Controls on Soil Respiration

Our analysis indicates significant moisture controls on global soil respiration. Soil moisture from the ERA-Interim data displays a much different relationship to Rs than mean annual precipitation. Mean annual precipitation shows a strong positive and linear relationship with Rs at the global scale (Figure 4a), as has been shown in previous studies, but the soil moisture relationship is much more variable. The highest Rs values occur around 27% volumetric water content (Figure 4b), but Rs values are variable throughout the soil moisture range. Arctic and tropical soils show the greatest coefficient of variation in soil moisture values within their datasets. In tests for linear correlation with other variables (Table 2), soil moisture shows the strongest relationship with soil carbon content when accounting for the influence of other variables (Pearson Correlation=0.53), and its other significant relationships are generally weaker.

Within biome datasets, soil moisture is the dominant predictor in regression tree analysis only in temperate evergreen and temperate deciduous forests (Appendix C). In mixed forests, savannahs and shrublands, and boreal forests, it is a dominant secondary predictor of Rs, once accounting for high temperature levels. In the global PCA, soil moisture explains largely the residual variability in PC2, plotted on the y axis (Loading=0.64, Figure 6). It appears to describe more variability within biomes, such as in arctic and tropical forests with high moisture variation, than among biomes.

In statistical models with a Michaelis-Menten mechanistic framework, soil moisture does not improve model fit over MAP, which has been shown to predict global annual Rs in other studies, and has a larger RMSE (Table 4a). NLS models with the CASA framework and a parabolic soil moisture function each explain more Rs variability than those with the Michaelis-Menten framework (Table 4b); the soil moisture optimum in the strongest of these (Table 4b-3; r2=.65) is around 38% volumetric water content.

c) Carbon Supply Controls on Soil Respiration

Our use of modeled NPP data from satellite measurements further corroborates the early relationship described by Raich and Schlesinger. At the global scale, NPP is a strong positive and linear predictor of Rs (Figure 5a), 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 (Appendix B: g).

In regression tree analysis, NPP is second to temperature in partitioning Rs variability in croplands, grasslands, and boreal forests (Appendix C). It does not emerge as an important predictor for any other biomes. NPP plays a similar role to soil moisture in the PCA, where it loads the second principal component the most strongly (0.71, Figure 6) and appears to explain greater variability within biomes than between them. This is particularly evident in the cropland and grassland biomes, whose values parallel the vector of NPP loadings.

In NLS models with the Michaelis-Menten framework, NPP performs marginally better than soil pH as the single additional linear predictor of Rs (Table 4a). In the CASA-framework models, a linear NPP function improves the fit of the model incorporating topsoil carbon, but reduces the explanatory power and increases the error in the model incorporating total soil carbon (Table 4b).

Soil Carbon estimates show a strong negative relationship with Rs at the global scale (Figure 5b). Arctic and boreal datasets, with the highest soil carbon estimates, have the lowest Rs values and may limit our ability to construct empirical models of Rs based on soil carbon availability at the global scale. Grasslands, savannahs and shrublands, and arctic biomes show the highest coefficients of variation in soil carbon.

In regression tree analysis, topsoil carbon is a strong predictor of Rs variability in temperate evergreen and boreal forests (Appendix C). Soil carbon loads the first principal component in the PCA with equal strength to temperature, but in the opposite direction, negatively to higher Rs values (Figure 6), suggesting that total soil carbon reflects the carbon remaining in soils as the result of temperature-mediated respiration rates.

In the CASA-framework NLS models, the model with total soil carbon but no NPP coefficient explains the most variability in Rs (Table 4b-3; r2=.65), and improves the fit over the same model with topsoil carbon (Table 4b-2; r2=.37). With a calibrated NPP coefficient, however, the topsoil carbon model explains more variability and greatly reduces the RMSE

(Table 4b-1).

d) Predictive Models of Global Soil Respiration

At the scale of annual Rs measurements and coarse global climatic measurements, each of our predictive modeling efforts captured between 29 and 65% of the variability in observed Rs_annual. This is suggestive not only of the limitations of these functions in accurately predicting these values but also of the difficulty in corroborating the mechanistic relationships we model with empirical observations at broad scales. Our statistical, polynomial models performed best for boreal forests (r2=.55) and mixed forests (r2=.55), which were the only biomes in which additional linear NPP coefficients were statistically significant and improved the model fit (Table 3). The differences between these biome-parameterized models and the global model are most evident when compared spatially (Figure8). Between figures 8a and 9a, 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 a lack of data in this region, its moisture-temperature function has the greatest degree of error among the biomes (RMSE=573.01).

Each of the model structures used in the NLS process were able to converge on global functions relating soil moisture, temperature, and NPP, but insufficient variability in the data within biomes prevented 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 4a). NPP as an additional variable improved the fit of each model, as did pH though it added little explanatory power (r^2=.29, .3, respectively, table 4a). Using the CASA model structure improved explanatory power both with and without the inclusion of a linear NPP function (Table 4b). The total soil carbon model with CASA structure explains nearly half of the Rs variability in cross-validation, but spatial comparison shows that it greatly overestimates Rs predictions in tropical areas with high NPP and a lack of Rs observations (Figure 8). The topsoil carbon model improved the explained variability even without the inclusion of an NPP component, yet with a greater degree of RMSE (Table 4b). Total annual global Rs was 93.9±25.11 Pg C/yr in the global GAM. The global Michaelis-Menten model with precipitation estimated and Rs rate of 80.3±24.6 Pg C/yr globally, and the CASA-framework model with soil moisture and a linear NPP function estimated Rs=108.6±69.6 Pg C/yr. Differences in the totals and error ranges of these estimates are the results of compounded error and uncertainty in certain regions, especially the highly productive tropics, which is evident in the spatial differences of Figure 9.

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, Falkowski et. al. 2000, Trumbore 2006). At the broad spatial and temporal scales explored in this study, there are important and unfortunate limits to scaling up predictions of Rs as a function of climatic and environmental factors with known mechanistic relationships at focused scales (Ryan et. al. 2005). Nonetheless, both expected and novel patterns emerge at global and biome scales which serve to elucidate the most dominant effects in different biomes and offer insight regarding future carbon cycle-climate interactions.

This analysis corroborates prior research which has described positive correlation of mean annual Rs values at the global scale with mean atmospheric temperature and annual precipitation (Raich, J.; Potter, C.; Bhagawati 2002, Chen et. al 2014), and shows where soil moisture measurements explain further soil respiration variability. Global-scale correlation between temperature, precipitation, and NPP have shown how climatic drivers regulate total Rs. Autotrophic and heterotrophic respiration are highly correlated and climatic drivers of Rs are less significant when considering only one of these components (Bond-Lamberty et al 2004). Earlier research has shown global Rs estimates to be approximately 24% greater than NPP (Raich et al 1995). Our analysis, with additional observations and satellite-derived NPP, corroborates this finding (22%, Figure 5a); the additional variation in soil respiration is attributed to the consumption of soil organic carbon by heterotrophs. The additional variability that results from heterotrophic respiration is explained in part by soil carbon and soil moisture measures.

At the global scale, the highest Rs values seem to occur where volumetric soil water content approaches ~25% (Figure 4b), which could corroborate the functions of recently constructed models (Yi and Kimball 2011, Faloon et. al. 2011, Davidson et. al. 2012), but high degrees of variation at this scale obfuscate a more focused understanding. Our NLS model which incorporated a parabolic moisture function as used in several ESMs (Mellilo et. al. 2000, Exbrayat et. al. 2013) performed significantly better than models which relied upon precipitation as seen in previous studies (Table 4a) (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 variability in temperature and NPP within these ecosystems (Figure 3, Appendix B) and in part to the mediating influence on soil moisture of snowpack dynamics (Brooks et al 2005, 2011, Oquist et al 2009), especially in the boreal forests (Du et al 2013). Because of the strong correlation between precipitation and NPP (Table 2), 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 supply 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, Du et al 2013, Hartley et al 2008). There is significant uncertainty regarding climate change’s potential to drive the release of the large amounts of soil carbon found at high latitudes (Shurr et al. 2008), and changing precipitation and snow dynamics are likely to affect soil moisture conditions (Euskritchen, McGuire, and Chapin 2007). Relatively low rates of NPP in these biomes amplify the importance of climatic factors in driving the decomposition of large soil carbon pools, especially when considering that error in global models is a greater percentage of total Rs estimates at high latitudes.

In forested biomes, conversely, high rates of NPP and high Rs relative to model error may overwhelm the temperature and moisture influences on Rs uncertainty (Jannsens et al. 2001). Overestimates of Rs in our statistical models are underscored by uncertainty in the tropics (Figure 8, 9c). Prior research has shown local soil moisture characteristics to affect Rs variability within tropical forests, and has stressed the need to measure soil moisture at varying depths with soil properties (Davidson et al 2000). Seasonal precipitation dynamics in tropical ecosystems also likely contribute to the high soil moisture variability shown in this study, but at annual timescales temperature still emerges as the dominant Rs control despite the control of moisture in some site-scale studies (Hashimoto et al 2004).

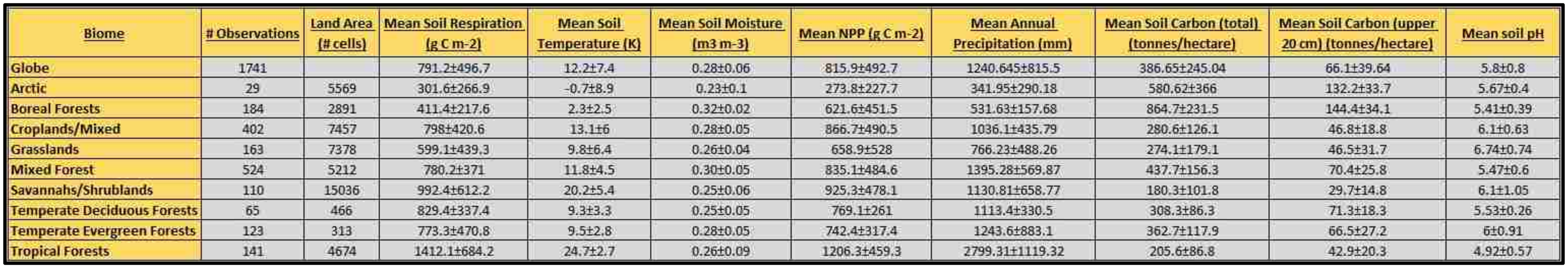
The general additive model used in this study describes an over-fit statistical relationship between the satellite-derived variables and the observations in the SRDB, but it provides an empirically-driven benchmark estimate against which to compare fitted models with mechanistic bases. The results of the models with Michaelis-Menten moisture or precipitation parameters corroborate prior research which has been performed for mainly temperate ecosystems, and clarifies the margin of error by which such analyses can be applied to the globe. Models with a quadratic soil moisture function as in the CASA equation improve explained variance but often at the cost of increased mean squared error. The addition of a fitted NPP coefficient in the total soil carbon model, for example, leads to significant over-prediction of Rs in areas of high NPP when compared to the GAM (Figure 9). 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).

Two primary complications limit our insight in this analysis. Firstly, 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 Figure 8 and Table 3, smooth functions of soil moisture and temperature were fit for each biome; relative differences in the performance of these models and in Rs estimates made in Figure 9 show that without enough data to explain variability within biomes as a function of NPP, for example, error in Rs estimates can vary significantly. Secondly, a global-scale analysis of soil respiration variability relies upon annual Rs measurements and the horizontal mismatch of scale 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 grid-scale predictions (Reichstein and Beer, 2008). The mathematical relationships between climatic variables and Rs used in ESMs must manifest even in annual observations at large scales. The relative differences in the outputs of these models suggests the importance of considering soil moisture influences on respiration and where areas of uncertainty in our global understanding of soil respiration necessitate further broad-scale research.

This study provides a clear overview of the importance of integrating soil moisture 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 models of Rs. 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 at various scales.

Tables

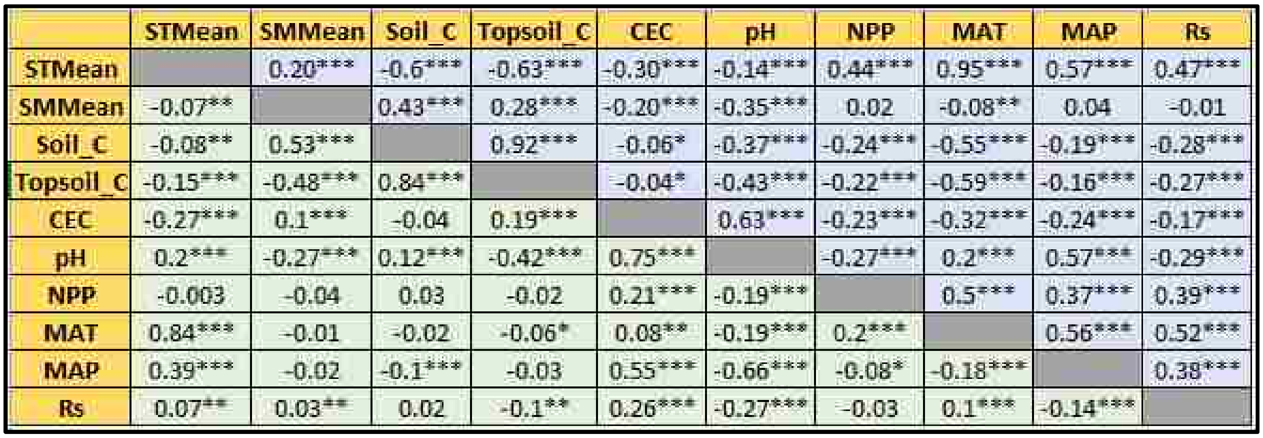
1. Global summary of variable means by biome



Biome	# Observations	Land Area (# cells)	Mean Soil Respiration (g C m-2)	Mean Soil Temperature (K)	Mean Soil Moisture (m3 m-3)	Mean NPP (g C m-2)	Mean Annual Precipitation (mm)	Mean Soil Carbon (total) (tonnes/hectare)	Mean Soil Carbon (upper 20 cm) (tonnes/hectare)	Mean soil pH
Globe	1741		791.2±496.7	12.2±7.4	0.28±0.06	815.9±492.7	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	273.8±227.7	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	621.6±451.5	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	866.7±490.5	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	658.9±528	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	835.1±484.6	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	925.3±478.1	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	769.1±261	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	742.4±317.4	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	1206.3±459.3	2799.31±1119.32	205.6±86.8	42.9±20.3	4.92±0.57

Table 1: Summary of mean values for each biome. Error bars = +/- 1 S.D.

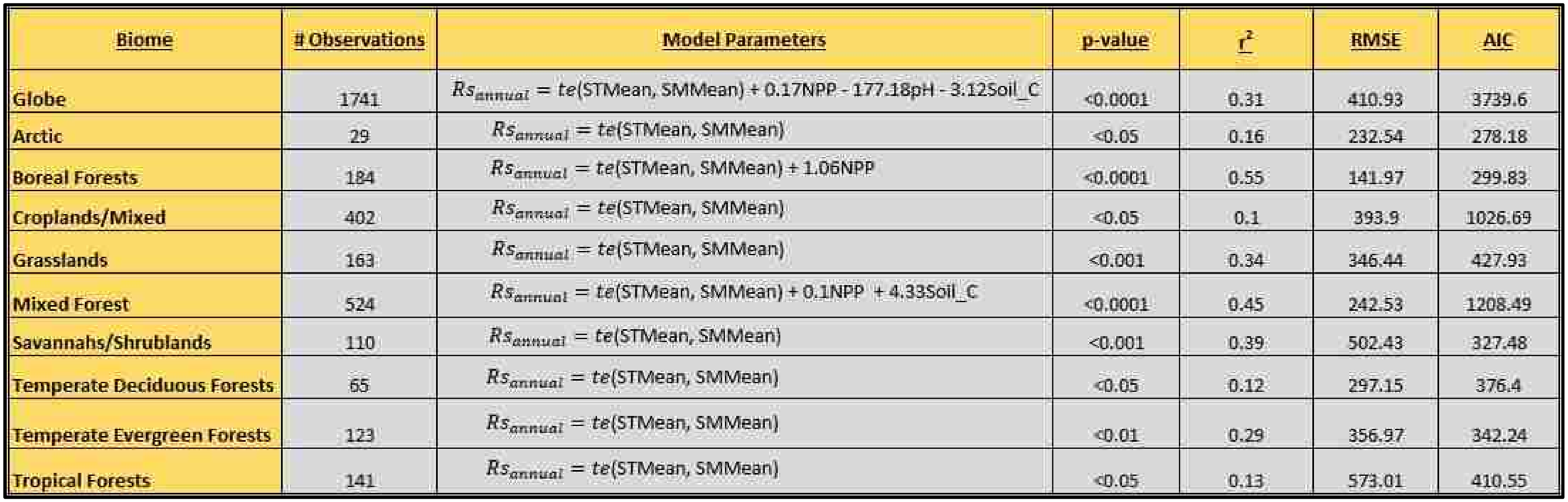
2. Pairwise and Pearson Product-Momentum Correlations



	STMean	SMMean	Soil_C	Topsoil_C	CEC	pH	NPP	MAT	MAP	Rs
STMean		0.20***	-0.6***	-0.63***	-0.30***	-0.14***	0.44***	0.95***	0.57***	0.47***
SMMean	-0.07**		0.43***	0.28***	-0.20***	-0.35***	0.02	-0.08**	0.04	-0.01
Soil_C	-0.08**	0.53***		0.92***	-0.06*	-0.37***	-0.24***	-0.55***	-0.19***	-0.28***
Topsoil_C	-0.15***	-0.48***	0.84***		-0.04*	-0.43***	-0.22***	-0.59***	-0.16***	-0.27***
CEC	-0.27***	0.1***	-0.04	0.19***		0.63***	-0.23***	-0.32***	-0.24***	-0.17***
pH	0.2***	-0.27***	0.12***	-0.42***	0.75***		-0.27***	0.2***	0.57***	-0.29***
NPP	-0.003	-0.04	0.03	-0.02	0.21***	-0.19***		0.5***	0.37***	0.39***
MAT	0.84***	-0.01	-0.02	-0.06*	0.08**	-0.19***	0.2***		0.56***	0.52***
MAP	0.39***	-0.02	-0.1***	-0.03	0.55***	-0.66***	-0.08*	-0.18***		0.38***
Rs	0.07**	0.03**	0.02	-0.1**	0.26***	-0.27***	-0.03	0.1***	-0.14***	

Table 2: Correlation Coefficient matrix. Upper triangle (blue) displays Pearson Product-Momentum Coefficients for each variable. Lower triangle (green) displays pairwise correlation coefficients between each set of variables after adjusting for influence of all others.

3. Generalized Additive Model Results



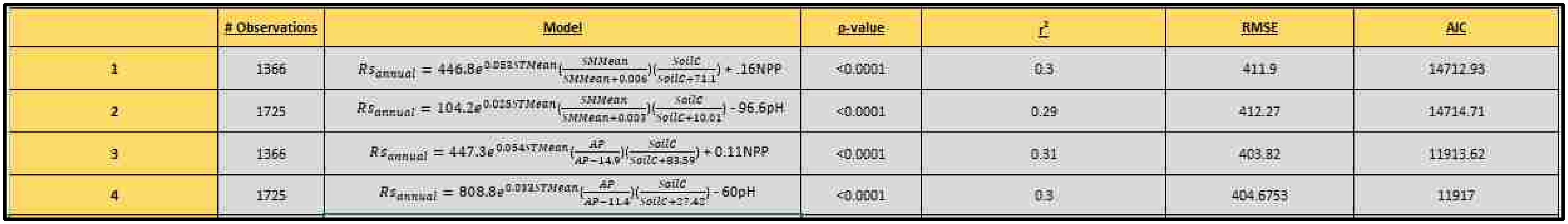
Biome	# Observations	Model Parameters	p-value	r^2	RMSE	AIC
Globe	1741	$Rs_{annual} = te(\text{STMean, SMMean}) + 0.17\text{NPP} - 177.18\text{pH} - 3.12\text{Soil\_C}$	<0.0001	0.31	410.93	3739.6
Arctic	29	$Rs_{annual} = te(\text{STMean, SMMean})$	<0.05	0.16	232.54	278.18
Boreal Forests	184	$Rs_{annual} = te(\text{STMean, SMMean}) + 1.06\text{NPP}$	<0.0001	0.55	141.97	299.83
Croplands/Mixed	402	$Rs_{annual} = te(\text{STMean, SMMean})$	<0.05	0.1	393.9	1026.69
Grasslands	163	$Rs_{annual} = te(\text{STMean, SMMean})$	<0.001	0.34	346.44	427.93
Mixed Forest	524	$Rs_{annual} = te(\text{STMean, SMMean}) + 0.1\text{NPP} + 4.33\text{Soil\_C}$	<0.0001	0.45	242.53	1208.49
Savannahs/Shrublands	110	$Rs_{annual} = te(\text{STMean, SMMean})$	<0.001	0.39	502.43	327.48
Temperate Deciduous Forests	65	$Rs_{annual} = te(\text{STMean, SMMean})$	<0.05	0.12	297.15	376.4
Temperate Evergreen Forests	123	$Rs_{annual} = te(\text{STMean, SMMean})$	<0.01	0.29	356.97	342.24
Tropical Forests	141	$Rs_{annual} = te(\text{STMean, SMMean})$	<0.05	0.13	573.01	410.55

Table 3: Generalized Additive Model statistics for each dataset. 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). AIC=Aikaike’s Information Criterion.

4. NLS Results

***Table 4a**: Model Summaries for Non-linear Least Squares fit procedure using Arrhenius temperature function and Michaelis-Menten soil moisture, precipitation, and carbon parameters. STMean=Mean Soil Temperature (C), SMMean=Mean Soil Moisture (m3 m-3), Soil C= Soil Carbon (tonnes/hectare), AP=Mean Annual Precipitation (mm). RMSE=Root mean squared error (g C m-2). AIC=Akaike's Information Criterion.*

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.



	# Observations	Model	p-value	r^2	RMSE	AIC
1	1366	$Rs_{annual} = 446.8e^{0.053STMean}(\frac{SMMean}{SMMean+0.006})(\frac{SoilC}{SoilC+71.1}) + .16NPP$	<0.0001	0.3	411.9	14712.93
2	1725	$Rs_{annual} = 104.2e^{0.025STMean}(\frac{SMMean}{SMMean+0.003})(\frac{SoilC}{SoilC+10.01}) - 96.6pH$	<0.0001	0.29	412.27	14714.71
3	1366	$Rs_{annual} = 447.3e^{0.054STMean}(\frac{AP}{AP-14.9})(\frac{SoilC}{SoilC+83.59}) + 0.11NPP$	<0.0001	0.31	403.82	11913.62
4	1725	$Rs_{annual} = 808.8e^{0.032STMean}(\frac{AP}{AP-11.4})(\frac{SoilC}{SoilC+27.40}) - 60pH$	<0.0001	0.3	404.6753	11917

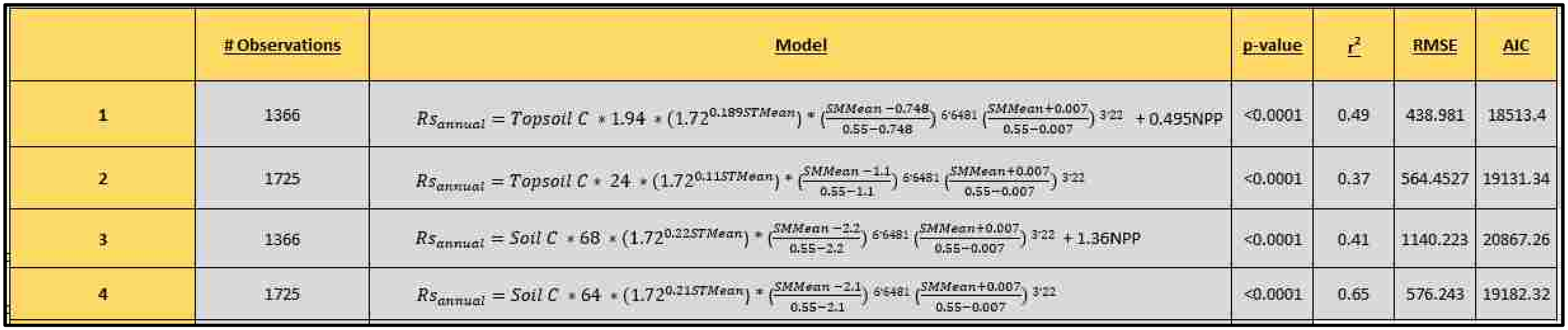
***Table 4b**: Model Summaries for Non-linear Least Squares fit procedure using CASA model framework. Procedure calibrated only 1st Soil Moisture function numerator, regulating optimum of parabolic curve. STMean=Mean Soil Temperature (C), SMMean=Mean Soil Moisture (m3 m-3), Soil C= Soil Carbon (tonnes/hectare), Topsoil C=soil carbon in upper 20 cm (tonnes/hectare). RMSE=Root mean squared error (g C m-2). AIC=Akaike's Information Criterion.*

1: Global model using topsoil carbon, CASA structure, and an additional linear NPP parameter.

2: Global model using topsoil carbon, CASA structure, and no additional linear NPP parameter.

3: Global model using total soil carbon, CASA structure, and an additional linear NPP parameter.

4: Global model using total soil carbon, CASA structure, and no additional linear pH parameter.



	# Observations	**Model**	**p-value**	**r^2**	**RMSE**	**AIC**
1	1366	$Rs_{annual} = Topsoil\ C * 1.94 * (1.72^{0.189STMean}) * (\frac{SMMean - 0.748}{0.55 - 0.748})^{6.6481} (\frac{SMMean + 0.007}{0.55 - 0.007})^{3.22} + 0.495NPP$	<0.0001	0.49	438.981	18513.4
2	1725	$Rs_{annual} = Topsoil\ C * 24 * (1.72^{0.11STMean}) * (\frac{SMMean - 1.1}{0.55 - 1.1})^{6.6481} (\frac{SMMean + 0.007}{0.55 - 0.007})^{3.22}$	<0.0001	0.37	564.4527	19131.34
3	1366	$Rs_{annual} = Soil\ C * 68 * (1.72^{0.22STMean}) * (\frac{SMMean - 2.2}{0.55 - 2.2})^{6.6481} (\frac{SMMean + 0.007}{0.55 - 0.007})^{3.22} + 1.36NPP$	<0.0001	0.41	1140.223	20867.26
4	1725	$Rs_{annual} = Soil\ C * 64 * (1.72^{0.21STMean}) * (\frac{SMMean - 2.1}{0.55 - 2.1})^{6.6481} (\frac{SMMean + 0.007}{0.55 - 0.007})^{3.22}$	<0.0001	0.65	576.243	19182.32

Figures

1. Global Rs Observations and Biomes

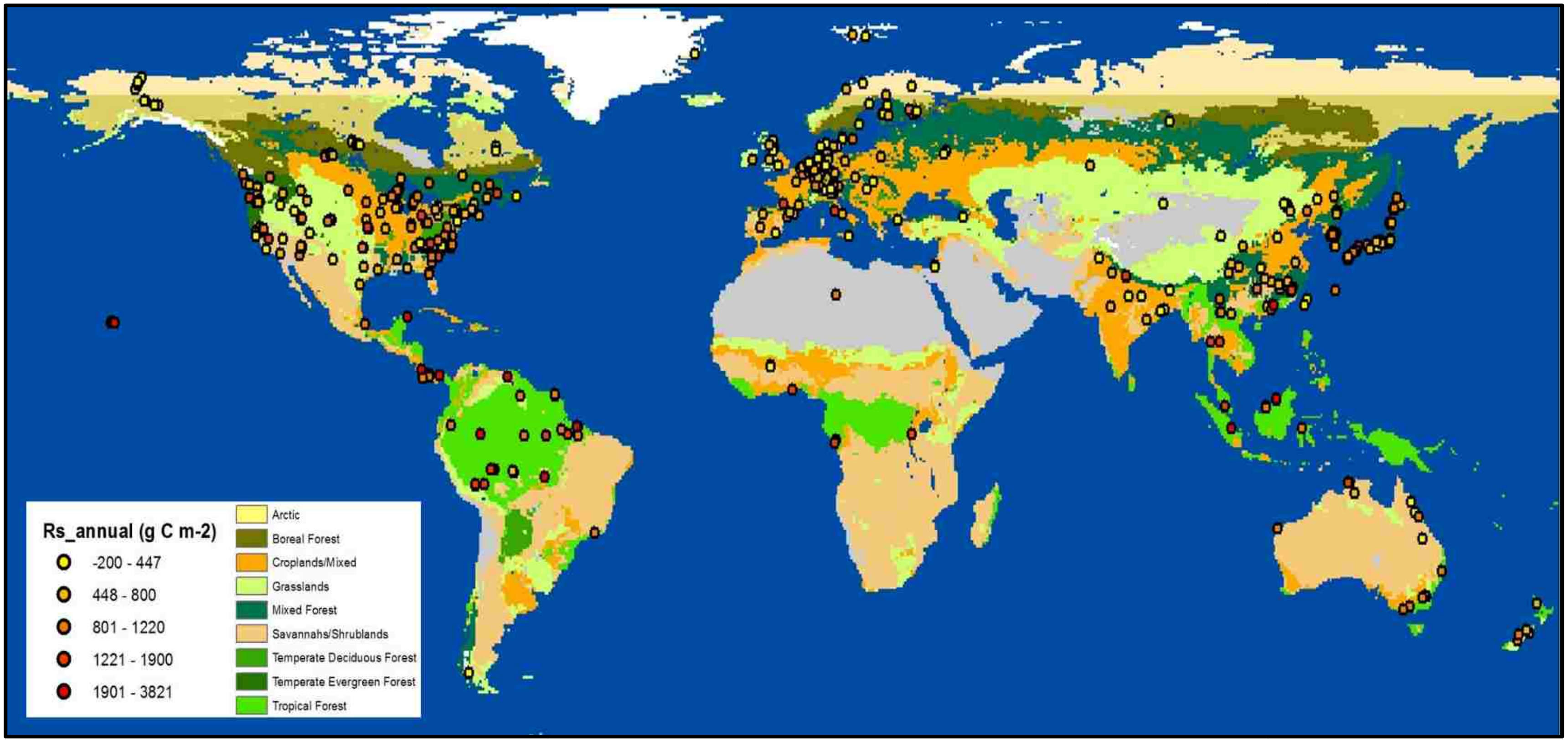


Figure 1: Biomes and global Annual Soil Respiration observations of the study set

2. Soil Respiration Overview by biome

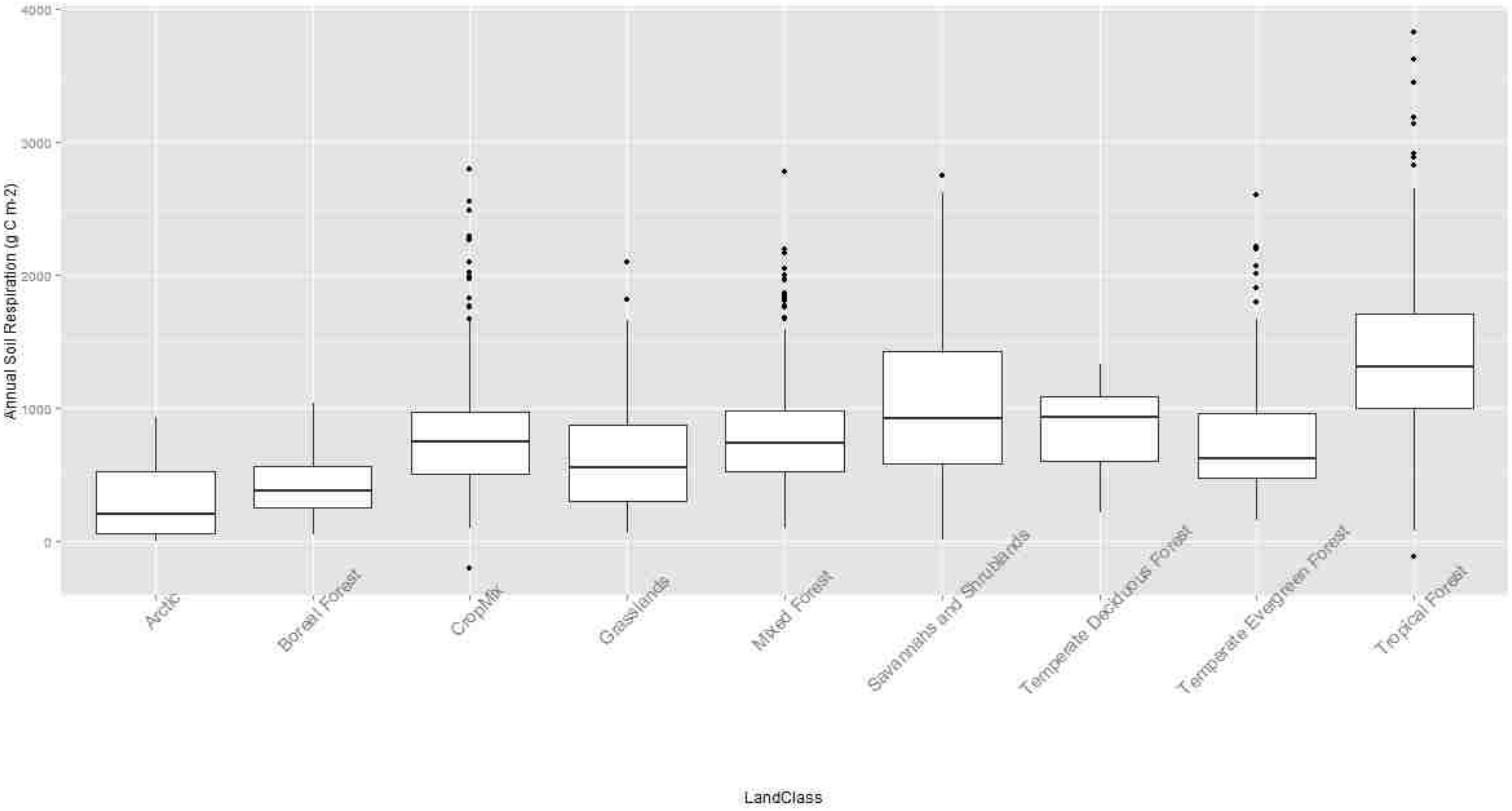
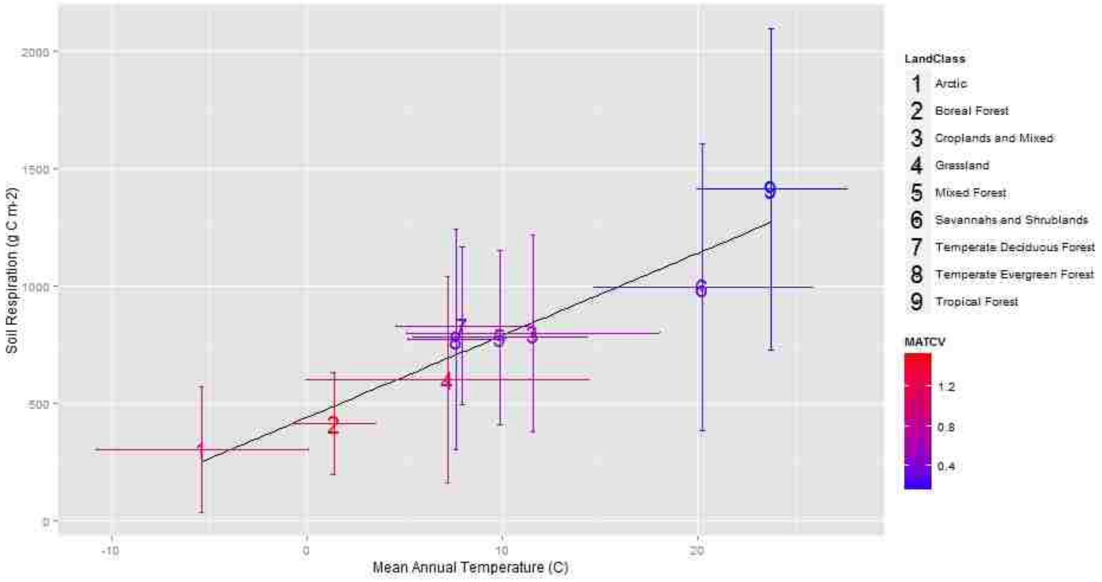


Figure 2: Annual soil respiration observations by Biome. Box plots display the mean values (center horizontal line) and ranges of the middle and outer quartiles of observations (boxes and vertical lines, respectively).

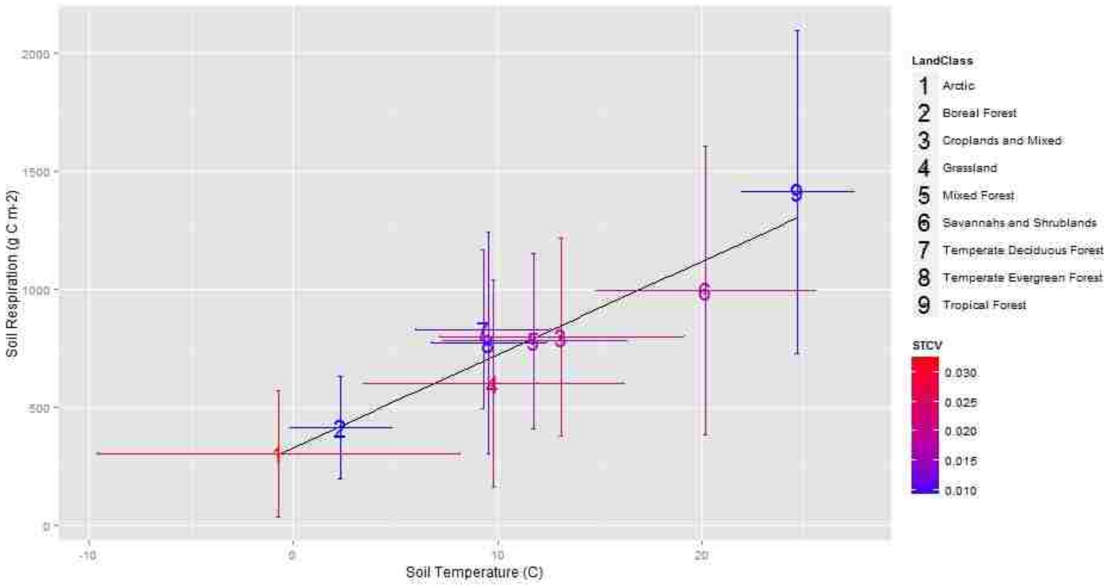
3. Global Temperature Relationships

Figure 3: Biome mean soil respiration values and temperature variables. Error bars represent +/- 1 standard deviation in each plot. Color is scaled according to the coefficient of variation of each biome's independent variable. ***(a)*** *Mean Annual Temperature (C), y=34.99x + 439.1; $p<0.01$; $R^2 = .89$;* ***(b)*** *Mean Soil Temperature (C), y=39.5x + 327.2; $p<0.01$; $R^2 = .91$*

(3a)



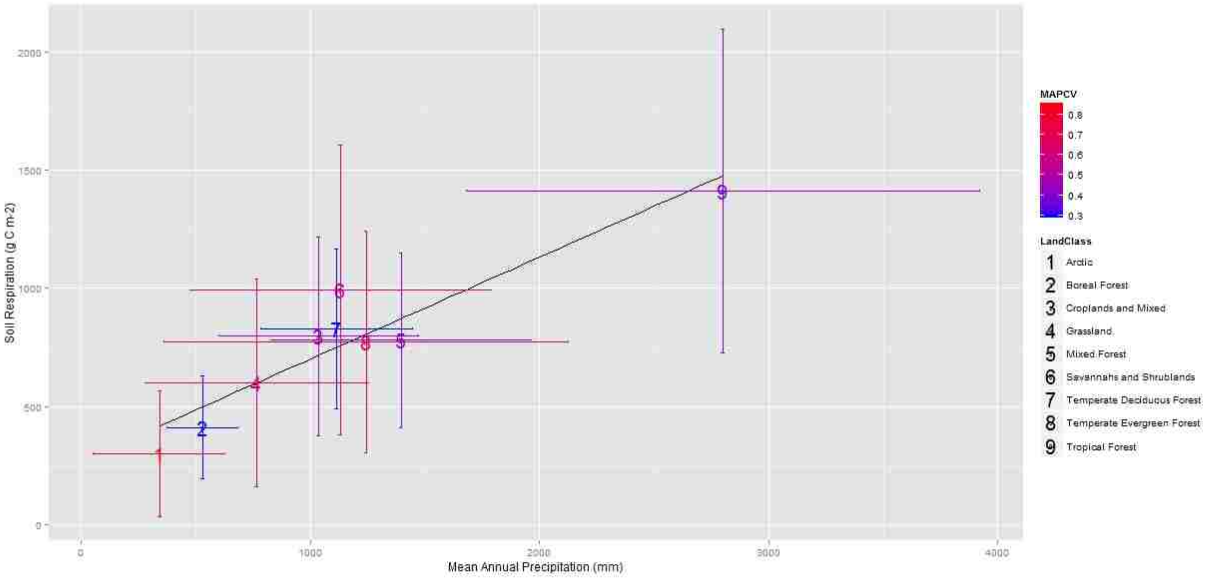
(3b)



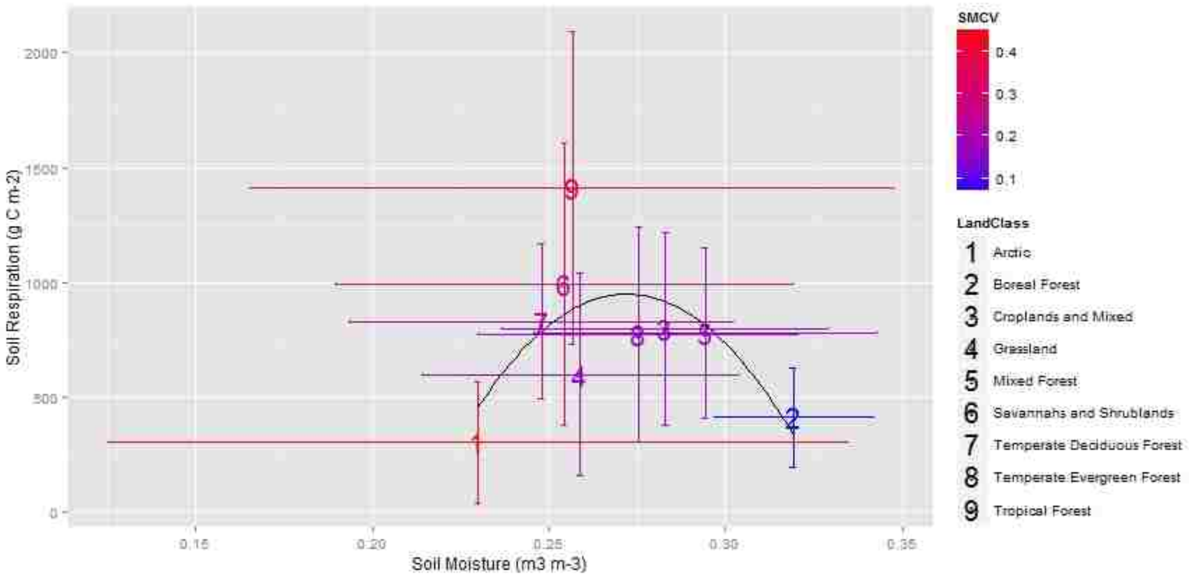
4. Global Moisture Relationships

Figure 4: Biome mean soil respiration values and moisture variables. Error bars represent +/- 1 standard deviation in each plot. Color is scaled according to the coefficient of variation of each biome's independent variable. ***(a)*** *Mean Annual Precipitation (mm), y=270.33+.43x. $p<0.05$; $R^2=0.88$;* ***(b)*** *Mean Soil Moisture (m3 m-3), $y=150803.45x - 277187.14x^2 - 19562.43$; $p<0.1$; $R^2= .45$*

(4a)



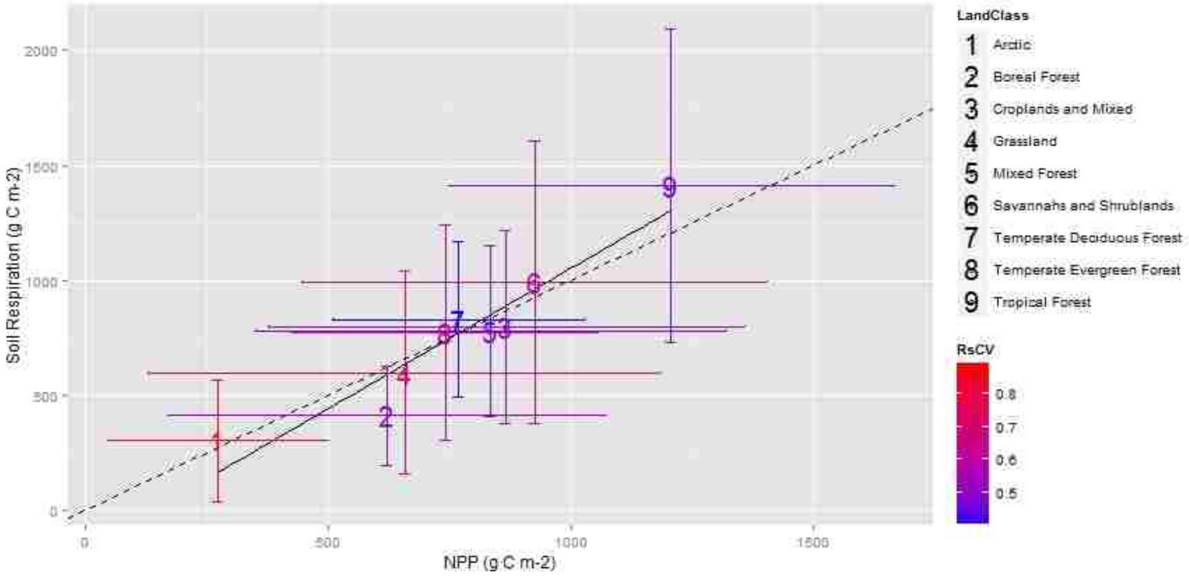
(4b)



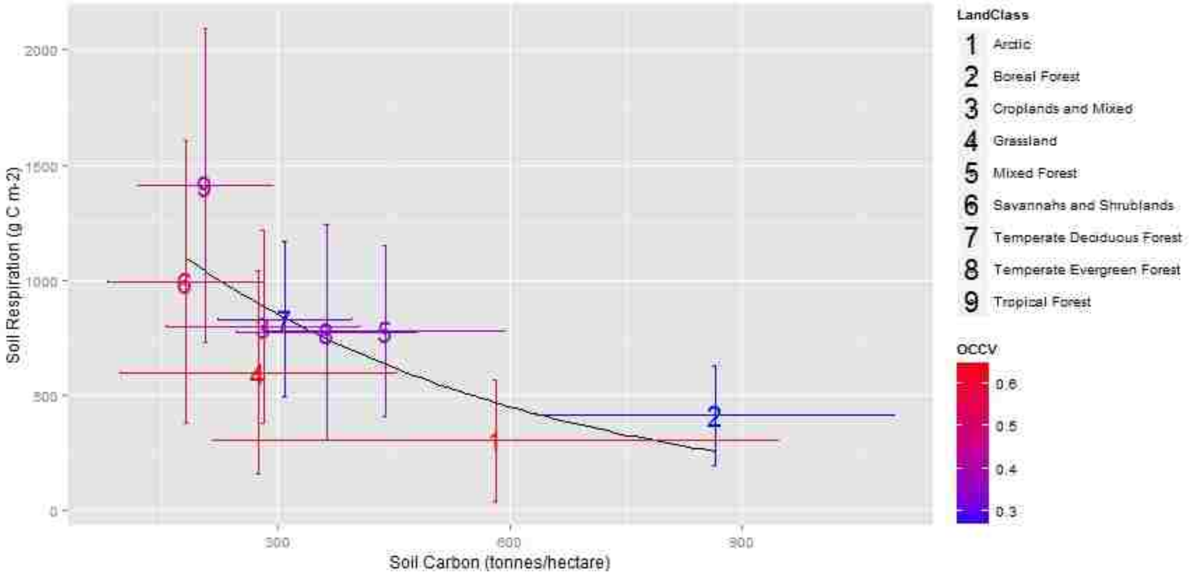
5. Global Carbon Supply Relationships

Figure 5: Biome mean soil respiration values and carbon supply variables. Error bars represent +/- 1 standard deviation in each plot. Color is scaled according to the coefficient of variation of each biome's independent variable. ***(a)*** *Net Primary Productivity (g C m-2), y=1.22x-170.5. Dashed line represents 1:1 relationship. p<0.05;* $R^2=0.9$*;* ***(b)*** *Total Soil Carbon (tonnes/hectare), y=7.382-0.002*log(x). p<0.05;* $R^2=0.34$

(5a)



(5b)



6. Global Principal Components Analysis

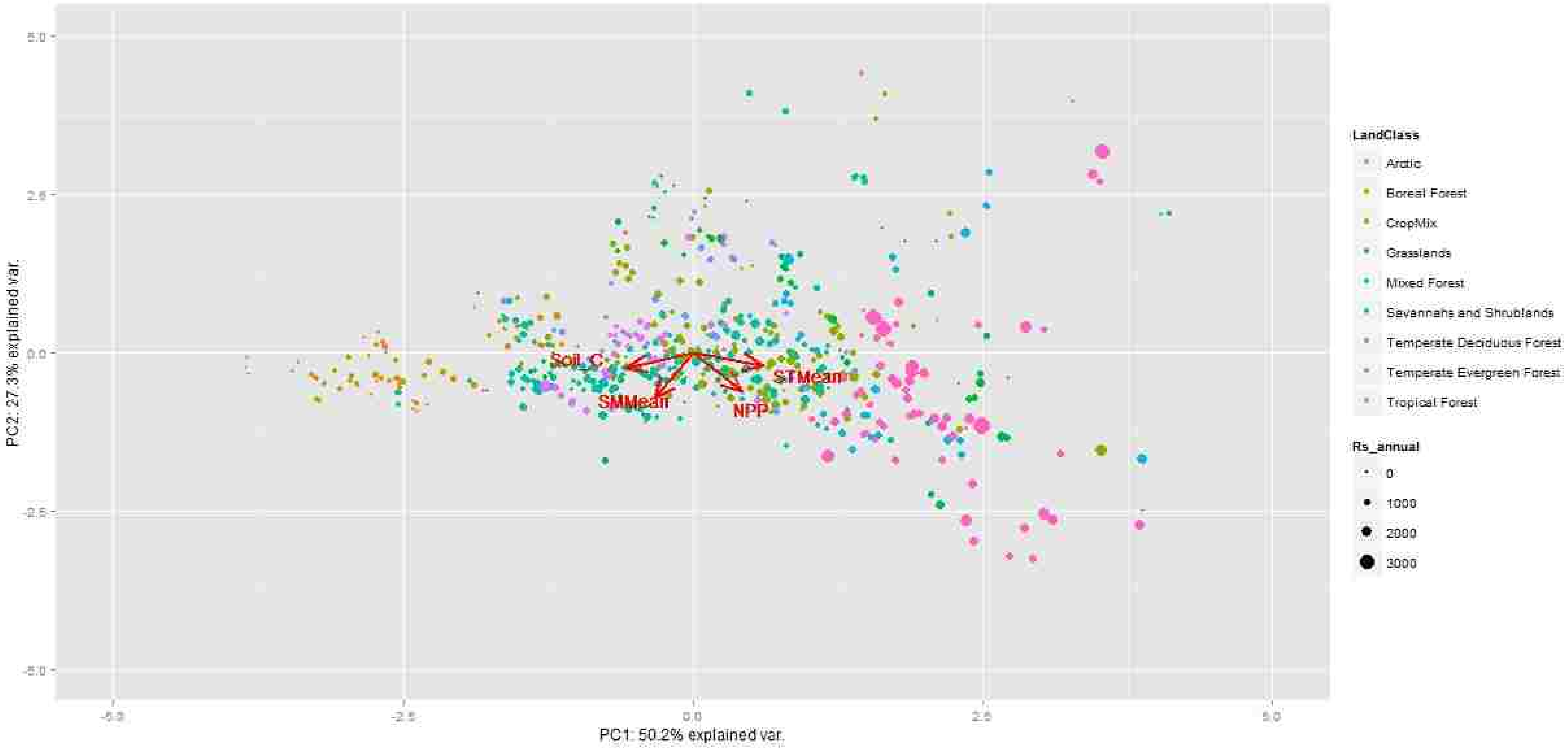


Figure 6. Principal Components Analysis biplot of variability in independent variables. Red vectors represent principal Component Loadings of each variable. Point size=Annual Soil Respiration (g C m-2):

	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*

7. Global Regression Tree

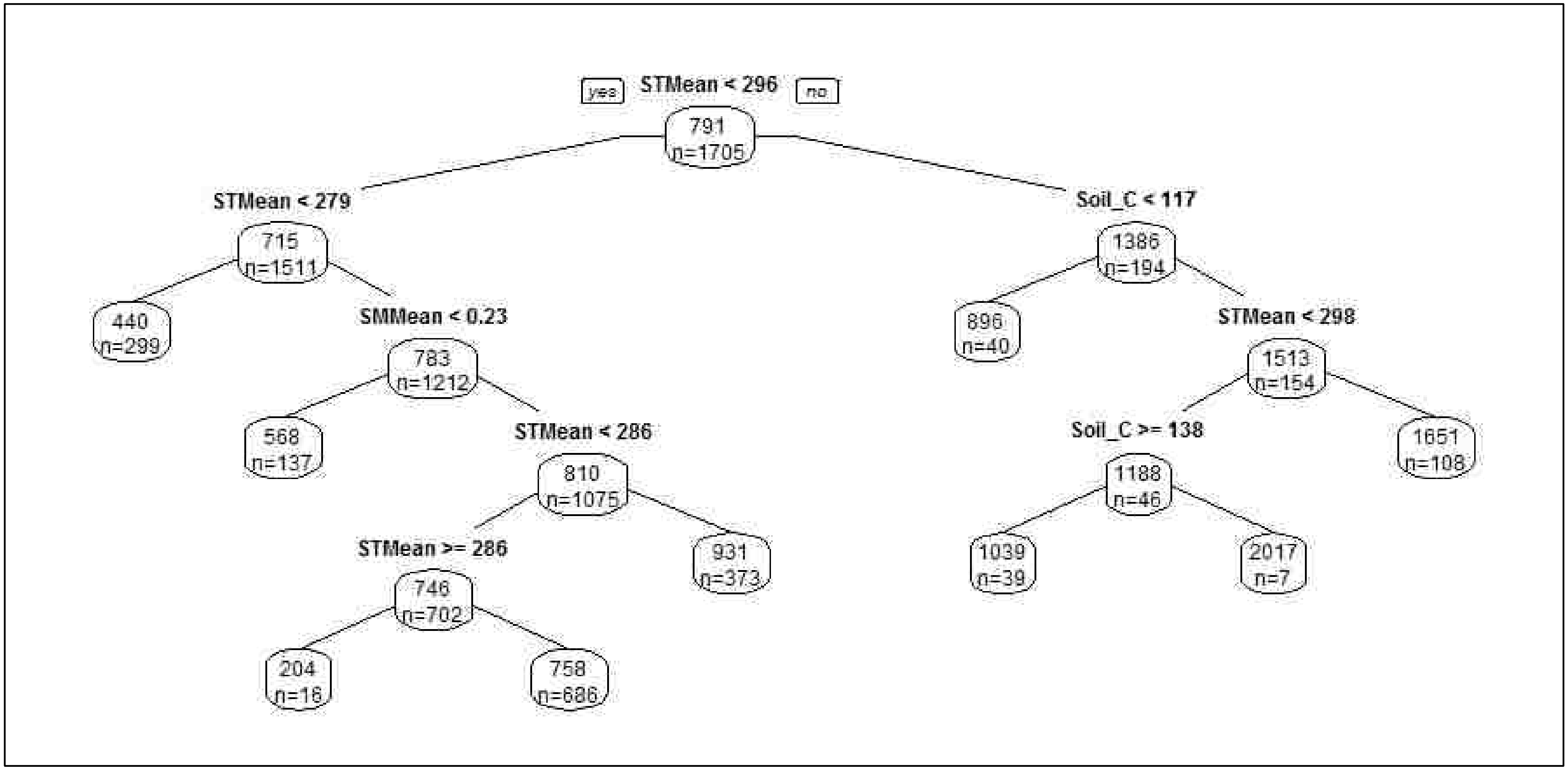
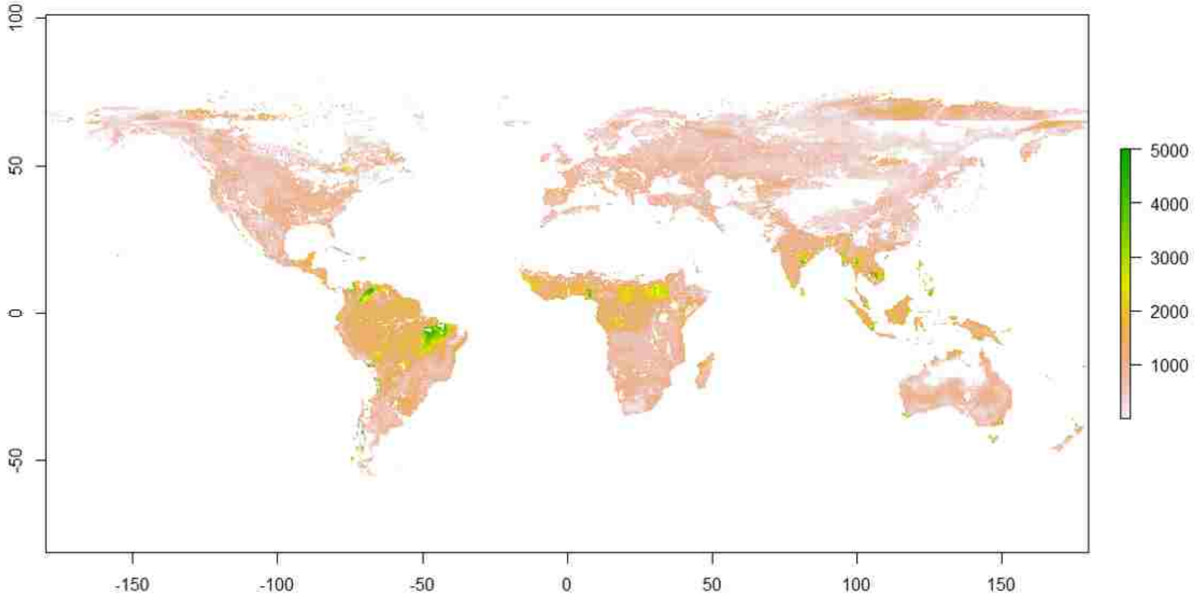


Figure 7: Regression tree for the global dataset. Predictor coefficients and number of observations reported at each node. STMean=mean annual soil temperature (C), SMMean=mean annual soil moisture (m3 m-3), Soil_C=total soil carbon (tonnes/hectare). NPP (g C m-2) also included as independent variable in model calibration.

8. Biome-Specific GAM Results

(8a)



(8b)

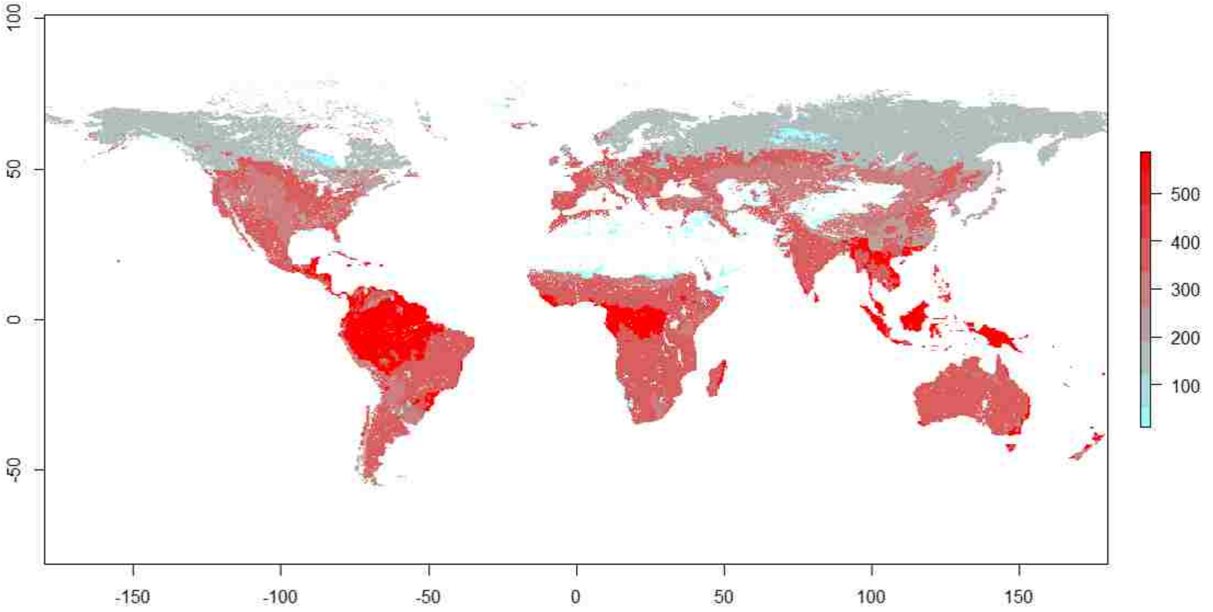


Figure 8. The predicted results of Rs_annual in 2014 using biome-specific models. (A): Predicted Rs_annual, g C m-2. (B): RMSE of model for each biome (g C m-2).

9. GAM and NLS spatial comparison

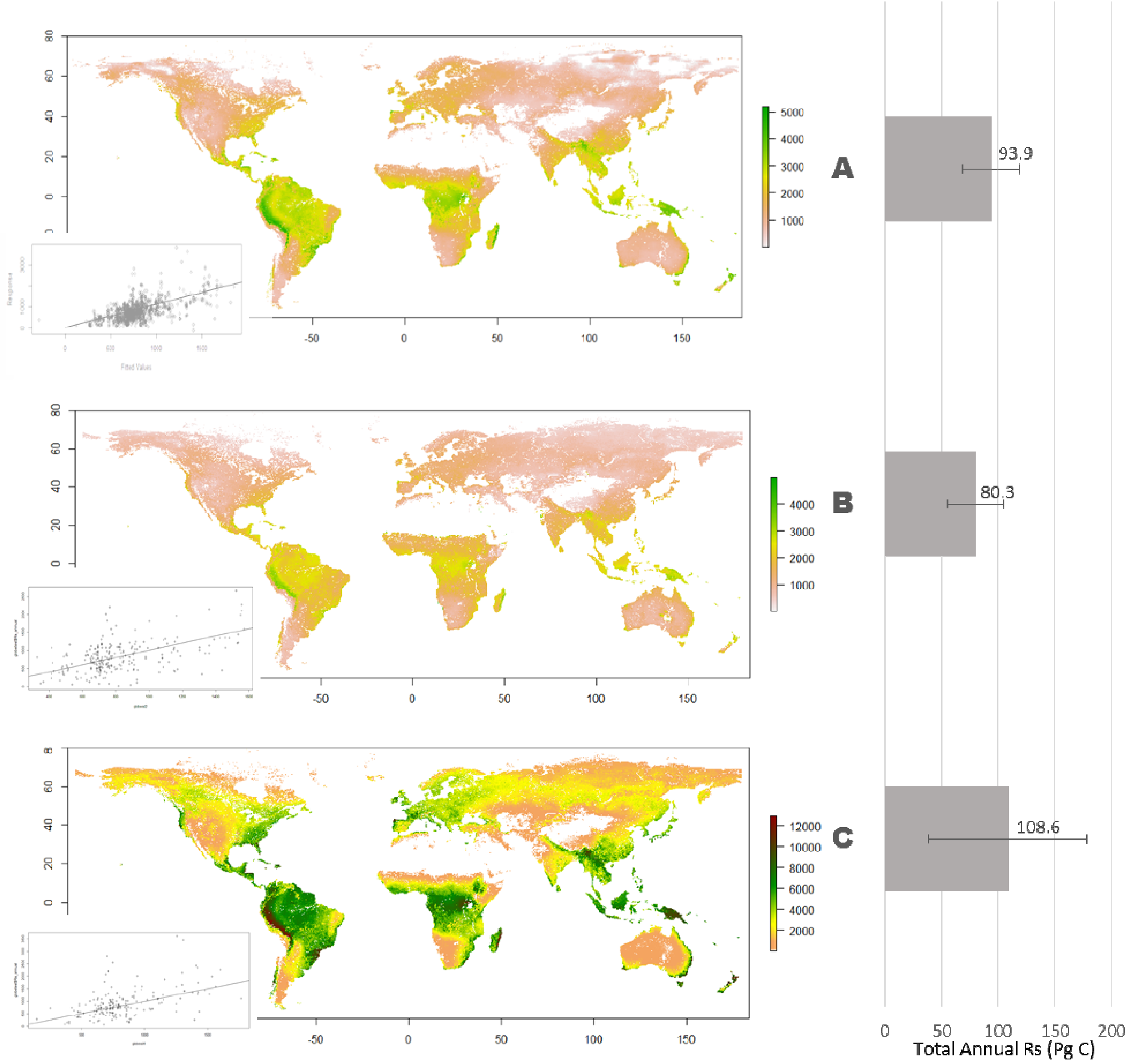


*Figure 9. The predicted results of Rs_annual in 2014 using global models. Lower left: Cross-validation results on one 20% testing set from k-fold procedure. Right panel: Total annual soil respiration=Σ(cell rate * cell area); Error bars =(*

A: Global generalized additive model (Table 3) RMSE; 410.93 g C m-2; R^2 *=.31.*
B: Global NLS model with precipitation michaelis-menten structure (Table 4a-3). RMSE=403.82 g C m-2; R^2 *=.31.*
C: Global NLS model with total soil carbon, CASA structure, and NPP (Table 4b-3). RMSE=1140.22 g C m-2; R^2*=.41*

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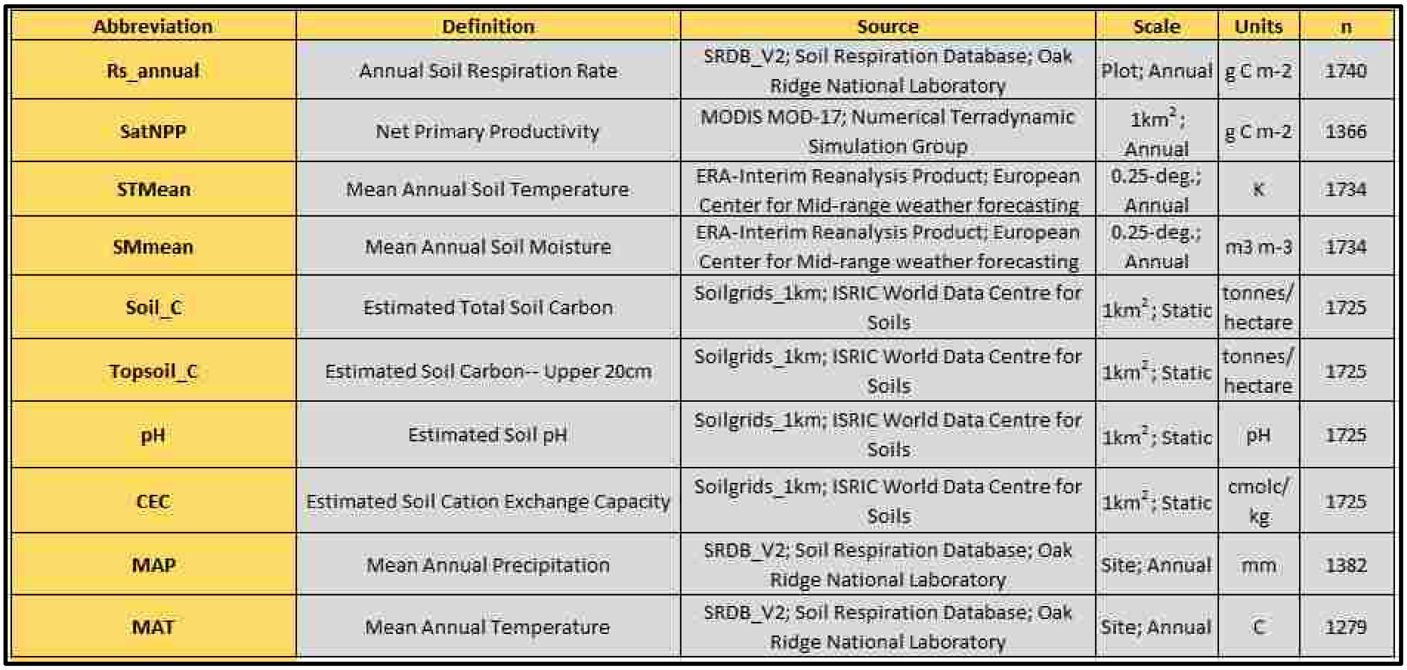
Appendix A: Data Sources

Table 5: Data Sources and Scales



Abbreviation	Definition	Source	Scale	Units	n
Rs_annual	Annual Soil Respiration Rate	SRDB_V2; Soil Respiration Database; Oak Ridge National Laboratory	Plot; Annual	g C m-2	1740
SatNPP	Net Primary Productivity	MODIS MOD-17; Numerical Terradynamic Simulation Group	1km^2; Annual	g C m-2	1366
STMean	Mean Annual Soil Temperature	ERA-Interim Reanalysis Product; European Center for Mid-range weather forecasting	0.25-deg.; Annual	K	1734
SMmean	Mean Annual Soil Moisture	ERA-Interim Reanalysis Product; European Center for Mid-range weather forecasting	0.25-deg.; Annual	m3 m-3	1734
Soil_C	Estimated Total Soil Carbon	Soilgrids_1km; ISRIC World Data Centre for Soils	1km^2; Static	tonnes/ hectare	1725
Topsoil_C	Estimated Soil Carbon-- Upper 20cm	Soilgrids_1km; ISRIC World Data Centre for Soils	1km^2; Static	tonnes/ hectare	1725
pH	Estimated Soil pH	Soilgrids_1km; ISRIC World Data Centre for Soils	1km^2; Static	pH	1725
CEC	Estimated Soil Cation Exchange Capacity	Soilgrids_1km; ISRIC World Data Centre for Soils	1km^2; Static	cmolc/ kg	1725
MAP	Mean Annual Precipitation	SRDB_V2; Soil Respiration Database; Oak Ridge National Laboratory	Site; Annual	mm	1382
MAT	Mean Annual Temperature	SRDB_V2; Soil Respiration Database; Oak Ridge National Laboratory	Site; Annual	C	1279

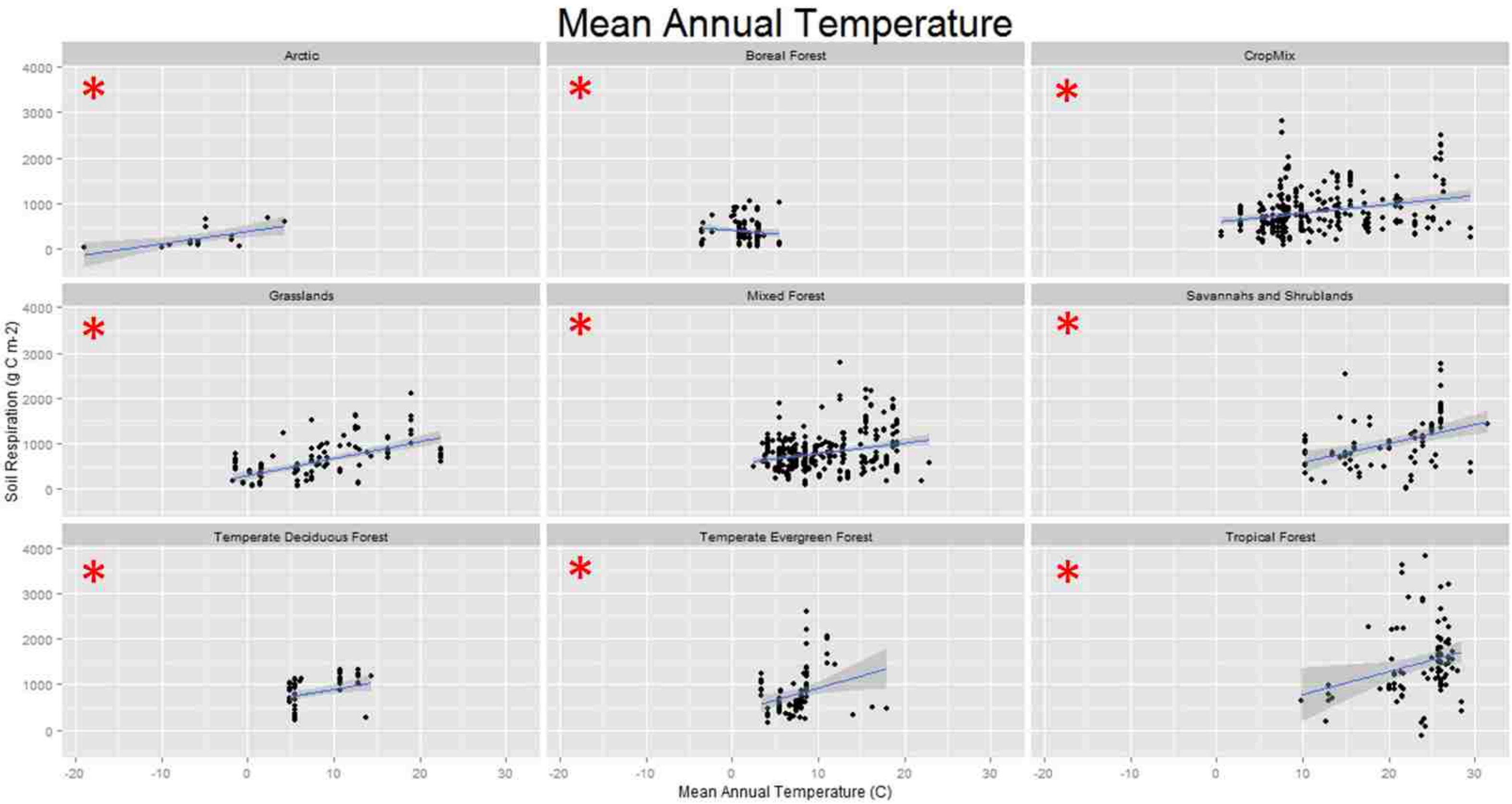
Table 5: Variable Abbreviations and data source information.

Appendix B: Univariate Analysis

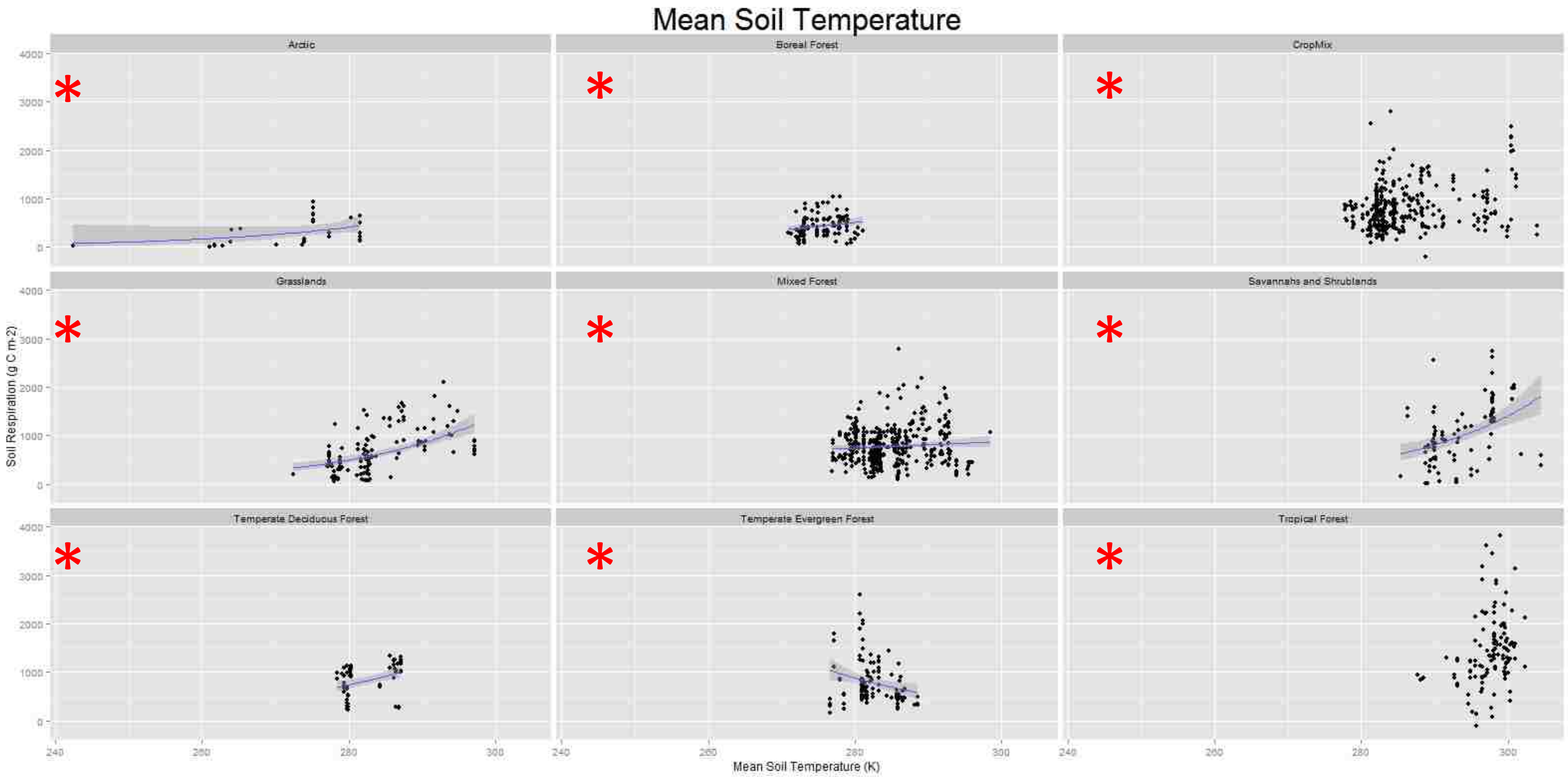
Figure 10: Univariate matrices

Figure 10: Relationships between annual soil respiration and each independent variable, partitioned by biome. Statistically significant relationships (p<0.05) denoted by red asterisk. Normalized soil temperature and soil moisture are calculated as: , for each data point relative to annual values 1979-2012.

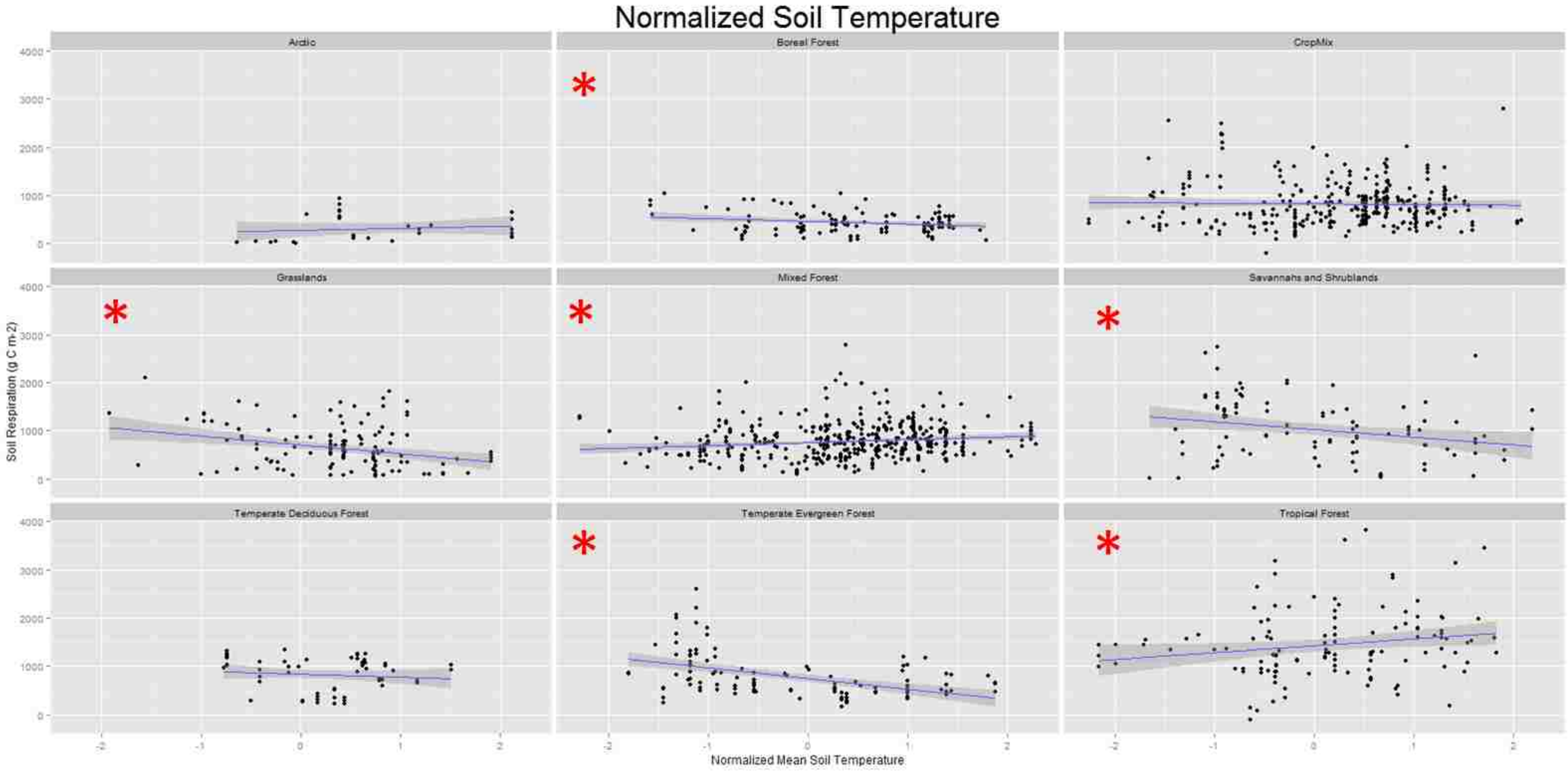
A: Mean annual temperature



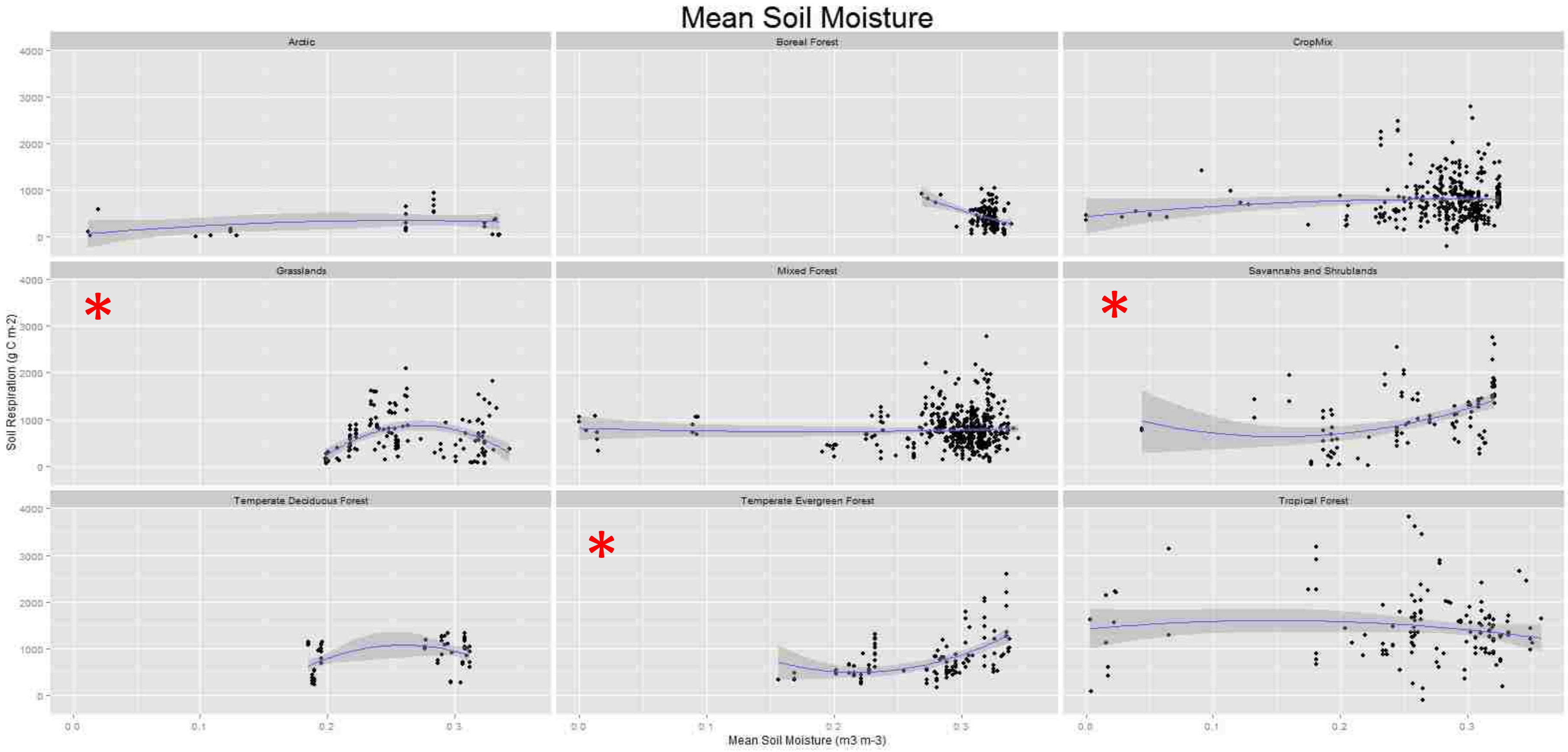
B: Soil Temperature



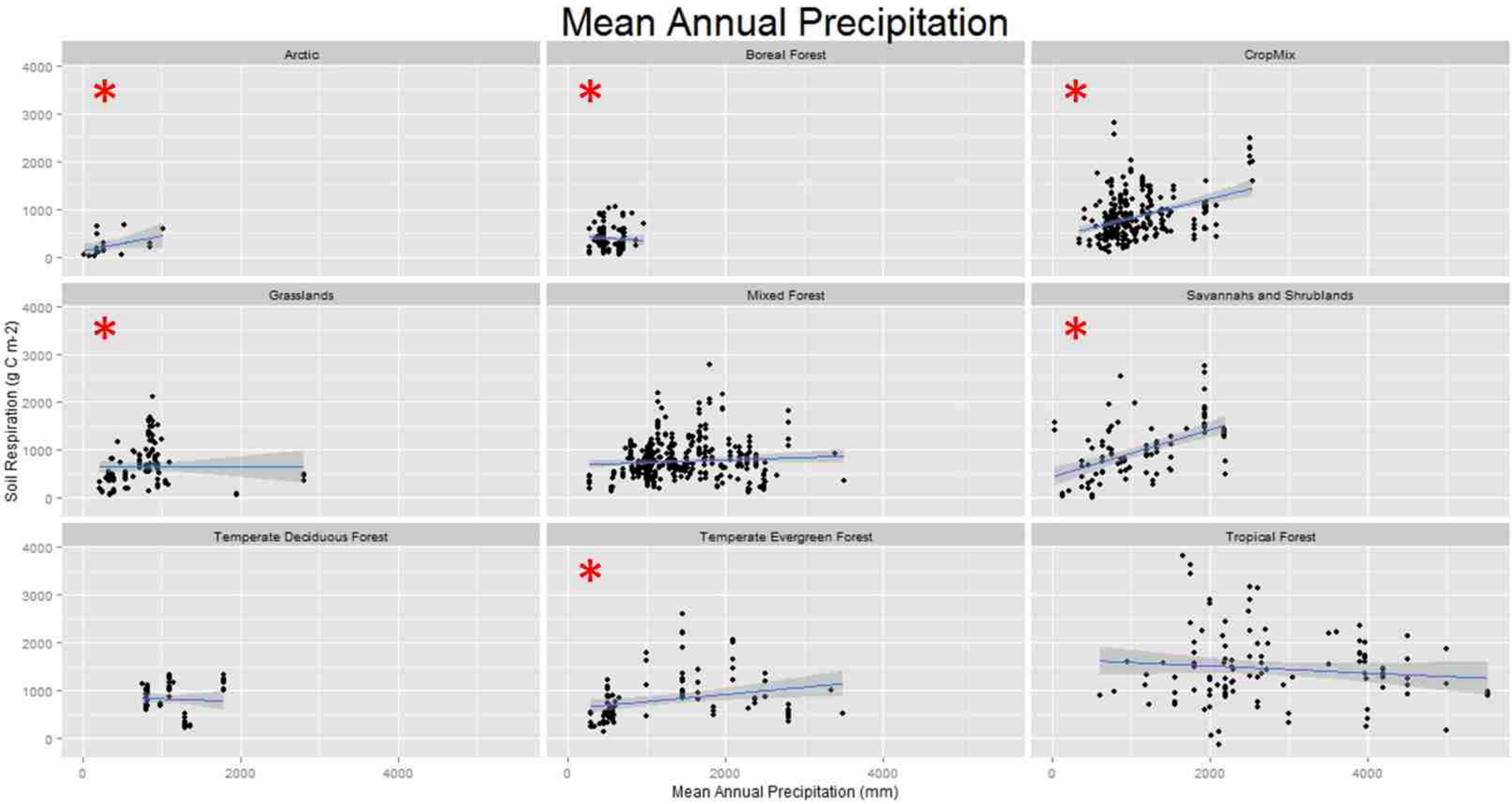
C: Normalized Soil Temperature



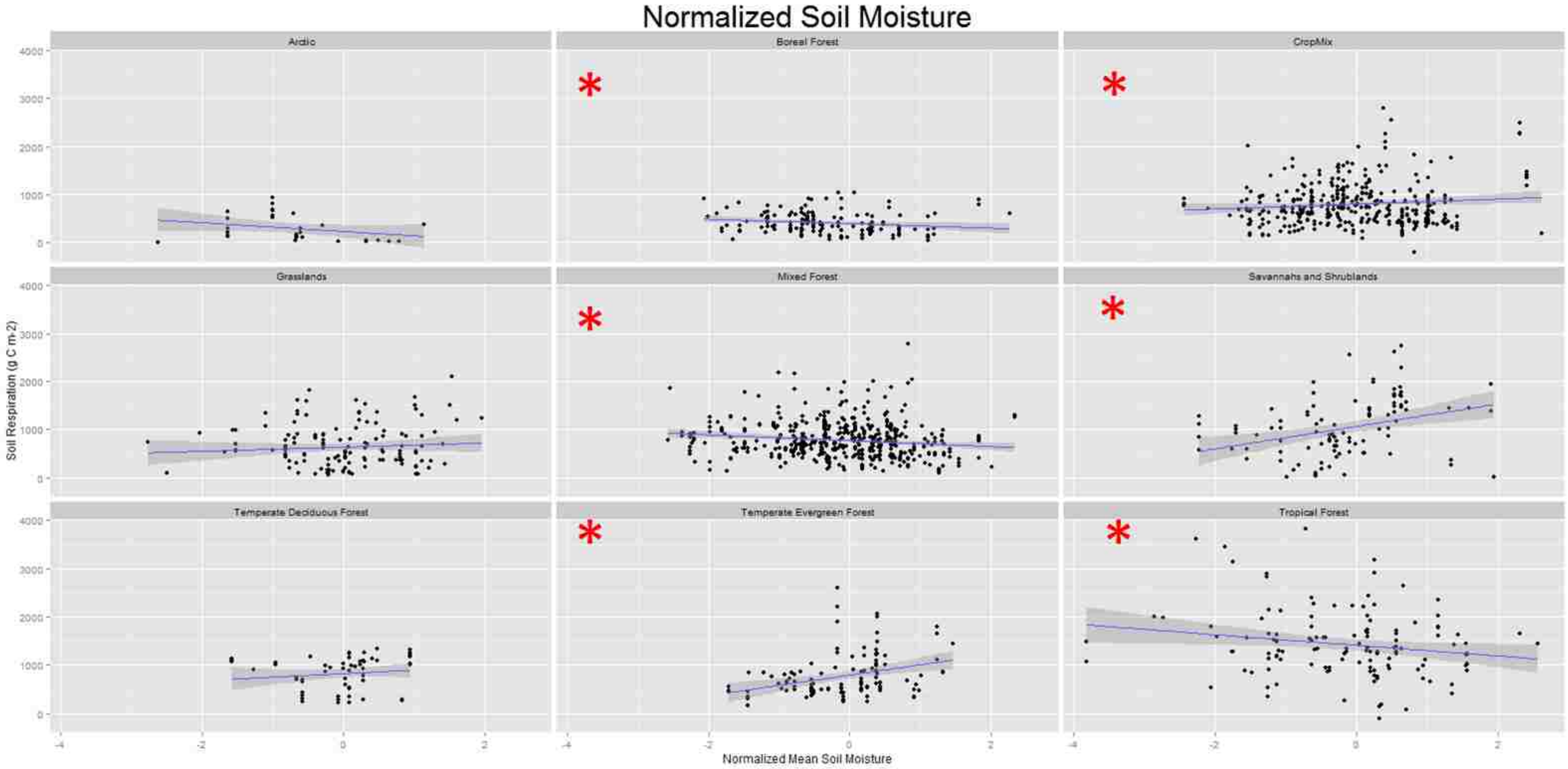
D: Soil Moisture



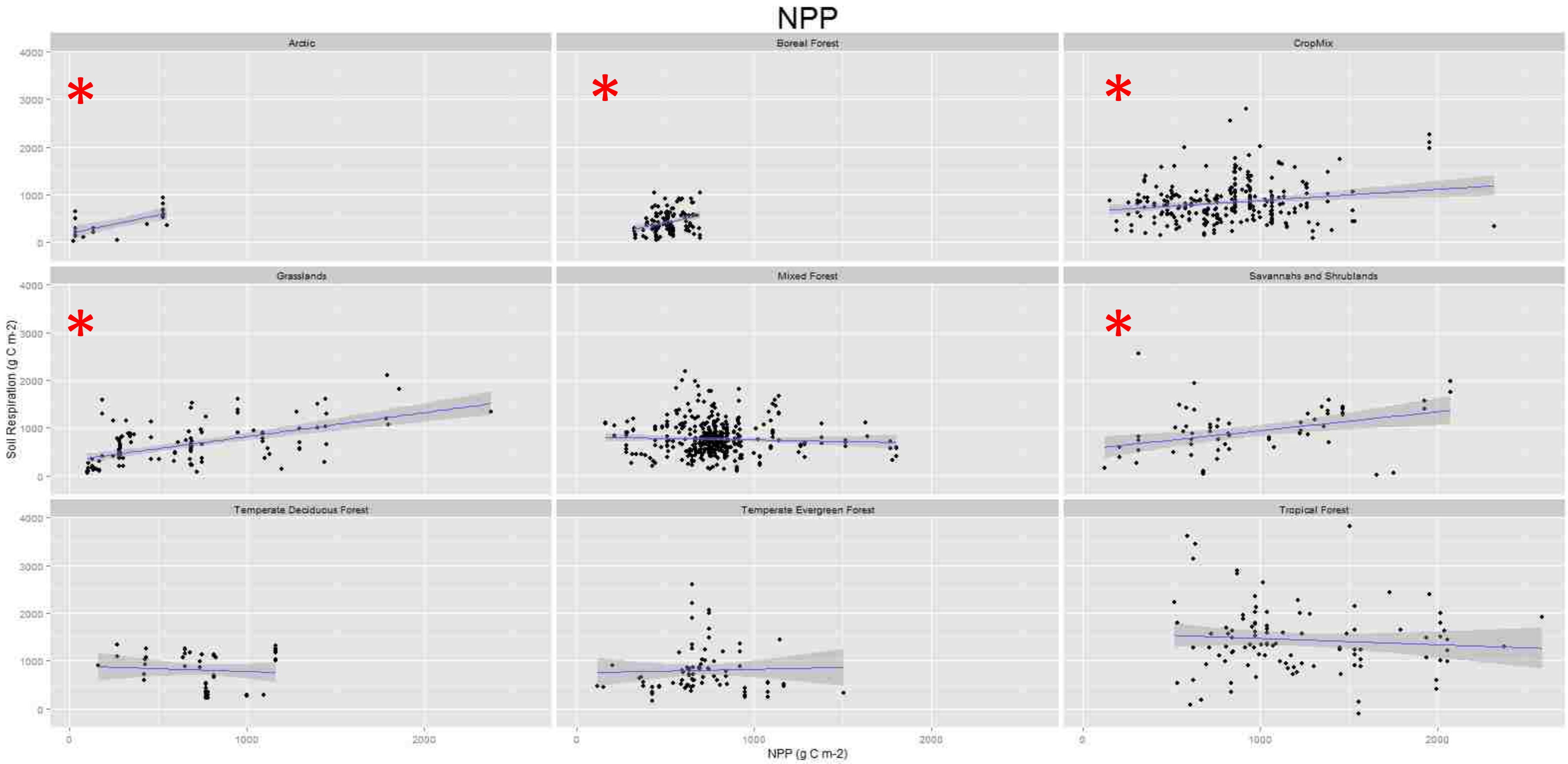
E: Mean Annual Precipitation



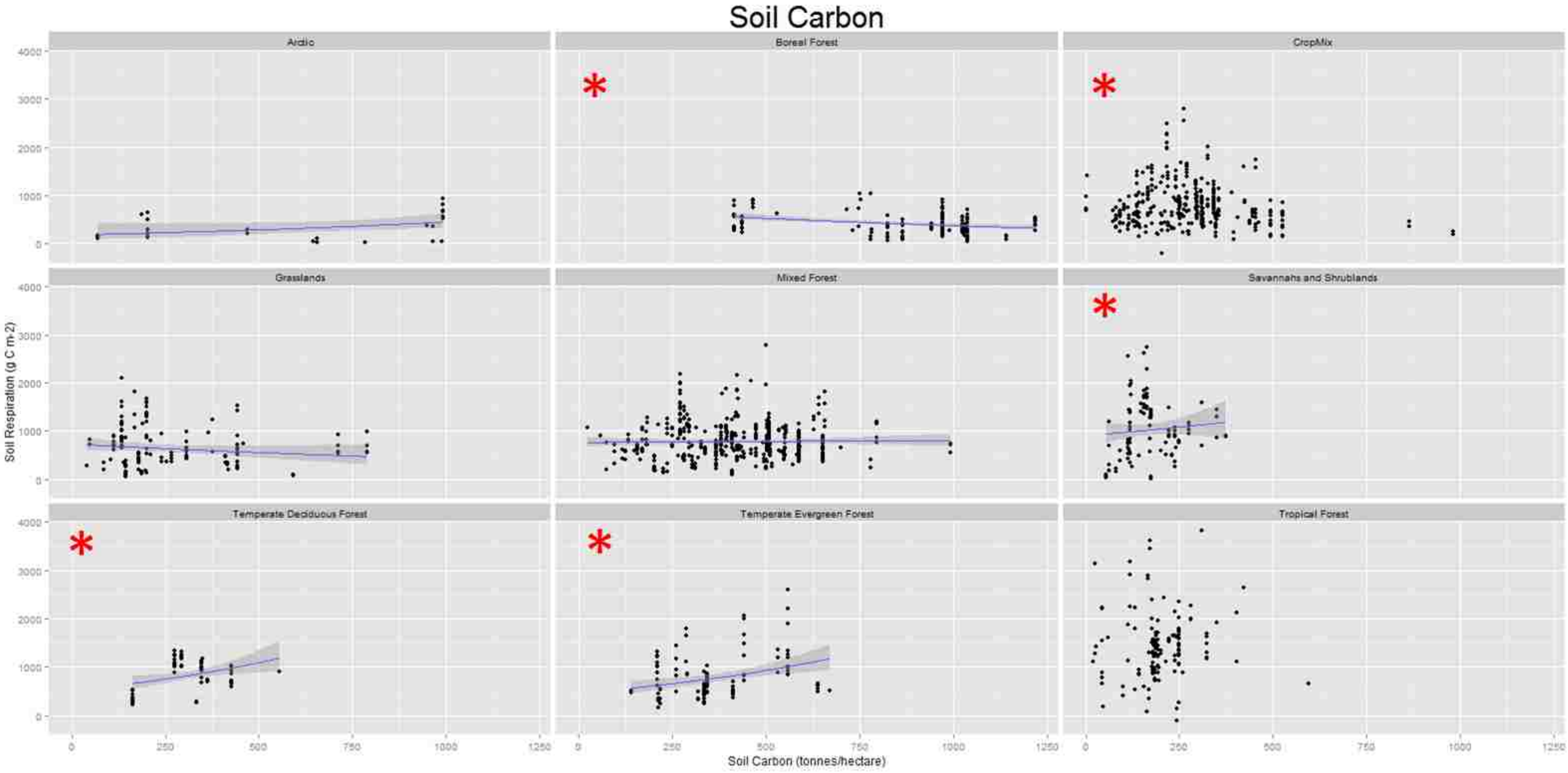
F: Normalized Soil Moisture



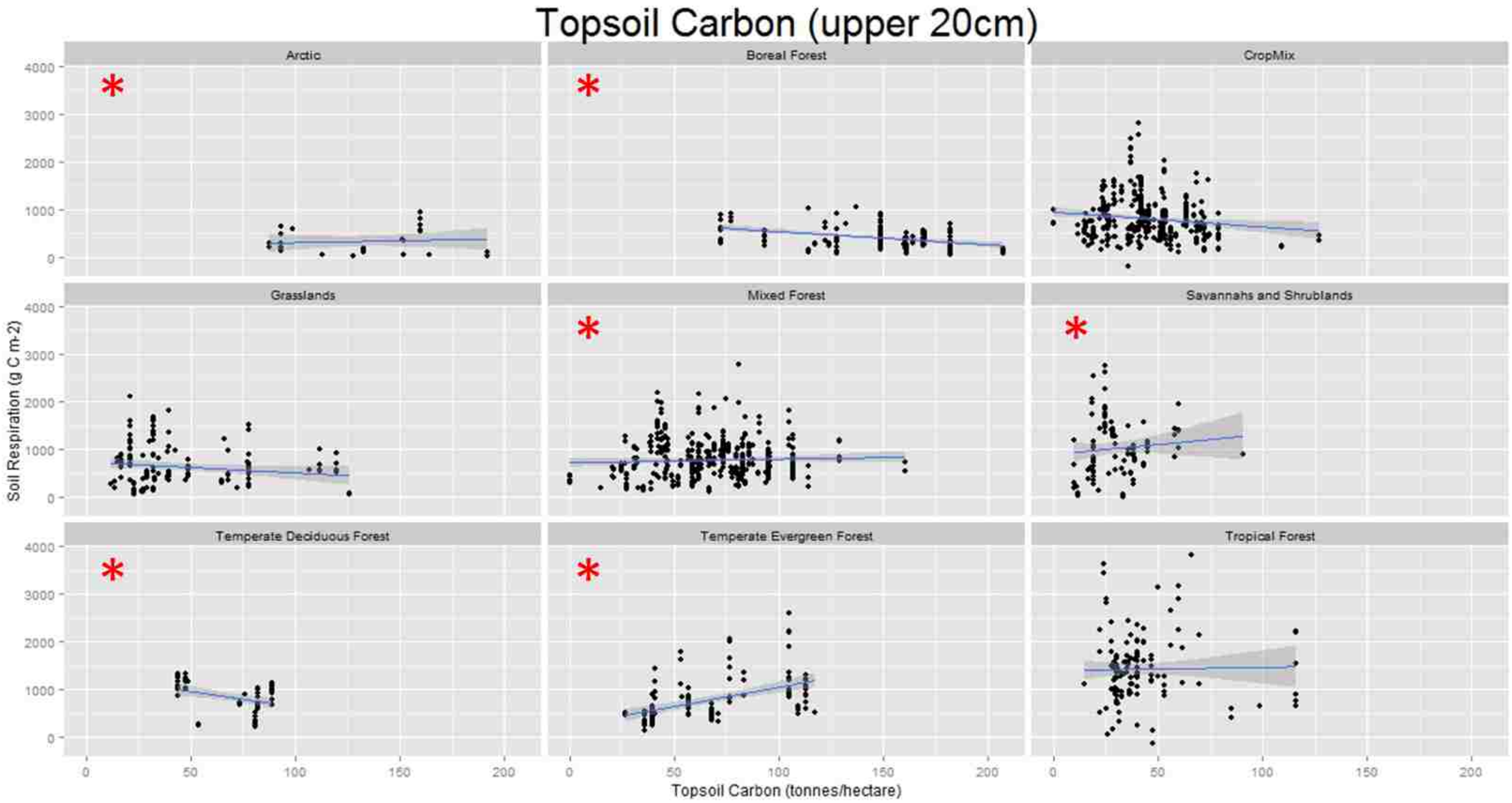
G: NPP


NPP
Arctic
Boreal Forest
CropMix
Grasslands
Mixed Forest
Savannahs and Shrublands
Temperate Deciduous Forest
Temperate Evergreen Forest
Tropical Forest
Soil Respiration (g C m-2)
0
1000
2000
3000
4000
NPP (g C m-2)
0
1000
2000

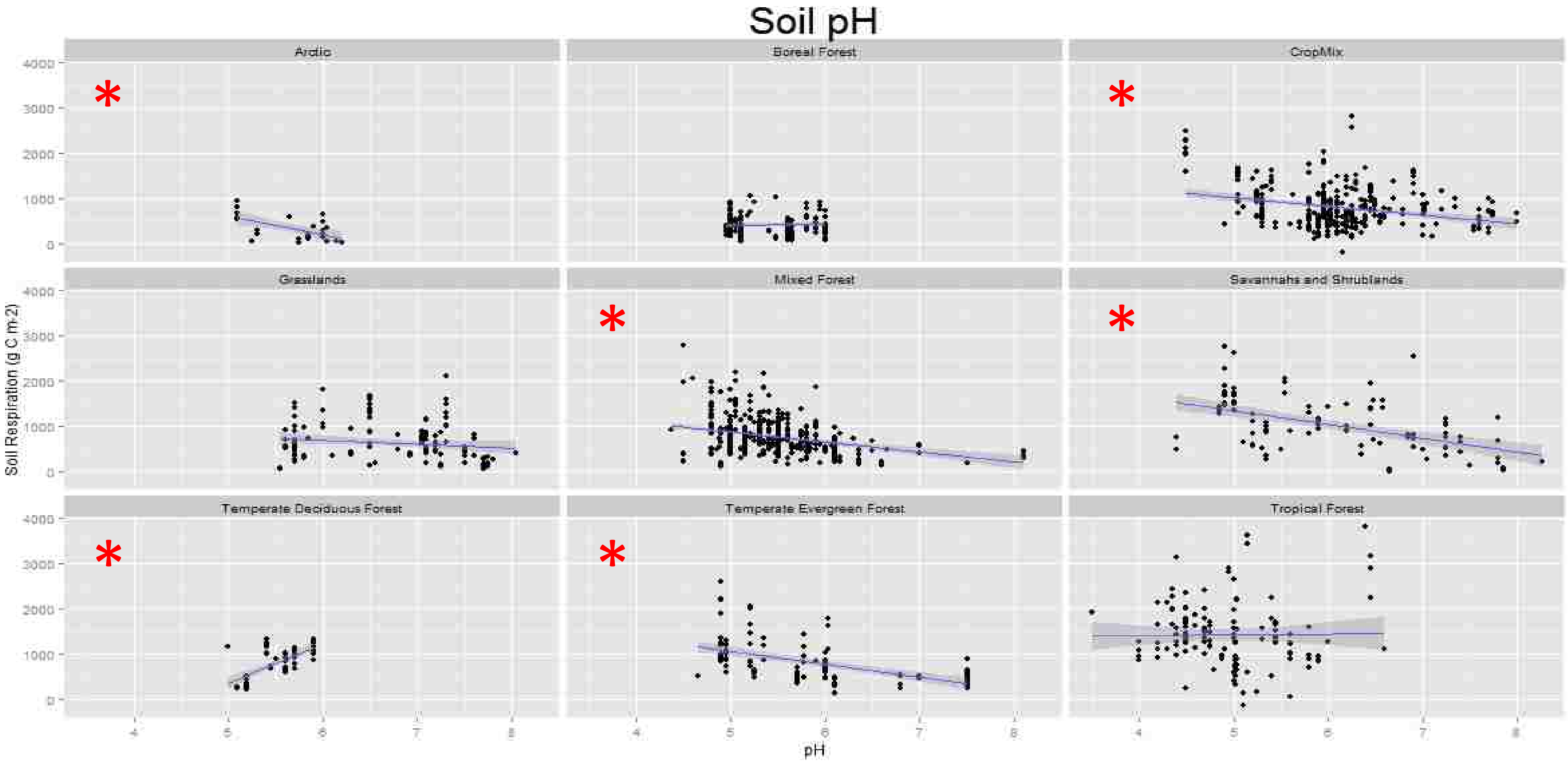
H: Soil Carbon



I: Topsoil Carbon



J: Soil pH

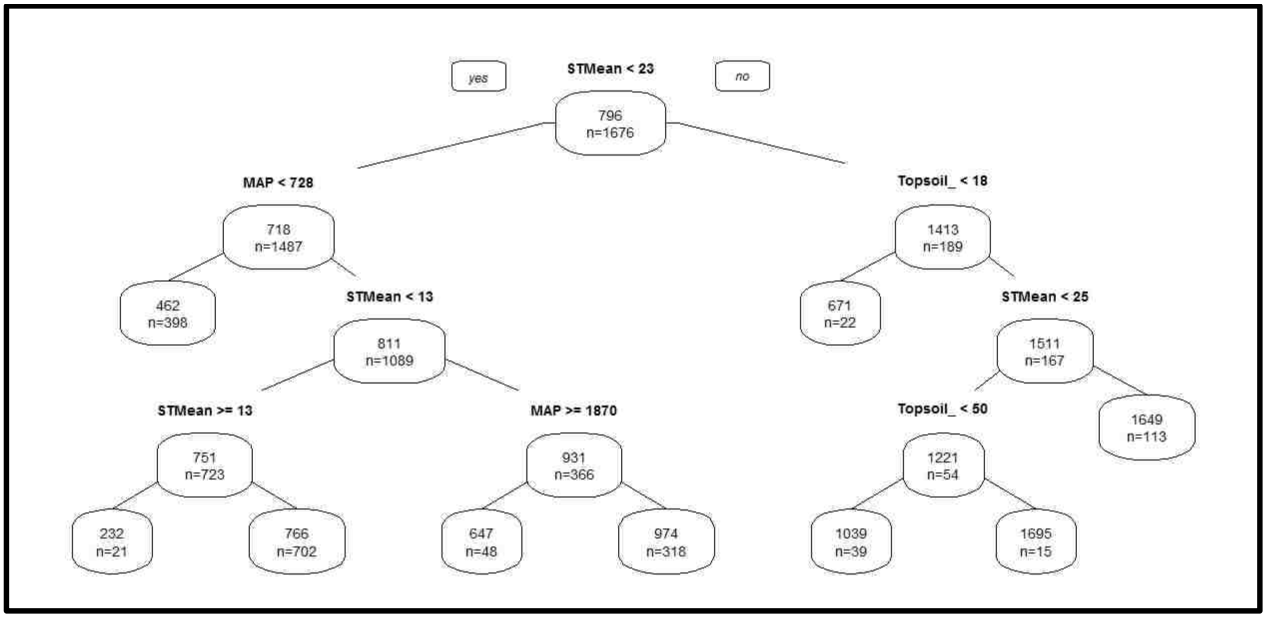

Soil pH
Arctic
Boreal Forest
CropMix
Grasslands
Mixed Forest
Savannahs and Shrublands
Temperate Deciduous Forest
Temperate Evergreen Forest
Tropical Forest
*
*
*
*
*
*
Soil Respiration (g C m-2)
4000
3000
2000
1000
0
4
5
6
7
8
pH

Appendix C: Classification and Regression Trees

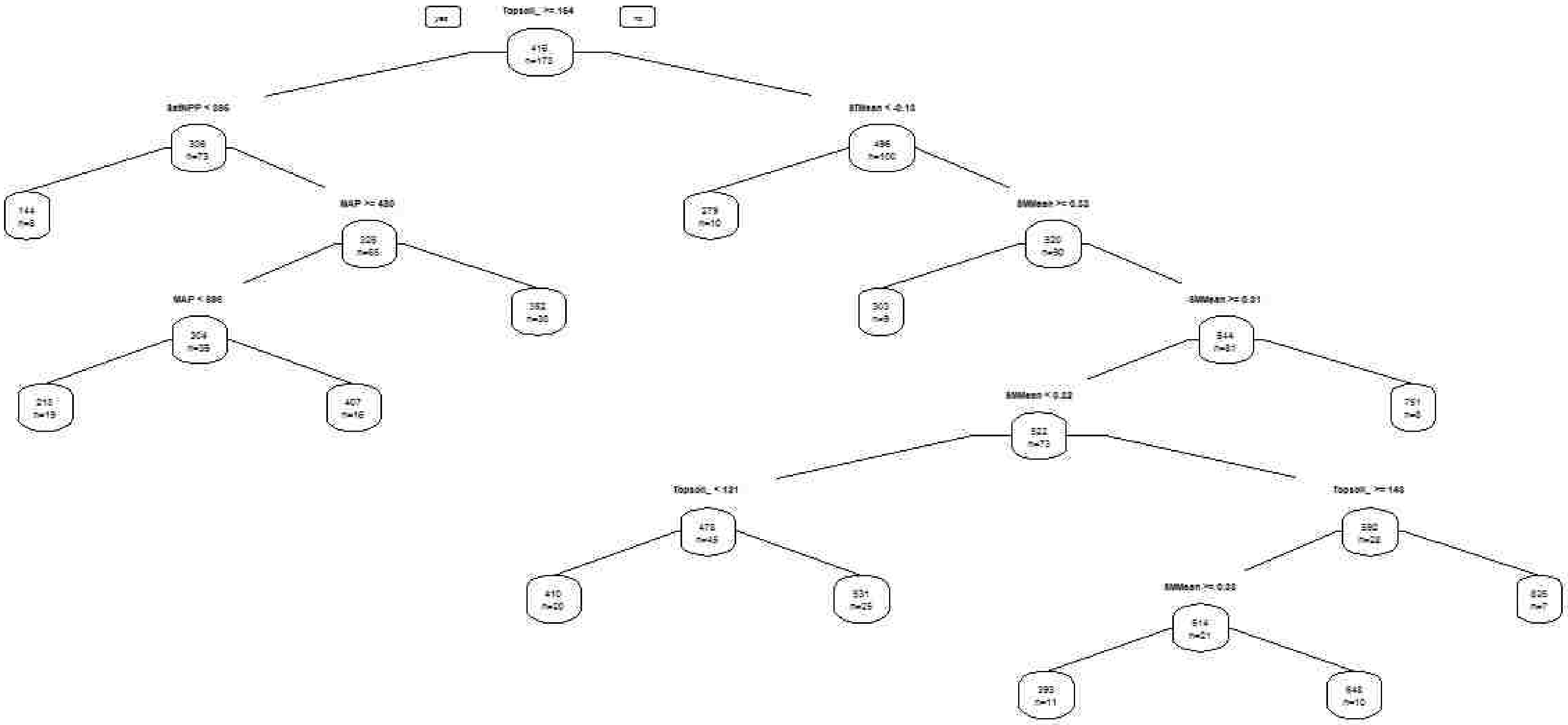
Figure 11: Regression Trees by Biome

Figure 11: Regression trees for the global dataset and individual biomes. Predictor coefficients and number of observations reported at each node. STMean=mean annual soil temperature (C), SMMean=mean annual soil moisture (m3 m-3), Soil_C=total soil carbon (tonnes/hectare). NPP=net primary productivity (g C m-2)

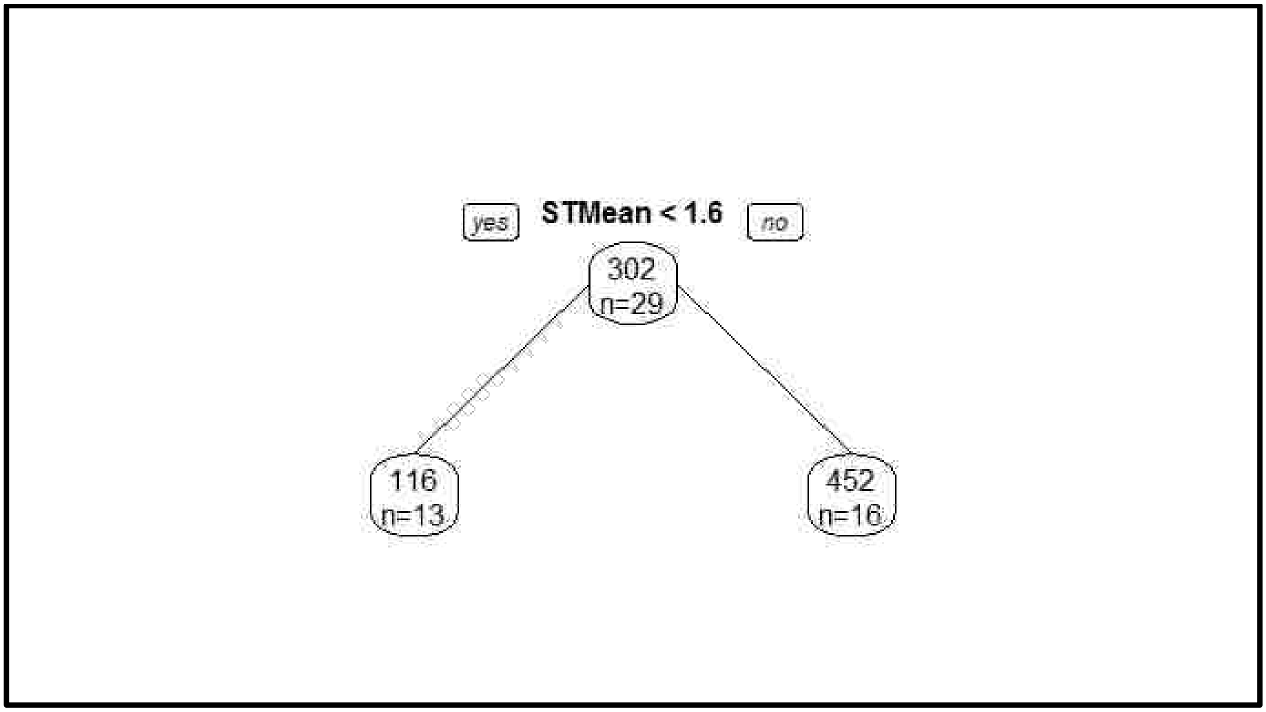
A: Global



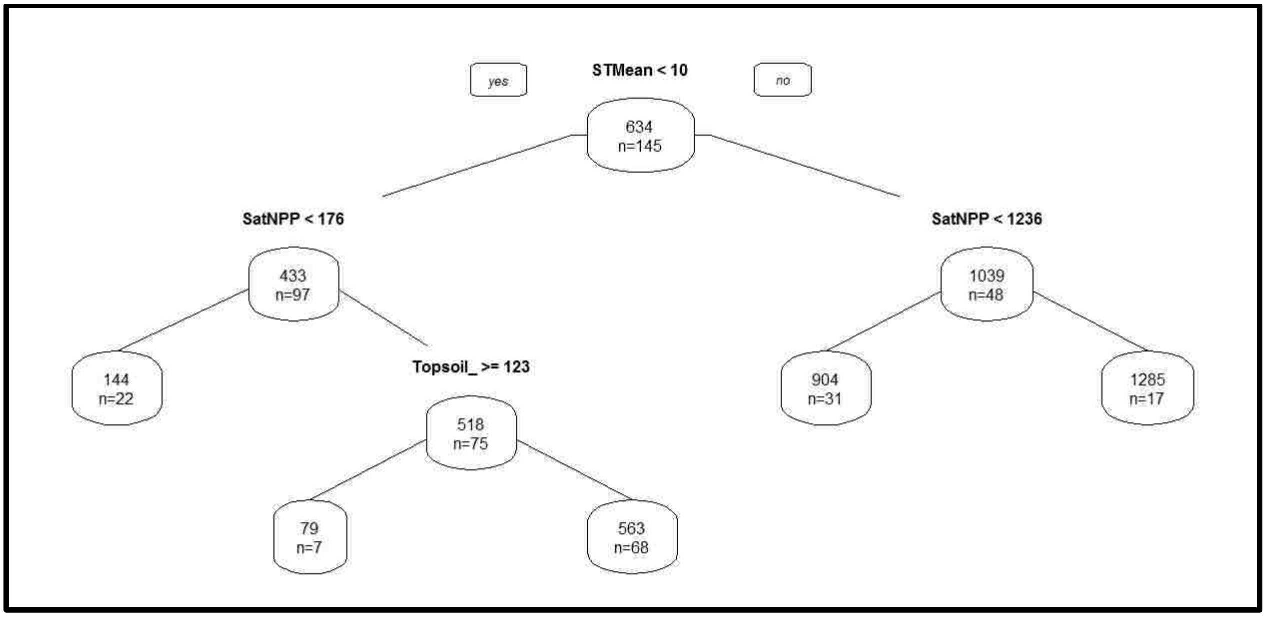
B: Boreal Forests



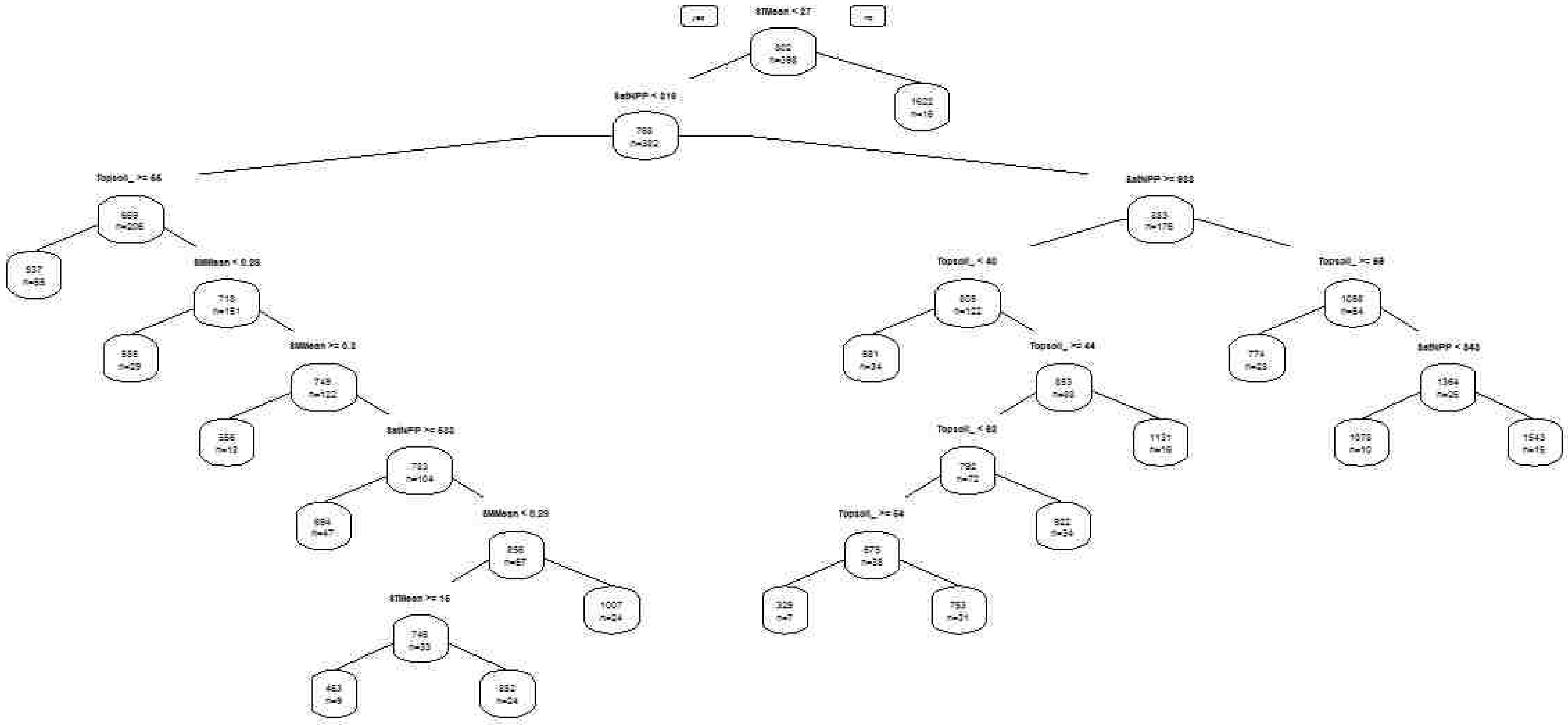
C: Arctic



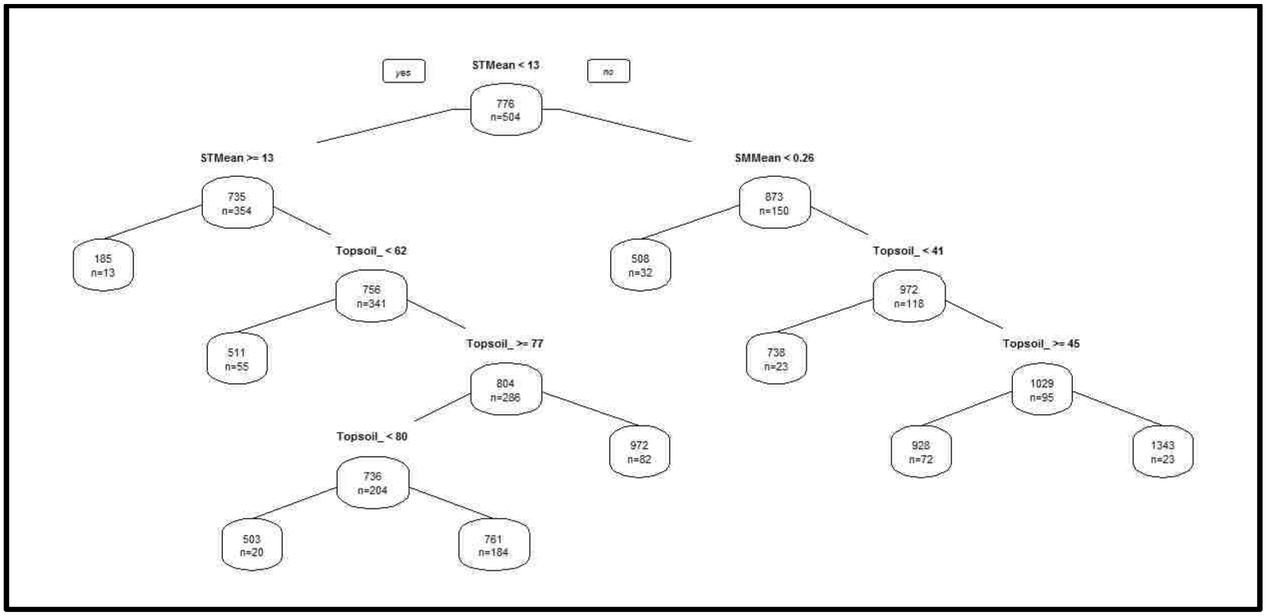
D: Grasslands



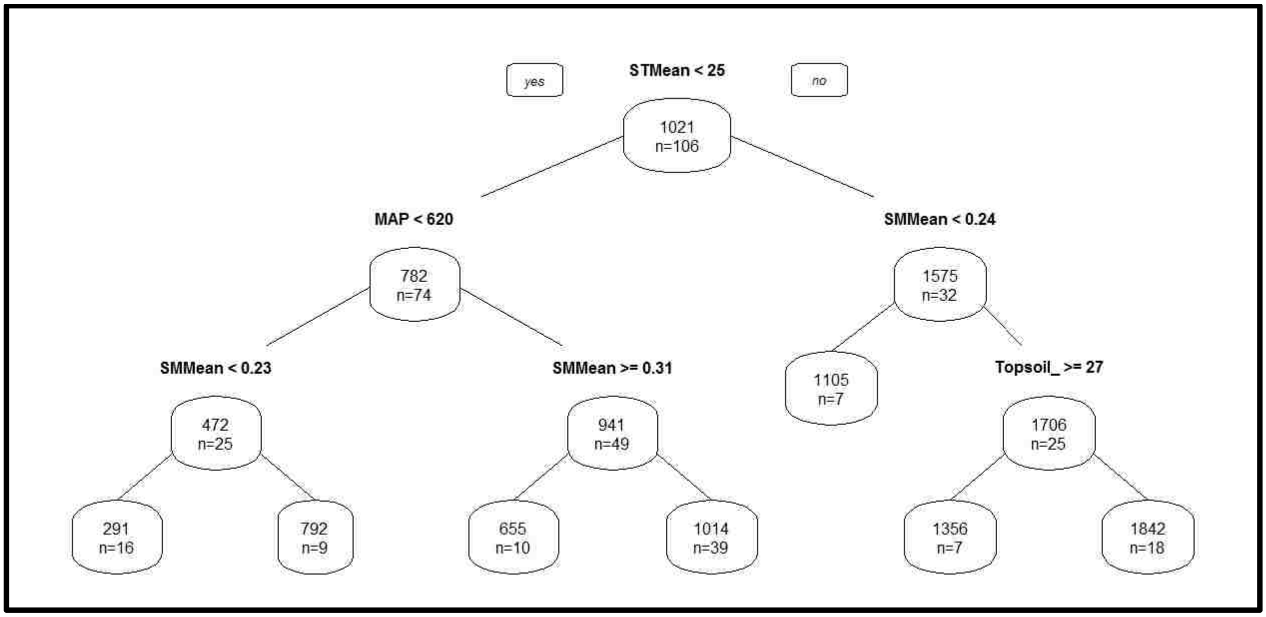
E: Croplands/Mixed



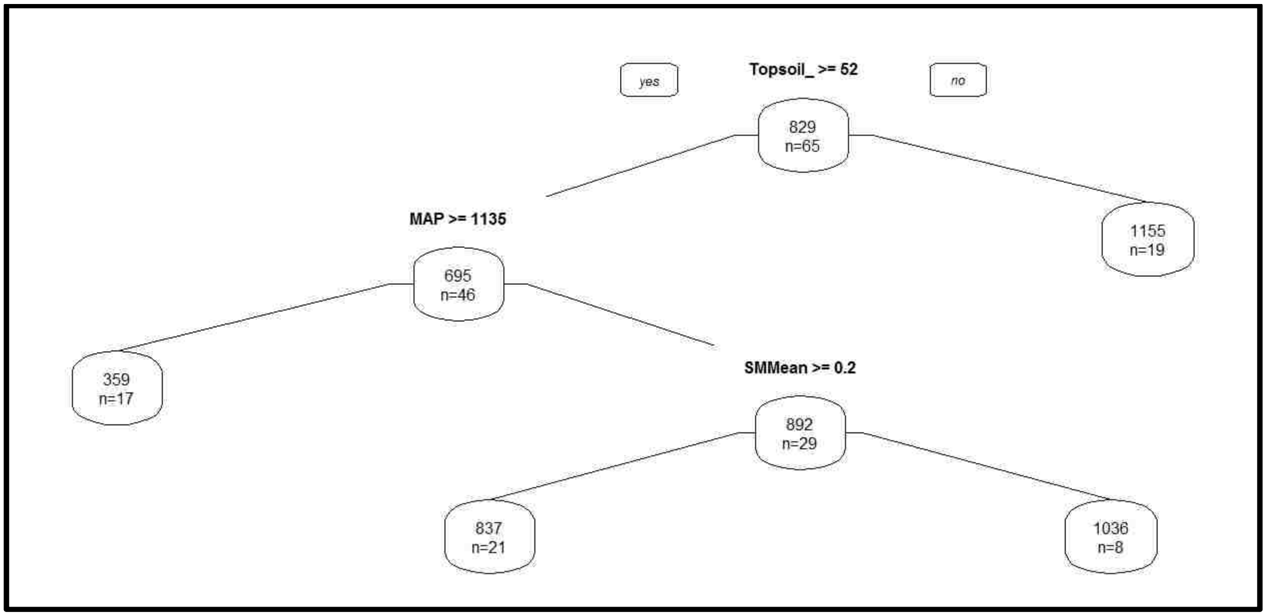
F: Mixed Forests



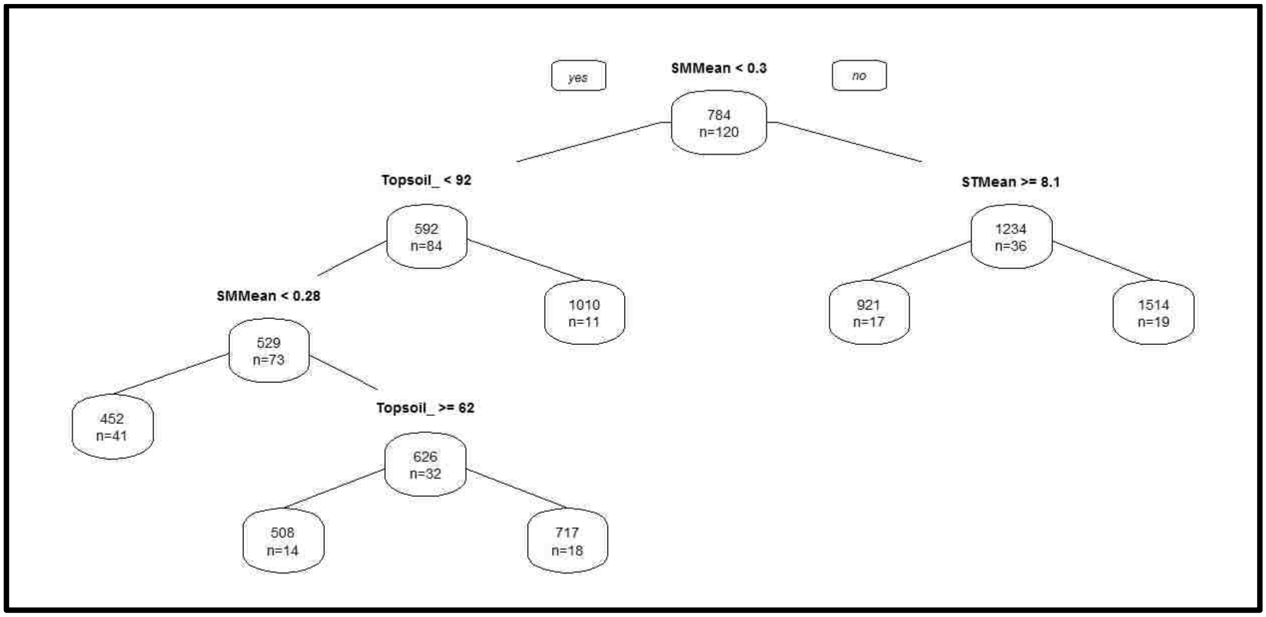
G: Savannahs and Shrublands



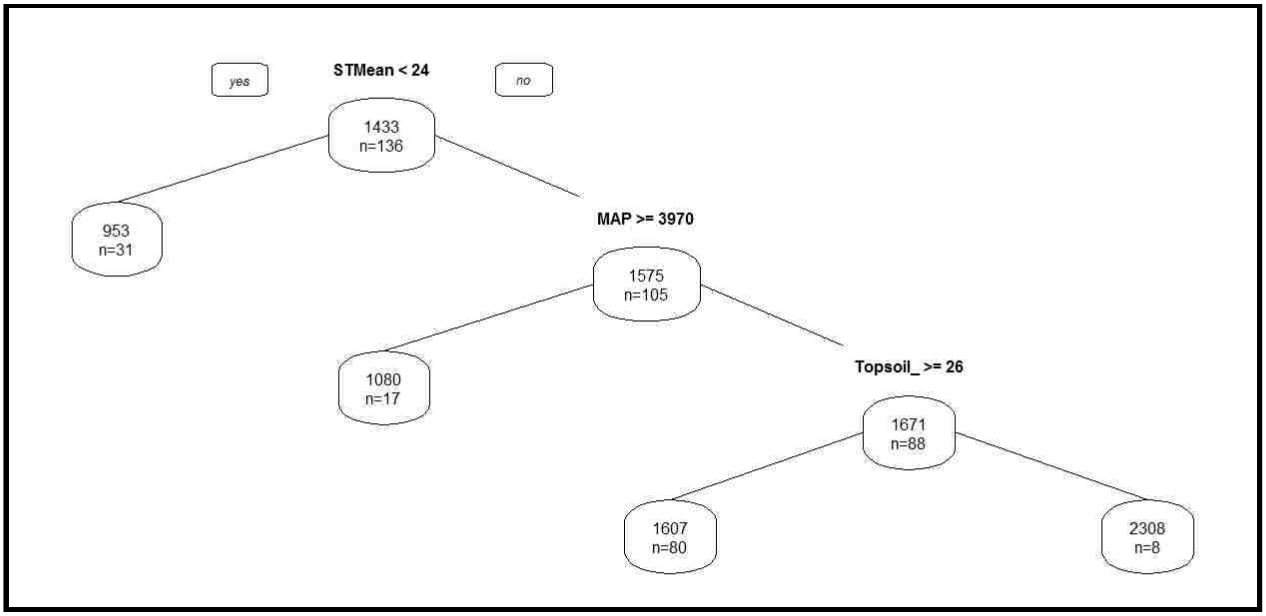
H: Temperate Deciduous Forests



I: Temperate Evergreen Forests



J: Tropical Forests



Appendix D: Principal Components Analysis

Figure 12: Global PCA v2

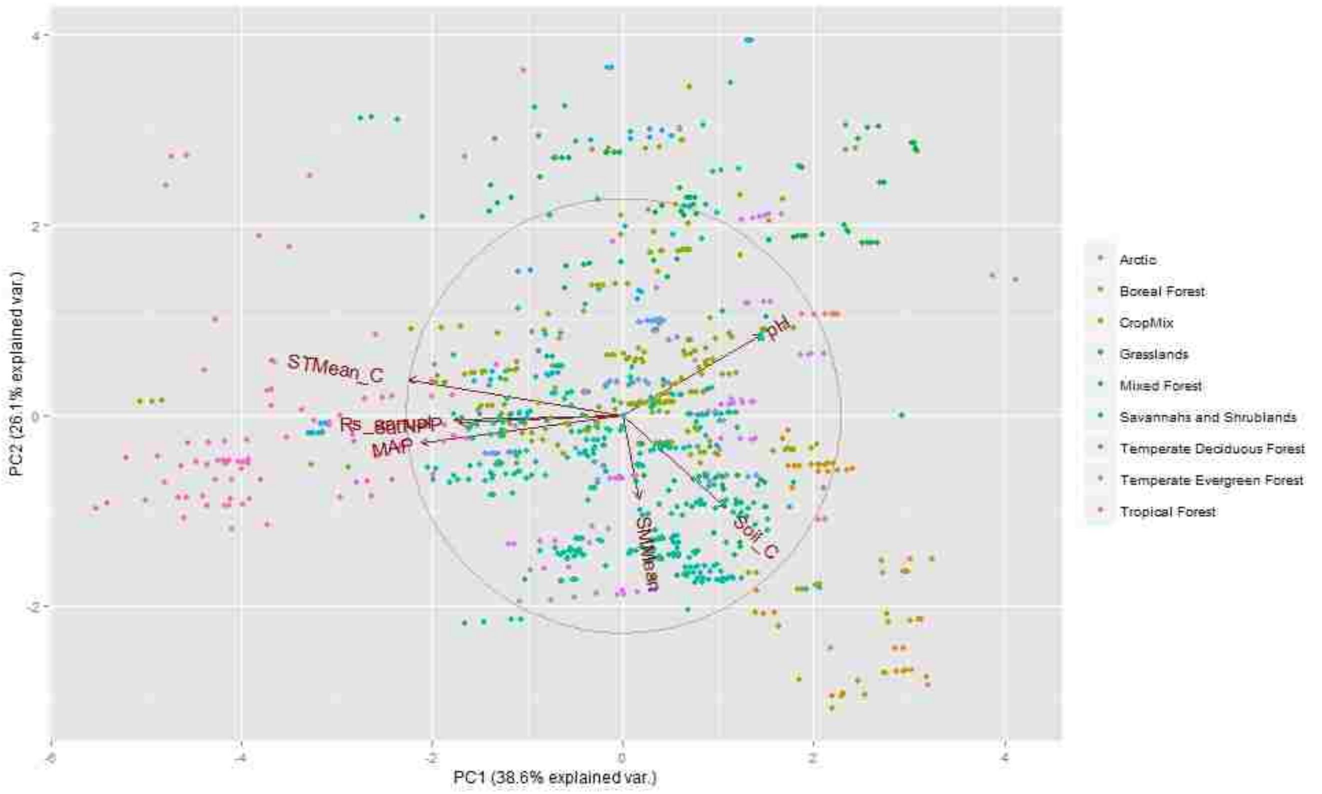


Figure 12. Principal Components Analysis biplot of variability in all variables. Red vectors represent principal Component Loadings of each variable:

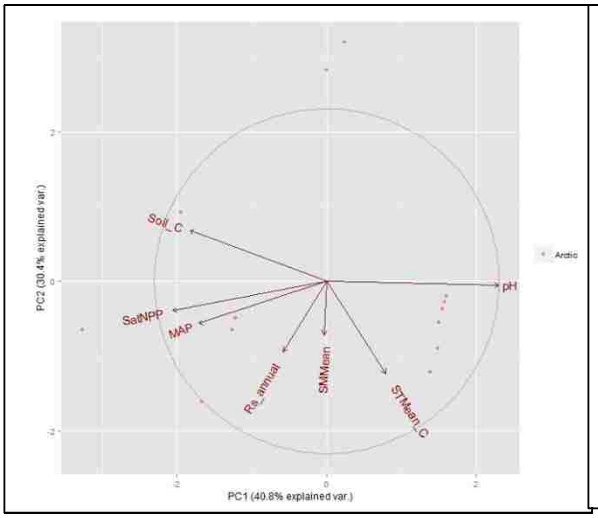
```
                 PC1          PC2         PC3         PC4        PC5
STMean     0.5929902  0.006531622 -0.01333823  0.03944419 -0.5052354
SMMean    -0.1810133  0.523537633 -0.41912846  0.70666733 -0.1344578
SatNPP     0.4499812  0.228597431  0.59605402  0.39175270  0.4837189
Soil_C    -0.4472493  0.449925459  0.20313244 -0.28359018  0.2496062
Rs_annual  0.4445251  0.246444759 -0.61447464 -0.33801943  0.4996778
pH        -0.1244154 -0.640656664 -0.22367647  0.38847747  0.4250800
                  PC6
STMean     0.625558385
SMMean     0.004032205
SatNPP    -0.050255367
Soil_C     0.643075175
Rs_annual -0.012176130
pH         0.438680872
```

Figure 13: Biome-Scale PCA

Figure 13: Principal components biplots for all variables in individual biome sub-datasets. Red vectors represent principal component loadings of each variable for PC1 and PC2 (x and y axis, respectively)

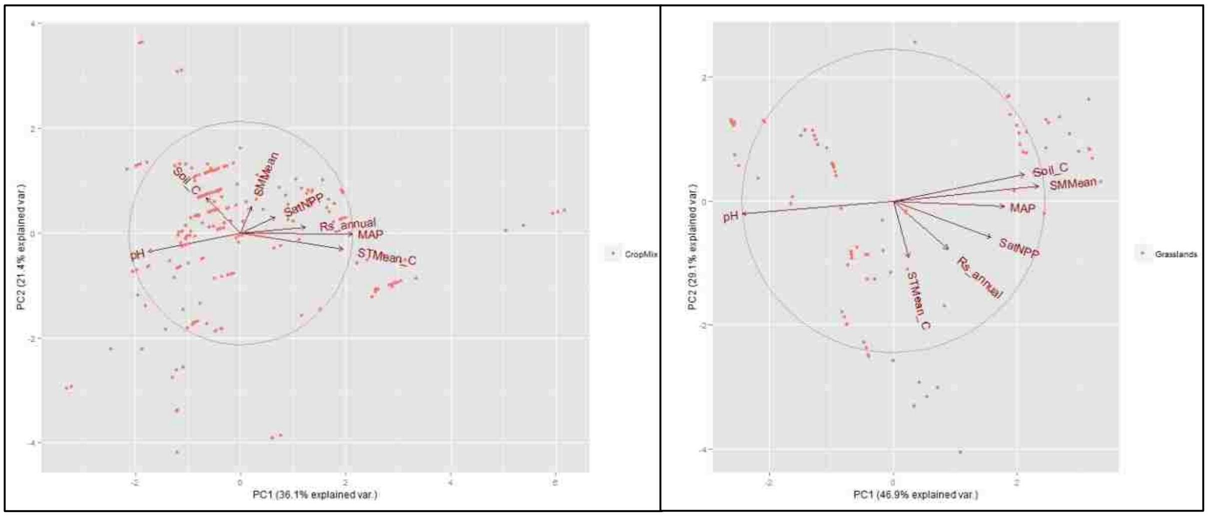
A: Arctic

B: Boreal

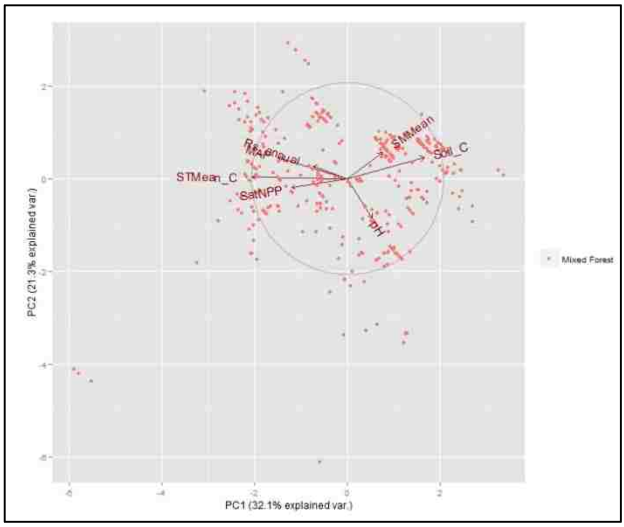


C:Croplands/Mixed

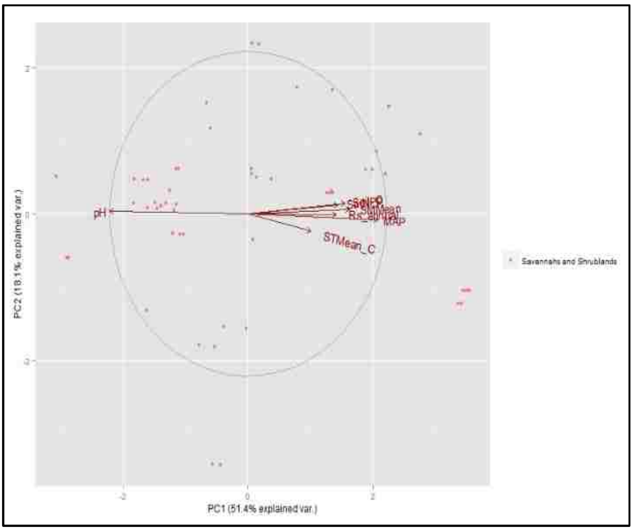
D: Grasslands



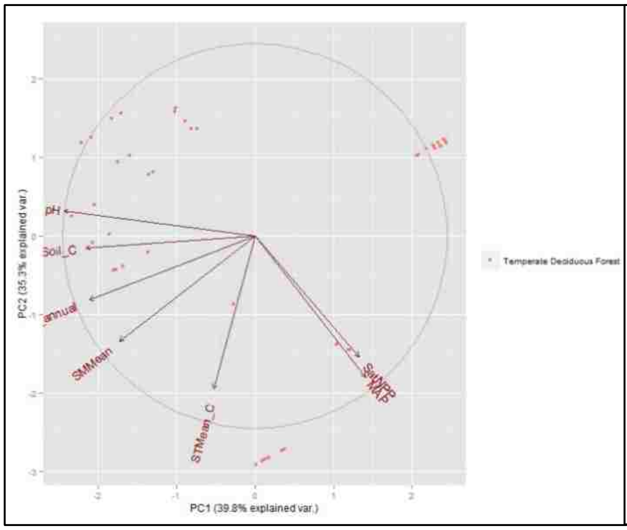
E: Mixed Forests



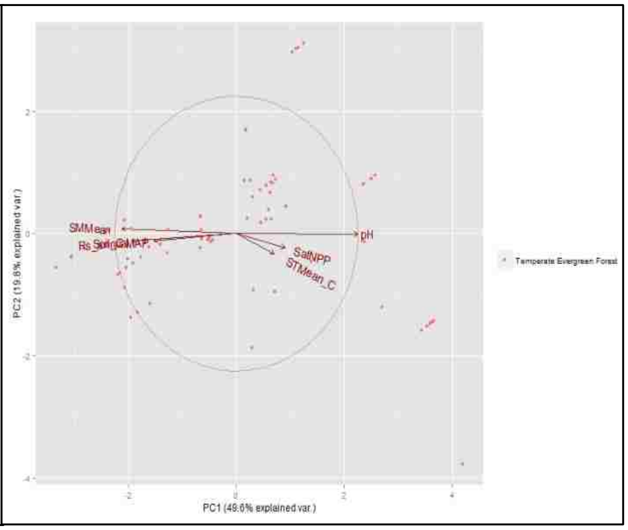
F: Savannahs/Shrublands



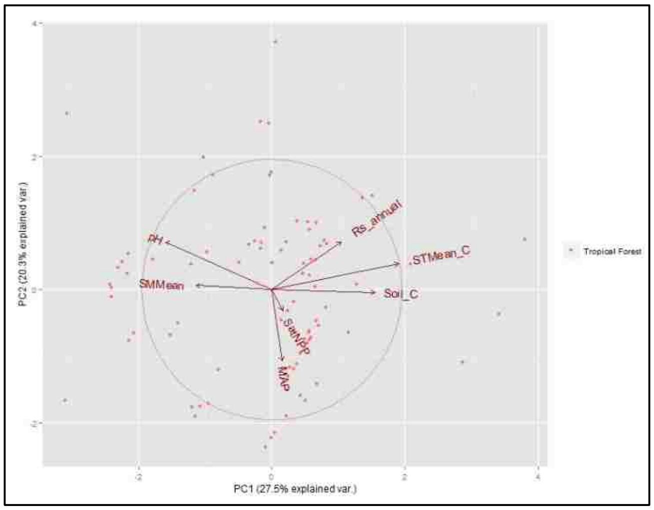
G: Temperate Deciduous Forests



H: Temperate Evergreen Forests



I: Tropical Forests

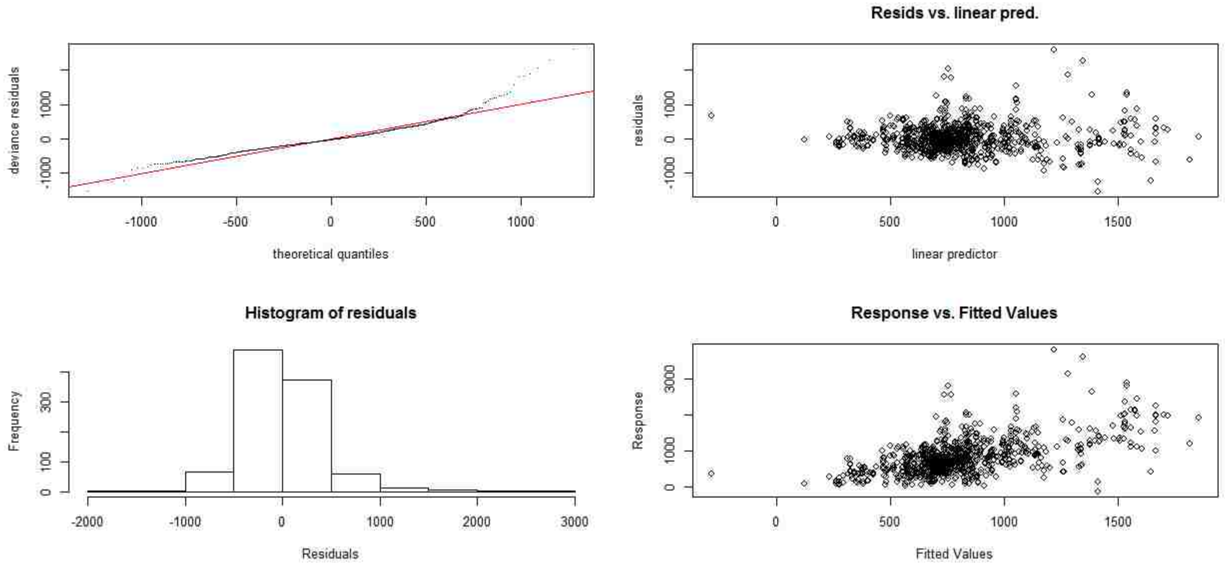


Appendix E: GAM Model Validation

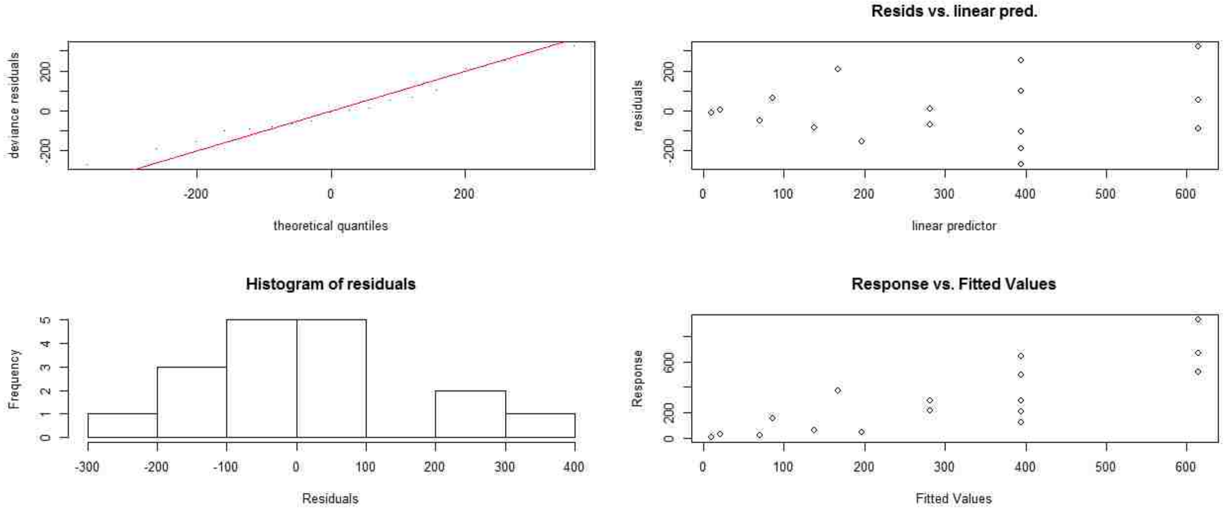
Figure 14: GAM Statistics

Figure 14: Statistical overview for GAM model performances.

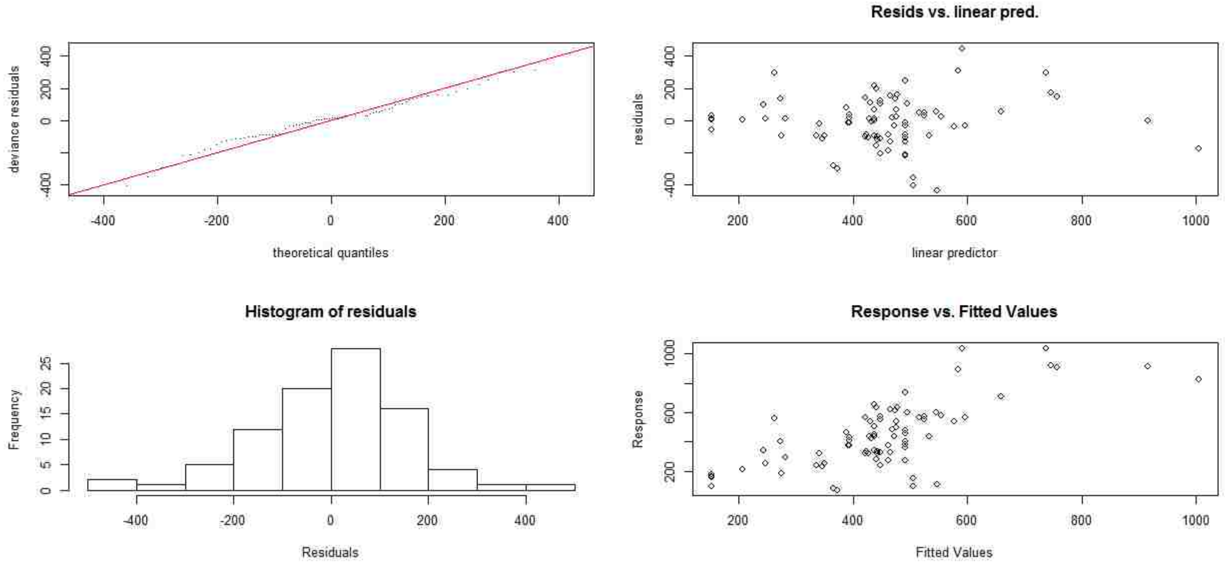
A: Global



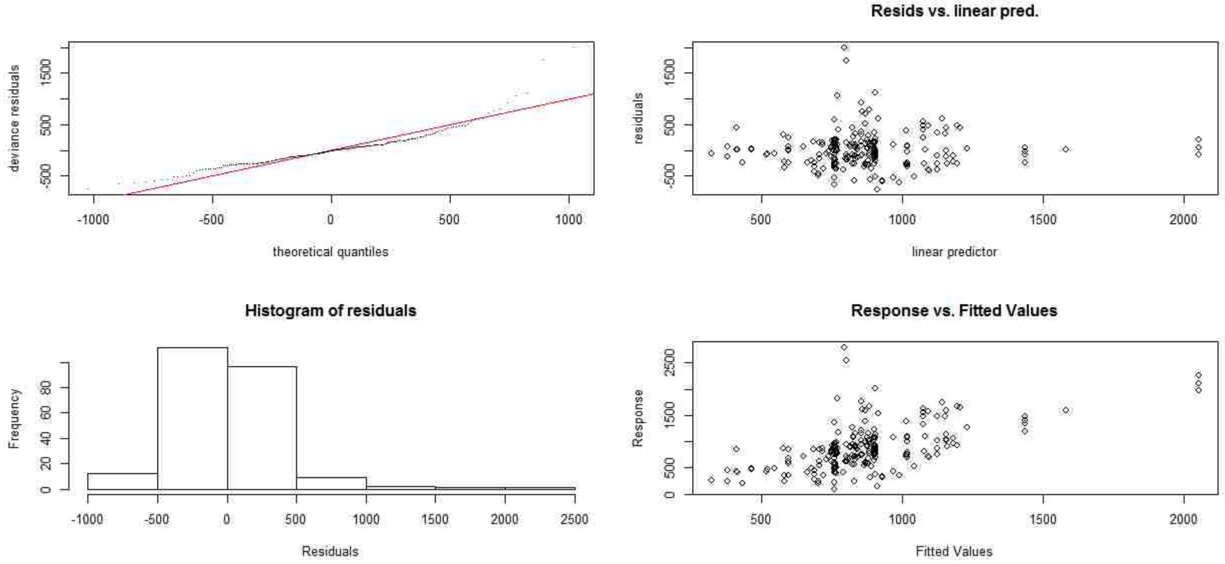
B: Arctic



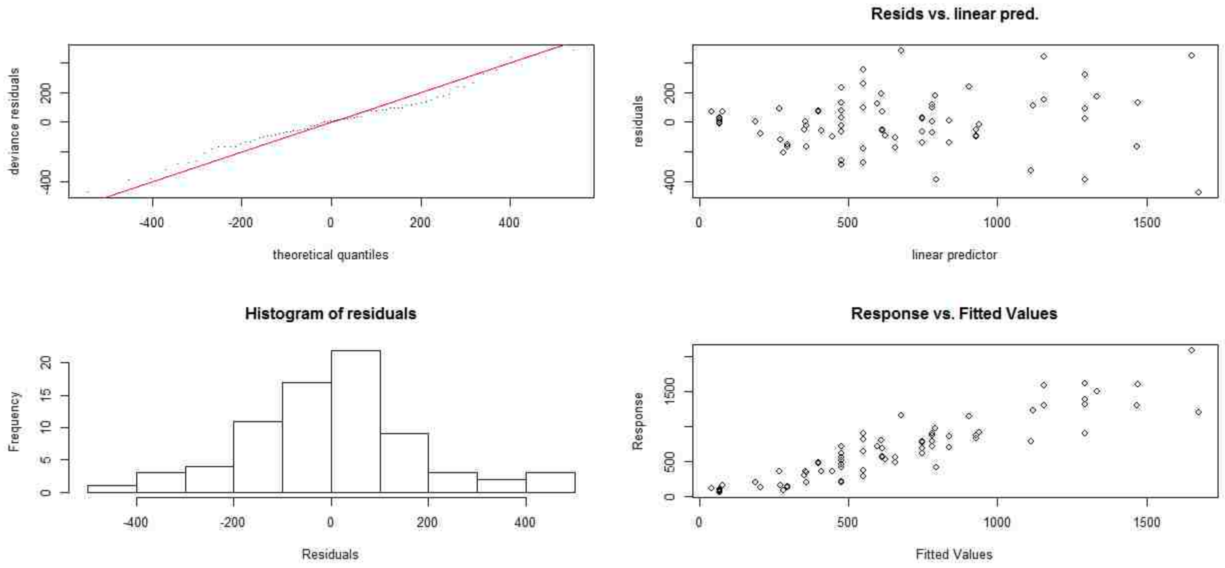
C: Boreal



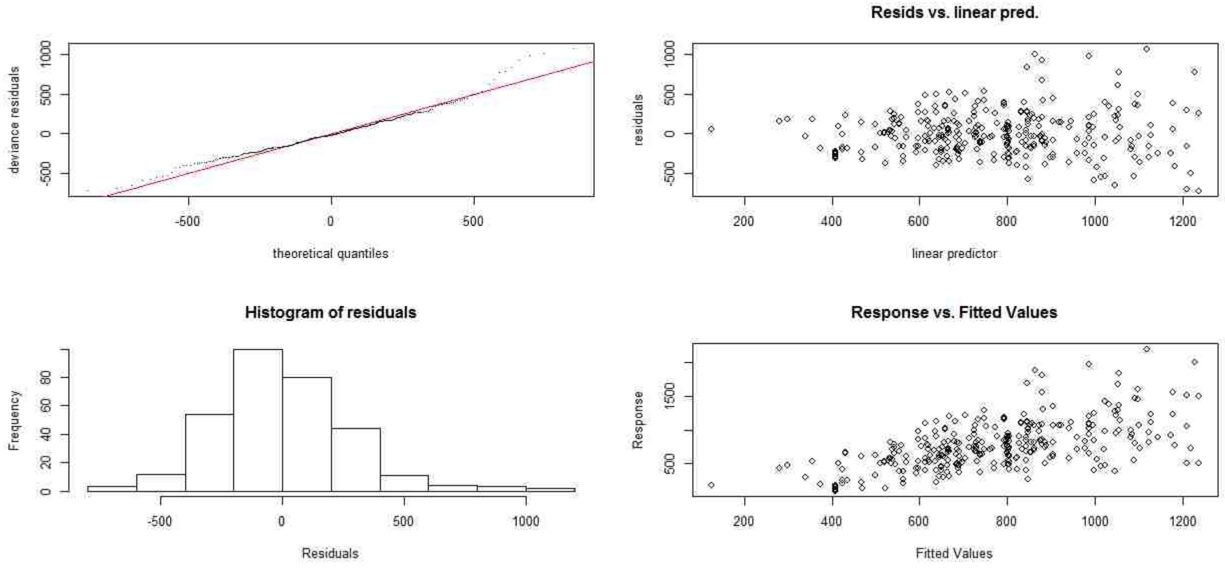
D: Croplands/Mixed



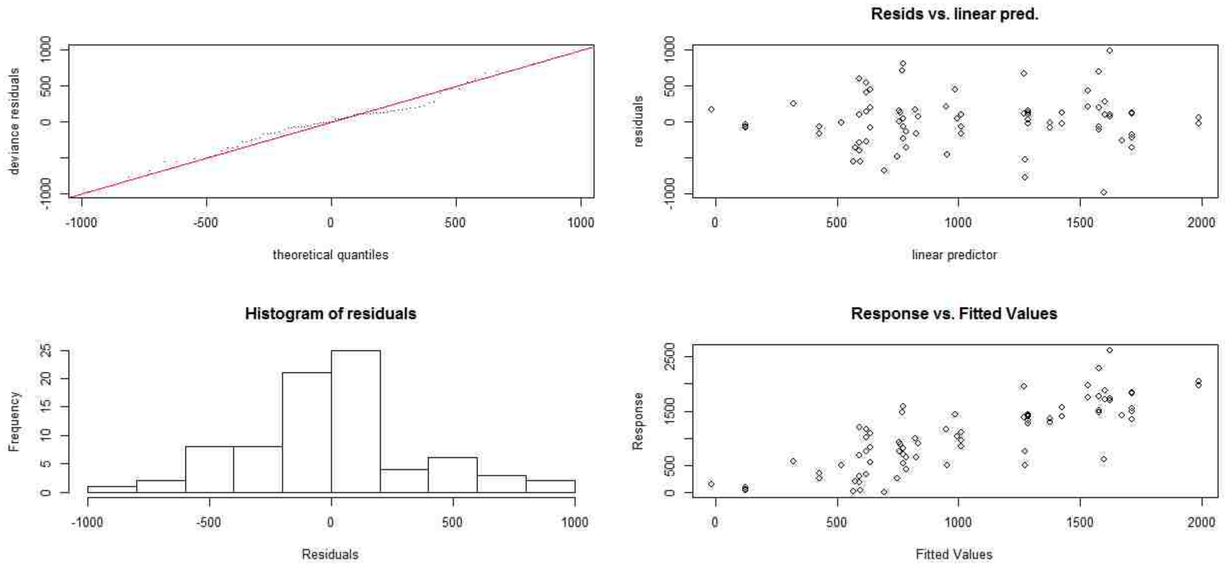
E: Grasslands



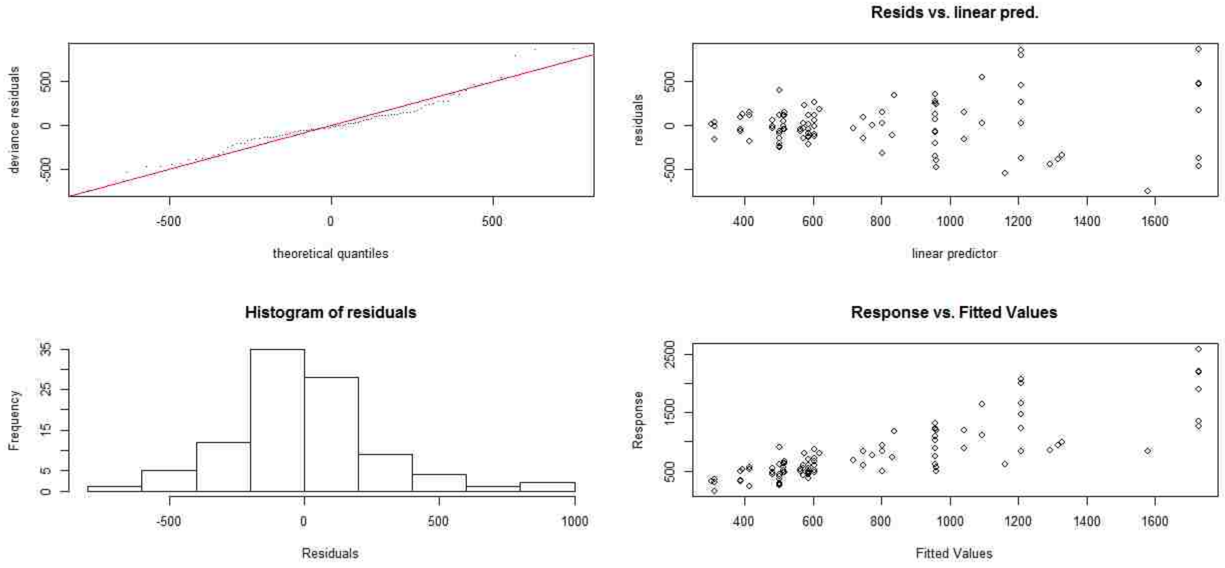
F: Mixed Forests



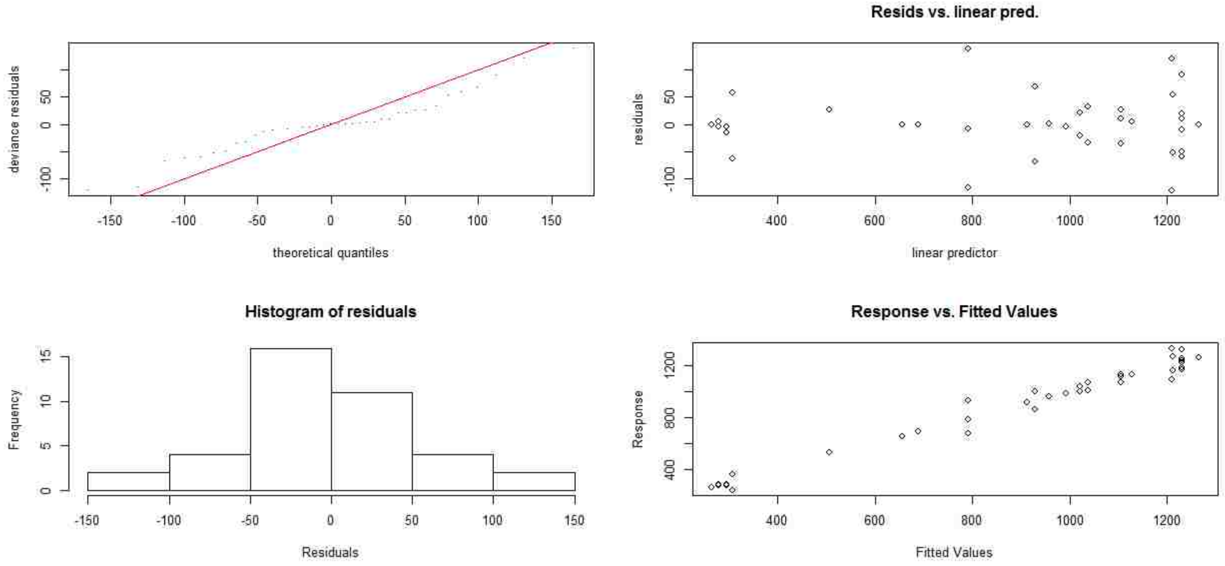
G: Savannahs/Shrublands



H: Temperate Deciduous Forests



I: Temperate Evergreen Forests



J: Tropical Forests