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DOI

[10.1002/2017GB005627](https://doi.org/10.1002/2017GB005627)

Publication date

2017

Document Version

Final published version

Published in

Global Biogeochemical Cycles

License

Article 25fa Dutch Copyright Act

[Link to publication](#)

Citation for published version (APA):

Serna-Chavez, H. M., Swenson, N. G., Weiser, M. D., van Loon, E. E., Bouten, W., Davidson, M. D., & van Bodegom, P. M. (2017). Strong biotic influences on regional patterns of climate regulation services. *Global Biogeochemical Cycles*, 31(5), 787-803.
<https://doi.org/10.1002/2017GB005627>

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Global Biogeochemical Cycles

RESEARCH ARTICLE

10.1002/2017GB005627

Key Points:

- Forest structure and successional stage strongly influence climate regulation processes at a regional, temperate extent
- The identity, strength, and direction of the main abiotic and biotic influences behind climate regulation process are not ubiquitous
- Multiple abiotic and biotic factors are needed to monitor and quantify the climate change-mitigation potential of temperate forests

Supporting Information:

- Supporting Information S1
- Table S1

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Citation:

Serna-Chavez, H. M., N. G. Swenson, M. D. Weiser, E. E. van Loon, W. Bouten, M. D. Davidson, and P. M. van Bodegom (2017), Strong biotic influences on regional patterns of climate regulation services, *Global Biogeochem. Cycles*, 31, 787–803, doi:10.1002/2017GB005627.

Received 24 JAN 2017

Accepted 12 APR 2017

Accepted article online 18 APR 2017

Published online 4 MAY 2017

Strong biotic influences on regional patterns of climate regulation services

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Abstract Climate regulation services from forests are an important leverage in global-change mitigation treaties. Like most ecosystem services, climate regulation is the product of various ecological phenomena with unique spatial features. Elucidating which abiotic and biotic factors relate to spatial patterns of climate regulation services advances our understanding of what underlies climate-mitigation potential and its variation within and across ecosystems. Here we quantify and contrast the statistical relations between climate regulation services (albedo and evapotranspiration, primary productivity, and soil carbon) and abiotic and biotic factors. We focus on 16,955 forest plots in a regional extent across the eastern United States. We find the statistical effects of forest litter and understory carbon on climate regulation services to be as strong as those of temperature-precipitation interactions. These biotic factors likely influence climate regulation through changes in vegetation and canopy density, radiance scattering, and decomposition rates. We also find a moderate relation between leaf nitrogen traits and primary productivity at this regional scale. The statistical relation between climate regulation and temperature-precipitation ranges, seasonality, and climatic thresholds highlights a strong feedback with global climate change. Our assessment suggests the expression of strong biotic influences on climate regulation services at a regional, temperate extent. Biotic homogenization and management practices manipulating forest structure and succession will likely strongly impact climate-mitigation potential. The identity, strength, and direction of primary influences differed for each process involved in climate regulation. Hence, different abiotic and biotic factors are needed to monitor and quantify the full climate-mitigation potential of temperate forest ecosystems.

1. Introduction

Carbon sequestration and the carbon stored in forest's trees are the ecological leverage of climate-mitigation treaties [McAlpine *et al.*, 2010; Agrawal *et al.*, 2011]. Offsetting carbon emissions, however, is only one of the ways through which forests influence the climate. Forests, and all other ecosystems, also influence the climate through water and energy fluxes [Pielke *et al.*, 1998; Bonan, 2008; Alkama and Cescatti, 2016; Naudts *et al.*, 2016]. Together, carbon, water, and energy fluxes between ecosystems and the atmosphere encompass the ecosystem services of climate regulation. The capture and emission of carbon and other greenhouse gases by vegetation and soils are biogeochemical fluxes [Bonan, 2008; Diaz *et al.*, 2009]. The interception and transpiration of water, and the reflection of solar radiation, are biophysical fluxes [Pielke *et al.*, 1998; Anderson-Teixeira *et al.*, 2012; Alkama and Cescatti, 2016]. Climate regulation services connect biophysical and biogeochemical fluxes to the maintenance of conditions favorable to human well-being and activities [House and Brovkin, 2005]. Though they can counterweigh benefits from the capture of carbon and other greenhouse gases [Anderson-Teixeira *et al.*, 2012; Naudts *et al.*, 2016], biophysical fluxes remain to be incorporated into climate-mitigation treaties [Jackson *et al.*, 2008]. To design and implement effective climate-change mitigation policies, we need to understand the individual and combined mitigation potential from biophysical and biogeochemical fluxes. A first step into that direction is to characterize how abiotic and biotic factors relate to patterns of both the biophysical and biogeochemical fluxes providing climate regulation services. This assessment can help us understand why and how the climate-mitigation potential varies within and across forest ecosystems, within and across nations.

For climate regulation services there is robust evidence of a strong abiotic influence behind biogeochemical and biophysical fluxes [Jobbagy and Jackson, 2000; Reichstein et al., 2002, 2007; Seddon et al., 2016]. Abiotic factors, however, have not fully explained the variation in spatial patterns of climate regulation services [Lavorel et al., 2010; Reichstein et al., 2014]. Though climate and the environment influence biological communities and their functional traits, there are theoretical and empirical bases for additional, strong biotic influences on irradiance scattering, carbon allocation, respiration, water use efficiency, and carbon stabilization in soils [Chapin, 2003; Eviner and Chapin, 2003; de Deyn et al., 2008]. What remains uncharacterized is the expression of this biotic influence on the different biogeochemical and biophysical fluxes, and how they compare to the abiotic, at spatial scales larger than landscape. Evaluating the influence of the functional [Diaz et al., 2009; Lavorel et al., 2010; Conti and Diaz, 2013] and structural [Ruiz Benito et al., 2014] compositions of biotic communities on climate regulation services is sorely needed [Diaz et al., 2007; Reichstein et al., 2014]. The scarce availability of spatially explicit data has delayed the characterization of biological influences on biogeochemical and biophysical fluxes regulating climate and many other ecosystem services. Going beyond assessments based on plant functional types is crucial to estimate how climate regulation services could be impacted by the ongoing losses in global biodiversity and by management practices altering vegetation density and community composition.

Here we aim to quantify the abiotic and biotic influences on climate regulation services in a regional extent of forests. Comprehensive metrics to represent climate regulation services are scarce; the few available are model-based and data-intensive [West et al., 2011; Anderson-Teixeira et al., 2012]. We individually evaluate for the influences of the main ecosystem properties and processes involved in the biogeochemical and biophysical fluxes providing climate regulation services: albedo, evapotranspiration, primary productivity, and soil organic carbon (hereafter referred as climate regulation processes). First, we quantify the statistical relation between climate regulation processes and factors from abiotic and biotic categories separately. This helped us contrast the influence of the functional and structural composition of biotic communities on climate regulation processes, to those of temperature, precipitation, and the environment. Second, we assess how the strongest abiotic and biotic factors, alone and combined, explain climate regulation processes. Overall, if biophysical and biogeochemical fluxes are influenced similarly by abiotic and biotic factors, a robust proxy can be identified for the temperate forest region. Differences in the relative influence of factors related to biophysical and biogeochemical fluxes would suggest trade-offs and different responses to environmental and biological pressures.

2. Materials and Methods

We focus on a regional extent of forests in the eastern United States (approximately 3.3×10^6 km², east of the 95°E meridian). Unlike for tropical forest, biophysical and biogeochemical fluxes in temperate regions do not seem as strongly coupled [Jackson et al., 2008]. Unlike for tropical forest, data on functional traits, forest carbon pools, and forest structure are often available for temperate forests.

The regional extent under analysis encompasses 16,955 forest plots from the Forest Inventory Data (FIA, phase 3). FIA plots under management were excluded from our study given lack of details on the different practices. Each FIA plot consists of four circular subplots of 170 m² where trees with a diameter of ≥ 12.7 cm are measured. In each subplot there is a microplot of 10 m² where all trees with a diameter of ≥ 2.54 cm are measured [Woudenberg et al., 2010]. We combined functional trait data from the georeferenced forest plots with gridded data on climate regulation processes, and abiotic and biotic input variables. We set a buffer area of 0.8 km in radius around each forest plot and estimated the mean values of gridded data. This addressed the spatial dislocation in georeferenced plots applied by FIA to protect landowner's privacy [Woudenberg et al., 2010].

2.1. Climate Regulation Services: Biophysical and Biogeochemical Fluxes

We represent the biophysical and biogeochemical fluxes providing climate regulation individually. We chose to use remotely sensed data on the main ecosystem processes and properties behind the different fluxes, instead of using a single or proxy metric for climate regulation services. Remotely sensed data are currently the most independent source of data for large-scale assessment such as ours. Spatially explicit data on biophysical and biogeochemical fluxes from international flux networks have been interpolated

by using environmental information [Jung *et al.*, 2011], which hinders its use for characterizing the influences of abiotic and biotic variables thereupon.

We used albedo and evapotranspiration data to represent biophysical fluxes involved in climate regulation. Albedo and evapotranspiration provide local-to-regional climate services by modulating the amount of solar energy and air moisture used and emitted by forest ecosystems [Pielke *et al.*, 1998; Anderson-Teixeira *et al.*, 2012; Alkama and Cescatti, 2016]. To represent land-surface albedo, we averaged 16 day composite data on black-sky, short-wave albedo from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor (albedo (AB), fraction, no units, product MCD43B3 [Moody *et al.*, 2005]). We used black-sky short-wave albedo because it follows patterns of blue-sky, actual surface albedo better than white-sky or the average of black- and white-sky estimates [Liu *et al.*, 2009]. We used the average of annual MODIS data on evapotranspiration (ET, mm yr⁻¹, product MOD16A3 [Mu *et al.*, 2011]). The MODIS evapotranspiration algorithm is based on the Penman-Monteith equation [Monteith, 1965] and considers dry canopy transpiration, wet canopy, and soil surface evaporation in its calculations [Mu *et al.*, 2011]. AB and ET data were obtained at 1 × 1 km grid-cell resolution. AB and ET data represent the average from the 2000–2009 decade to smooth seasonal and/or annual fluctuations.

We used primary productivity and soil carbon storage to represent biogeochemical fluxes of climate regulation. The capture and storage of carbon in vegetation and soils influence atmospheric concentrations of greenhouse gases, providing lagged, global climate benefits [Bonan, 2008; Diaz *et al.*, 2009]. We used the average of annual MODIS data on gross and net primary productivity (GPP and NPP, g carbon m⁻² yr⁻¹, product MOD17A3 [Zhao *et al.*, 2005]). The MODIS NPP algorithm estimates autotrophic respiration from leaf area index, surface temperature, and respiration rates based on MODIS land-cover type [Zhao *et al.*, 2005]. MODIS NPP estimates are independent from GPP [Zhang *et al.*, 2009]. Including both GPP and NPP also allowed us to contrast the differences between correlates of the gross carbon uptake and the actual amount incorporated in vegetation. Data on GPP and NPP represent the average of the 2000–2009 decade at 1 × 1 km grid-cell resolution. We used data on soil organic carbon content in first-meter depth developed for the 2000–2009 decade (soil organic carbon (SOC), Mg ha⁻¹ [Wilson *et al.*, 2013]). For consistent spatial grain in our input data, we aggregated SOC data from 250 × 250 m to 1 × 1 km by calculating the average of values encompassed in the new grid-cell resolution. The aggregation did not bias patterns in input data (see Text S1 and Figure S1 in the supporting information).

2.2. Abiotic and Biotic Factors

In order to quantify and contrast the primary influences on climate regulation processes, we selected variables representing abiotic and biotic factors known to influence the different processes (Table 1). We used data on bioclimatic factors, soil physical-chemical characteristics, and topography to represent abiotic factors. We calculated bioclimatic variables by using mean monthly climate normals at 1 × 1 km grid-cell resolution (1981–2010) [Daly *et al.*, 2008]. Including bioclimatic variables permitted us to quantify effects of annual and seasonal means and ranges, and climatic limits on climate regulation processes (Table 1). The bioclimatic variables included precipitation of the wettest period (mm), precipitation seasonality (estimated as the quotient of the standard deviation of the monthly mean temperatures and the mean annual temperature, %), precipitation warmest quarter (mm), diurnal temperature range (°C), isothermality (mean diurnal range divided by temperature annual range), temperature annual range (°C), and temperature of the driest quarter (°C). Soil physical-chemical characteristics, known to influence water-holding capacity, carbon accumulation, and aboveground productivity, were extracted from gridded data (1 × 1 km grid-cell resolution) [Hengl *et al.*, 2014]. We included pH (in H₂O solution), cation exchange capacity (cmol⁺ kg⁻¹), bulk density (kg cm⁻³), and soil texture (sand, silt, and clay, % kg kg⁻¹) in the first-meter depth. As a proxy for abiotic conditions not accounted by the above factors, we included an elevation estimate from a 1 × 1 km resolution digital model (meters) [Gesch and Verdin, 1999].

To represent biotic factors, we used data on functional diversity, forest carbon pools, and vegetation cover (Table 1). We included the plot-level estimates of the functional traits presented in Swenson and Weiser [2010]: leaf nitrogen, maximum height, wood density, and seed mass. Leaf nitrogen content (mass %N) influences the quality and decomposability of organic matter [de Deyn *et al.*, 2008; Ordonez *et al.*, 2009]. Leaf nitrogen also influences the carbon cycle at the ecosystem level, varying positively and linearly with

Table 1. Abiotic and Biotic Variables Used to Characterize the Primary Influences of Climate Regulation Processes

Category	Type	Variable	Description
Abiotic	Bioclimatic factors ^a	Precipitation of the wettest period	Seasonal and annual means and ranges, for example, temperature annual range (°C), precipitation in the wettest quarter (mm)
		Precipitation seasonality	
		Precipitation warmest quarter	Climatic limits, for example, temperature and precipitation in coldest and driest periods
		Diurnal temperature range	
		Isothermality	
		Temperature annual range	
		Temperature of the driest quarter	
	Soil	pH	• pH index in water solution
		CEC	• Cation exchange capacity in the fine earth fraction (cmol ⁺ kg ⁻¹)
		Bulk density	• Density in fine earth fraction (kg m ⁻³)
Biotic	Topography	Texture factors	• Gravimetric content of clay, sand, and silt (% kg kg ⁻¹)
		Elevation	Meters above sea level
		Leaf nitrogen	• Percentage of nitrogen content in leaf (mass %N)
		Maximum height	• Height of adult tree (meters)
	Functional diversity ^b	Wood density	• Mass of wood divided by green volume (g cm ⁻³)
		Seed mass	• Average weight of seeds (mg)
		Species richness	• Number of species recorded in survey plots
		Understory	• Carbon of live seedlings, shrubs, bushes in the aboveground and belowground portions
	Carbon pools ^c	Dead wood	• Carbon in standing and downed dead wood
		Litter	• Organic material on the forest floor: woody debris, humus, and fine roots above the mineral soil layer
		Aboveground	• Carbon in the aboveground portion of the tree, excluding foliage
		Belowground	• Carbon in the belowground portion of the tree. Includes coarse roots >0.254 cm in root diameter
	Vegetation cover	Tree cover	Proportion of grid cell covered by tree canopies (%)

^aBioclimatic factors related to precipitation are in millimeters (mm) of water and those related to temperatures are in °C.

^bFor each functional trait (leaf nitrogen, maximum height, wood density, and seed mass), we calculated the community-weighted mean, minimum, maximum, range, and variance metrics.

^cAll forest carbon pool variables are in mg ha⁻¹.

photosynthesis [Reich *et al.*, 1992; Reich, 2012]. Maximum height (m) and wood density (g cm⁻³) are functional traits associated with plant biomass and investment in structure per unit of biomass, both relating to aboveground carbon storage [Chave *et al.*, 2009; Moles *et al.*, 2009]. Larger plants also make larger contributions to the accumulation of organic matter in soils [de Deyn *et al.*, 2008]. Seed mass (mg) increases with seedling survival and relates to forest successional development [Douma *et al.*, 2012]. Leaf nitrogen, seed mass, maximum height, and wood density reflect community responses to environmental conditions at regional [Freschet *et al.*, 2011] and global scales [van Bodegom *et al.*, 2014].

We used abundance-weighted, single-trait community metrics of functional traits multiplying species abundance by their trait values. Tree species presence and abundance (number of individual stems) estimates are from the 2006 inventory year, except for plots in the state of Louisiana where information comes from 2005 [Swenson and Weiser, 2010]. For each forest plot, we calculated the community mean, minimum, maximum, variance, and range metrics for each functional trait. As a community index of diversity, we included a plot-level estimate of species richness. Community mean trait values are generally associated to ecosystem functioning [Suding *et al.*, 2008; Lavorel, 2013]. In the case of, for example, canopy height, maximum trait values may more strongly relate to ecosystem functioning given the unidirectional impacts of light availability. On the other hand, the species with the lowest wood density in a community are most vulnerable to drought stress [Poorter *et al.*, 2010]. Trait ranges and variances in a community reflect limiting similarity and partly express the strength of competition and facilitation processes. Limiting similarity has been associated to ecosystem functioning in a wide range of studies [Diaz *et al.*, 2007; Lavorel *et al.*, 2010; Cardinale *et al.*, 2012].

To represent the different forest carbon pools, vertical structure, and successional stage, we used data on forest understory, dead wood, litter, and live tree aboveground and belowground carbon (Table 1). Forest structural and successional attributes determine the dominant species, and the vertical and canopy densities, which in turn influence the absorption of radiation, transpiration rates, productivity, and decomposition rates [Dixon *et al.*, 1994; Wardle, 2004; Bonan, 2008; de Deyn *et al.*, 2008]. Data on forest understory carbon represent the carbon of live seedlings, shrubs, bushes in the aboveground and belowground portions

[Woudenberg *et al.*, 2010]. Downed dead wood represents woody material of >7.62 cm in diameter and stumps and their roots >7.62 cm in diameter. Standing wood represents dead standing trees, including coarse roots [Woudenberg *et al.*, 2010]. We combined the estimates of standing and downed dead wood into one variable (dead carbon = standing + downed). Forest litter carbon data represent the organic material on the forest floor: fine woody debris, humus, and fine roots above mineral soil layer [Woudenberg *et al.*, 2010]. Forest litter estimates are derived from a model that considers geographic area, forest type, and stand age [Woudenberg *et al.*, 2010]. We did not include forest stand age from FIA inventories because many of plots did not have a stand age estimate reported in the 2000–2009 period, because it is used in the estimation of forest litter carbon [Woudenberg *et al.*, 2010] and because of the concerns over its estimation [Purves *et al.*, 2008; Stevens *et al.*, 2016; U.S. Department of Agriculture Forest Service FIA Program, 2016] (see Text S2). Exploratory analyses with forest stand age (following the statistical analyses described in section 2.3) are presented in Figures S2 and S3. Data on live aboveground carbon represent that of live timber and woodland trees species with a diameter of ≥ 2.54 cm and dead trees with a diameter of ≥ 12.7 cm [Woudenberg *et al.*, 2010]. Aboveground carbon data exclude carbon in foliage. Live belowground carbon represents that of coarse roots >0.254 cm in root diameter, calculated for live timber and woodland trees species with ≥ 2.54 cm in diameter, and dead trees with ≥ 12.7 cm in diameter [Woudenberg *et al.*, 2010]. All forest carbon data (in Mg ha^{-1}) were collated and validated by Wilson *et al.* [2013], using inventory data for the 2000–2009 decade.

Finally, to account for effects of canopy surface roughness on the surface-energy budget, we averaged annual data on MODIS tree canopy cover for the 2000–2009 decade (% cover, product MOD44B [DiMiceli *et al.*, 2011]). Tree cover data represent the proportion of canopy cover in a given grid cell. For uniformity in spatial grain, tree cover and forest carbon data were aggregated from 250×250 m to 1×1 km grid-cell resolution (see Text S1 and Figure S1). Data on leaf area index, photosynthetically active radiation, and radiation were not included in our analyses because they are used in the MODIS algorithms to estimate AB, ET, GPP, and NPP [Moody *et al.*, 2005; Zhao *et al.*, 2005; Mu *et al.*, 2011], and including them would introduce circularity of arguments.

2.3. Statistical Analyses

All input variables were standardized to avoid biases from different measurement scales (mean = 0, SD = 1). Climate regulation processes (AB, ET, NPP, and SOC) were left untransformed. Descriptive statistics of unstandardized input variables are presented in Table S1 in the supporting information.

To characterize the factors influencing climate regulation processes, we performed a two-step selection process before quantifying the statistical relation between variables and individual climate regulation processes [after Murray and Conner, 2009]. First, we eliminated likely spurious correlations by discarding variables with $R^2 \leq 0.05$ in bivariate linear regressions with the climate regulation process in turn. Second, we eliminated highly collinear variables by calculating variance inflation factors (VIF). We calculated VIF in a stepwise manner, discarding at each step the variable with the highest VIF, until all variables met the $\text{VIF} < 10$ threshold [Dormann *et al.*, 2013]. We grouped the resulting set of nonspurious, nonhighly collinear variables into abiotic and biotic categories. The abiotic category includes bioclimatic factors, soil characteristics, and topography. The biotic category includes functional trait metrics, forest carbon pool variables, and vegetation cover. These two steps were conducted for each climate regulation process.

We quantified the statistical relations between each climate regulation process and abiotic and biotic variables, separately, by using the hierarchical partitioning (HP) R package [Walsh and Mac Nally, 2013]. We chose HP because it quantifies the independent and joint influence of variables in a robust manner, unbiased by any degree of collinearity between input variables [Chevan and Sutherland, 1991; Mac Nally, 2000; Murray and Conner, 2009]. The independent influence of a variable is the averaged unique contribution to the explained variance, quantified by comparing all nested models containing the variable to those without it [Chevan and Sutherland, 1991; Mac Nally, 2000]. The joint influence represents the degree to which the contribution of a variable to the explained variance overlaps with that of others [Chevan and Sutherland, 1991; Mac Nally, 2000]. The sum of independent and joint influences of a variable approximates the magnitude of the univariate R^2 , but not the direction of the correlation [Mac Nally, 2000]. The HP analyses were conducted first for the abiotic and biotic variables separately then in combination, using the top variables from each category with the highest independent influence.

Table 2. Comparison Between the Best Multivariate Model Sets and the Full Models

	$\Delta(\text{Best Model Sets}^{\text{a}}\text{-Full Models}^{\text{b}})$	
	ΔR^2_{adj}	$\Delta \text{RMSE}^{\text{c}}$
<i>Albedo</i>		
Abiotic	−0.066	0.021
Biotic	−0.014	0.005
Combined ^d	−0.035	0.014
<i>Evapotranspiration</i>		
Abiotic	−0.044	5.86
Biotic	−0.012	1.50
Combined	−0.025	3.48
<i>Gross primary productivity</i>		
Abiotic	−0.080	27.3
Biotic	−0.010	2.60
Combined	−0.041	13.8
<i>Net primary productivity</i>		
Abiotic	−0.081	12.0
Biotic	0.00	0.00
Combined	−0.061	8.80
<i>Soil organic carbon</i>		
Abiotic	−0.062	1.80
Biotic	−0.039	1.10
Combined	−0.101	4.00

^aBest model set is defined as the collection of multivariate models in the upper 10th percentile of RMSE values obtained from tenfold cross validation.

^bFull models are the multivariate models fitted by using all the variables chosen through the variables selection process.

^cRMSE is the average root-mean-square error calculated from tenfold cross validation.

^dIn all cases, the combined set is fitted by using the up-to-six variables from the abiotic and biotic categories that showed the highest independent influence on each climate regulation process.

We then selected the variables with highest independent influences from HP analyses and used a multimodel inference framework to assess how abiotic and biotic variables explain the variance in climate regulation processes. This approach is complementary to HP, as it also helped us quantify the model coefficients of variables, and hence the direction of their influence on climate regulation processes. As for HP analyses, for each climate regulation process, we constructed sets of multivariate linear regression models by using the top variables from the abiotic and biotic categories separately, then using a combination of these variables. We conducted tenfold cross validation to compare the model accuracy and to base multimodel selection on root-mean-square-error (RMSE; Text S3) [James *et al.*, 2013; Burnham and Anderson, 2002]. Here we define the best model set as the set of multivariate models with the lowest 10% of RMSE values. To account for model selection uncertainty and to obtain robust estimates, we averaged the regression coefficients in the set of multivariate models in the lower 10% of RMSE values. We did not use Akaike's Information Criterion (AIC) as weighting criterion for model selection (or to rank variable importance) because it was affected by our large sample size [Burnham and Anderson, 2002; Hoeting *et al.*, 2006; Murray and Conner, 2009].

In building our models, we considered multivariate combinations of up to five regressors and nonlinear relationships. The restriction in the number of regressors in models to avoid model overfitting did not compromise explanatory power: The differences in explained variance between the best model sets and full models were $\leq 10\%$ (Table 2). If residual-versus-variable plots suggested deviations from linearity, we added polynomial terms into the model sets [Zuur *et al.*, 2007]. We did not include first-order interactions in models given limitations on processing power. The evaluation of ordinary least squares assumptions did not show major deviations (see Texts S3–S5). All best model sets (abiotic, biotic, and combined) were fitted by using the same set of complete observations. We do not report significance levels of the results from HP analyses or of model coefficients given our large sample size and spatial autocorrelation in some residuals. The spatial autocorrelation in model residuals did not show considerable deviations. In spatial correlograms, only the biotic model for NPP showed Moran's *I* between 0.15 and 0.20 at small distance intervals. All other residuals showed Moran's *I* between −0.1 and 0.1 at all distance intervals (see Figure S4) [Rhodes *et al.*, 2006]. Statistical analyses were conducted in R statistical software v3.1.2. Gridded data were processed with ArcGIS v10.1.

3. Results

3.1. Abiotic Influences

The variable selection process resulted in a different set of abiotic variables being chosen for each climate regulation process (Figure 1). Still, temperature and soil texture variables were more strongly related to climate regulation processes than other abiotic variables (Figures 1a–1e). For ET, GPP and NPP, temperature annual range, precipitation seasonality, and temperature of the driest quarter

Figure 1. Abiotic influence on climate regulation processes: independent contributions to models and standardized coefficients. The same x axis is used for all panels in order to facilitate comparisons; variable names in the x axis without value were those left out of the analyses because they did not fulfill the requirements of our variable selection process. (a–e) The height of bars represents the sum of independent and joint influences, which approximates the univariate R^2 of the variable. The independent influence of an abiotic variable is its averaged unique contribution to the explained variance; the joint influence represents the degree to which the contribution of the abiotic variable to the explained variance overlaps with that of others. (f–j) Standardized model coefficients for the best 10% abiotic model sets. The filled circles represent the average coefficient estimate over the models included in the best model sets; the error bars are the length of two standard deviations. Parameter n is the number of models included in the best model sets. $RMSE$ is root-mean-square error obtained from tenfold cross validation, averaged over the n models. R^2_{adj} represents the explained variance, averaged over n models. Coefficients for polynomial terms are presented in Table S3. Abbreviations: AB = albedo, ET = evapotranspiration, GPP = gross primary productivity, NPP = net primary productivity, SOC = soil organic carbon, CEC = soil cation exchange capacity, T = temperature, P = precipitation, qr = quarter of a year.

expressing temperature-precipitation interactions had the largest independent influence (Figures 1b–1d). For AB and SOC, the independent influence of soil texture variables was greater than that of most precipitation and temperature variables (Figures 1a and 1e). The independent-to-joint ratios of sand on AB and of silt on SOC were >0.8 . This suggests that soil variables have large, unique influences on the explained variance of AB and SOC. In all other cases, abiotic variables had independent-to-joint ratios <0.5 . The large joint influence reflects a considerable overlap in the variance explained by abiotic variables.

Using the abiotic factors that showed the greatest independent influence on each climate regulation process, we constructed model sets to quantify how much variance they can explain and the direction of their effects. The best 10% abiotic model sets explained on average $\geq 60\%$ of the variance in most climate regulation processes (Figures 1f–1j), although the abiotic model set for NPP explained only 34% of the variance (Figure 1i). In the best model sets we also found that abiotic factors with strong influence on climate regulation processes had opposing effects. Such differences in direction of abiotic influences were not consistent between processes behind biophysical (AB and ET) and biogeochemical (GPP, NPP, and SOC) fluxes. For example, temperature annual range had the largest (negative) averaged coefficient in the best model sets for ET, GPP, and NPP (Figures 1g–1i), while the coefficient was positive for SOC and AB. Other abiotic variables shared between climate regulation processes such as elevation and temperature of the driest quarter showed similar differences in direction of effects (Figures 1f–1j). Moreover, the standard deviation of coefficients was large, suggesting a considerable variation in the magnitude and direction of the influence.

3.2. Biotic Influences

The selection of biotic variables based on their influence on climate regulation processes differed more strongly than with abiotic variables. Not one biotic variable was strongly related to all four climate regulation processes (following our variable selection process, section 2.3). The largest independent influences on climate regulation processes were associated to forest litter (AB and SOC) and understory (ET, GPP, and NPP) carbon (Figures 2a–2e). With independent-to-joint ratios >0.9 , the influences of litter and understory carbon were largely independent from that of other biotic variables. Belowground and dead forest carbon variables were only moderately related to GPP, and to AB and SOC, respectively. Only for NPP, community leaf nitrogen traits had greater influence than understory carbon (Figure 2d). Trait ranges, trait variances, species richness, and forest aboveground carbon had $R^2 < 0.05$ in bivariate regressions with any climate regulation process and, hence, were not included in HP or multimodel analyses.

The best biotic model sets often performed as well as their abiotic counterparts. Surprisingly, the best 10% biotic model set for AB explained more variance and had a lower RMSE value than the abiotic counterpart ($R^2_{\text{adj}} = 78\%$ and 68% , respectively; Figure 2f). The explanatory power of the best biotic model set for SOC was only 2% less than that of the abiotic counterpart and had similar RMSE value. The best biotic model sets for ET, GPP, and NPP explained between 7% and 16% less of the variance and had considerably greater RMSE values than the abiotic sets. In all cases, the averaged coefficients of the forest carbon pool variables were considerably larger than those of functional traits or tree cover, and often in opposite direction (Figures 2f–2i). In the case of GPP and ET, the influence of forest understory was greatest, while for AB and SOC, litter carbon had the largest influence. Here again the direction of coefficients was not similar between the different climate regulation processes, or between the processes representing the two types of fluxes (AB and ET versus GPP, NPP, and SOC). The results for NPP need to be considered cautiously because only one model had been selected in the best 10% biotic model sets.

3.3. Combined Influence of Abiotic and Biotic Variables

We conducted again HP and multimodel analyses by using a combination of the four-to-six abiotic and biotic variables with the highest independent influence. Here, as expected, we found that the joint influence of abiotic and biotic variables on climate regulation services was greater than the independent (Figures 3a–3e and S5). This suggests that large fractions of variance explained separately by abiotic and biotic variables are accounted by the intrinsic overlap between them. Even so, HP analyses using a combination of the strongest abiotic and biotic influences on each climate regulation process showed the independent influence of forest litter and understory to be often greater than those of bioclimatic

Figure 2. Biotic influence on climate regulation processes: independent contributions to models and standardized coefficients. The same x axis is used for all panels in order to facilitate comparisons. (a–e) The height of bars represents the sum of independent and joint influences, which approximates the univariate R^2 of the variable. (f–j) Standardized model coefficients for the best 10% biotic model sets. The filled circles represent the average coefficient estimate over the models included in the best model sets; the error bars are the length of two standard deviations. Parameter n is the number of models included in the best model sets. RMSE is root-mean-square error obtained from tenfold cross validation, averaged over the n models. R^2_{adj} represents the explained variance, averaged over n models. Coefficients for polynomial terms are presented in Table S3. Abbreviations: AB = albedo, ET = evapotranspiration, GPP = gross primary productivity, NPP = net primary productivity, SOC = soil organic carbon.

and soil variables (Figures 3a–3e). The independent influence of forest litter on AB and SOC was the greatest (12.7% and 9.4%, respectively; Figures 3a and 3e). The independent influence of understory and temperature of the driest quarter on ET were similar (7.5% and 8.7%, respectively). For GPP, the independent influence of understory was similar to that of temperature of the driest quarter and

Figure 3. The combined influence of abiotic and biotic variables on climate regulation processes: contrasting independent contributions to explained variance. The blue is used to designate abiotic variables; the green is used for biotic variables. The same x axis is used for all panels in order to facilitate comparisons. (a–e) The bars represent independent and joint influences. (f–j) The model coefficients for the best 10% combined model sets. The error bars represent two standard deviations. Parameter n is the number of models included in the best model sets. $RMSE$ is root-mean-square error. R^2_{adj} represents the explained variance. Coefficients for polynomial terms are presented in Table S4. Abbreviations: AB = albedo, ET = evapotranspiration, GPP = gross primary productivity, NPP = net primary productivity, SOC = soil organic carbon, CEC = soil cation exchange capacity, T = temperature, P = precipitation, qr = quarter of a year.

precipitation of the warmest quarter but lower than that of temperature annual range (Figure 3c). The independent influence of soil silt on NPP was similar to that of temperature annual range (both about 6.9%), both greater than that of forest understory (4%; Figure 3d). For SOC, the independent influence of soil clay was similar to that of forest litter (both about 1.4%).

Figure 4. Spatial distribution of standardized residuals from the best 10% model sets. The best model sets are the multivariate models in the lower 10% of RMSE values. RMSE values were obtained from tenfold cross validation. The rows present the standardized residuals from the best (a–e) abiotic, (f–j) biotic, and (k–o) combined model sets. At each forest plot, standardized residuals are the average of residuals from each multivariate linear model in the set. To improve the visualization of patterns, we performed inverse distance squared weighted interpolation of the standardized residuals from the 16,955 forest plots. Interpolated grid on the area of study (approximately $3.3 \times 10^6 \text{ km}^2$) is composed of 3203 columns and 2706 rows. AB = albedo, ET = evapotranspiration, GPP = gross primary productivity, NPP = net primary productivity, SOC = soil organic carbon, Comb. = combined model sets.

The best 10% combined model sets had lower RMSE values, and tended to explain more variance in climate regulation processes, than the biotic or abiotic sets separately (Figures 3f–3j). The most striking improvement from using both abiotic and biotic variables in models was for SOC: a $>10\%$ increase in R^2_{adj} and a >3 decrease in RMSE value compared to both abiotic and biotic model sets. Only for NPP, abiotic model sets performed better than the combined model set. The difference in RMSE and R^2_{adj} between the combined and the abiotic model sets for ET and NPP was small ($\Delta R^2_{\text{adj}} = 1\%$, $\Delta \text{RMSE} \leq 4$), particularly when compared to the differences between the combined and the biotic model sets for ET and NPP ($\Delta R^2_{\text{adj}} = 8$ and 16% , $\Delta \text{RMSE} = 11.5$ and 40 , respectively). For AB, on the other hand, the difference in RMSE and explanatory power between the combined model and the biotic counterpart was smaller ($\Delta \text{RMSE} = 0.004$, $\Delta R^2_{\text{adj}} = 1.1\%$) than the differences between the combined and abiotic set ($\Delta \text{RMSE} = 0.04$, $\Delta R^2_{\text{adj}} = 12\%$).

In the combined model sets for AB and SOC, we found the coefficients of forest litter carbon to be larger than, and in opposing direction to, those of the strongest abiotic variables (Figures 3f and 3j). For SOC, though, the coefficients of forest litter and precipitation seasonality were similarly strong and positive (Figure 3j). The negative coefficient of temperature of the driest quarter on AB was equal to that of forest understory (Figure 3f). For ET and GPP, the strongest influence in the combined model sets were abiotic: The coefficient of temperature annual range was double than that of forest understory (the strongest biotic influence) and in the opposite direction (Figures 3g and 3h). The largest influence on NPP was abiotic, as expected given the greater explanatory power and lower RMSE from the abiotic-only model sets.

3.4. Heterogeneous Spatial Distribution of Model Residuals

Given the nature of our input data, we chose to study the spatial distribution of model residuals. The explanatory power of all best 10% model sets was heterogeneous across the spatial extent of assessment (Figure 4).

Except for AB, the best abiotic model sets tended to underpredict climate regulation processes in southern regions. Abiotic model sets overpredicted AB and SOC in northern regions. These residual patterns were similar to those from best biotic model sets (Figures 4a and 4e). This suggests that though the explanatory power of abiotic and biotic models differed, their ability to predict climate regulation processes in different areas remains relatively similar, which is most probably related to the strong joint effects. The best combined model set alleviated the slight overpredictions for ET (Figure 4l), while for SOC, the combined models increased the number of areas with moderate overpredictions (Figure 4o). For AB, residual patterns of biotic and combined model sets were more similar than those of any other climate regulation process (Figures 4f and 4k). This suggests that biotic variables alone can account spatial patterns of AB as well as models by using both abiotic and biotic variables combined. Only for GPP, the distribution of residuals from the abiotic, biotic, and combined model sets was similar (Figures 4c, 4h, and 4m). This suggests that the ability of abiotic and biotic variables to explain the spatial variance of GPP, separately, does not improve when using them in combination. Overall, no single model type (abiotic, biotic, or combined) consistently explained the spatial variation in climate regulation processes.

4. Discussion

A quantitative characterization of patterns and their drivers is key to understand the ecology of climate regulation services and, ultimately, to guide management practices. Biotic influence on ecosystem processes and properties is often expected to be of consequence at small spatial scales only [Sarr *et al.*, 2005; McGill, 2010]. However, we found that the relation between biotic factors and most climate regulation processes is strong at a regional scale (Figure 3). Moreover, for most climate regulation processes the inclusion of both abiotic and biotic variables in models increased explanatory power and accuracy compared to the individual abiotic and biotic models. Only for primary productivity, abiotic factors were more suited to account for the regional variation and even better than a combination of abiotic and biotic variables. The strongest abiotic influences on all climate regulation processes were temperature and precipitation ranges and seasonality. Another important finding from our analyses are the differences in primary abiotic and biotic influences on each climate regulation process (Figures 1–3). The sensitivities of each climate regulation process from temperate forests to biological losses and climatic changes are hence different. Given the differences in the main factors influencing the different climate regulation processes, a combination of abiotic and biotic variables should be considered to monitor climate regulation and to forecast changes after the impacts of global environmental change.

4.1. Strong Influence of Forest Structure and Successional Stage on Climate Regulation Processes

In the first part of our assessment, we quantified the statistical influence abiotic and biotic variables have on climate regulation processes. Biotic models for most climate regulation processes performed as well as the abiotic ones. Our findings suggest a strong biotic influence on climate regulation processes, as approximated by the statistical relations of forest litter and understory carbon. These results likely indicate that climate regulation processes in our regional scale of assessment are related to the combined effects of forest structure and successional stage. We base this suggestion on previous evidence of biotic mechanisms affecting climate regulation processes. Changes in understory carbon have been linked to mechanisms that influence carbon sequestration, water transpiration, and the absorption of solar radiation [Black and Kelliher, 1989; Nilsson and Wardle, 2005; Santiago and Wright, 2007]. Similarly, the influence of forest structure on productivity has been found in regional extents of temperate Mediterranean [Ruiz Benito *et al.*, 2014] and tropical forests [Poorter *et al.*, 2015]. The statistical relation between forest litter and AB and ET likely suggests an indirect influence through the vegetation and soil changes associated with the development of successional stage. Forests develop complex, dense canopies with successional stage, which increase the absorption of solar radiation and overstory evapotranspiration [Chapin, 2003; Parker and Russ, 2004; Wardle, 2004; de Deyn *et al.*, 2008; Douma *et al.*, 2012]. The strong influence we found between SOC and forest litter likely reflects the relation between soil carbon and litter accumulation and the changes in litter quality and decomposition rates associated with the progression of successional stage [Dixon *et al.*, 1994; Wardle, 2004; de Deyn *et al.*, 2008].

The influence that other biotic variables exhibited seems to support that forest structure and successional stage are strongly related to climate regulation processes. The influence of tree cover, height, and wood traits on AB likely reflects the relationship between canopy-level structural attributes and irradiance scattering

[Hollinger *et al.*, 2010]. Moreover, the influence of tree cover, height, and wood traits on ET likely reflects changes in aerodynamic roughness [Black and Kelliher, 1989]. These results, together with those of seed mass, support how forest structure and successional stage in combination likely influence patterns of AB and ET. On the other hand, the influence of height and wood traits on productivity and SOC was surprisingly small given their central role in the carbon gain strategy and storage capacity of plants, [Chave *et al.*, 2009; Moles *et al.*, 2009; Conti and Diaz, 2013; Finegan *et al.*, 2015]. The observed influence of community leaf nitrogen metrics likely reflects how leaf-level properties that directly influence photosynthetic gain scale-up to regional-level properties [Reich, 2012; Finegan *et al.*, 2015], though this influence is considerably smaller than that of forest structure, successional stage, and abiotic variables (Figure 3).

The effects of species richness and trait variance, as related to functional diversity, were small at this spatial extent. Diversity effects on climate regulation may be stronger in regions where biotic heterogeneity is large and in regions with strong environmental filters [Conti and Diaz, 2013; Finegan *et al.*, 2015; Poorter *et al.*, 2015]. In temperate regions, competitive exclusion can result in a strong underpinning of ecosystem processes and services by the most abundant species [Paquette and Messier, 2010], which may explain its limited impacts in our study.

4.2. Bioclimatic and Soil Influence on Climate Regulation Processes

The influence of abiotic factors on climate regulation processes was large even when considering biotic factors (Figures 1 and 3). Net primary productivity in particular was better explained by abiotic factors alone. This suggests that out of all climate regulation processes, NPP is likely more sensitive to changes in temperature and precipitation than to changes in biotic communities. Though this result is concordant to previous evidence on the large sensitivity of productivity to climatic extremes such as drought [Reichstein *et al.*, 2002; Williams *et al.*, 2012; Seddon *et al.*, 2016], our quantification of biotic influences of NPP is limited (see Figures 2d and 2i). Precipitation in the wettest period and seasonality, temperature of the driest quarter all were related to all climate regulation processes (Figures 1 and 3). These abiotic factors likely reflect a strong underlying mechanism of water supply on productivity, evapotranspiration, and soil organic matter accumulation [Reichstein *et al.*, 2002, 2007; de Deyn *et al.*, 2008; Williams *et al.*, 2012; Serna-Chavez *et al.*, 2013; Mao *et al.*, 2015; Seddon *et al.*, 2016]. Hence, a strong influence through water supply and availability on climate regulation processes is suggested. The statistical relations of soil factors such as texture and pH reinforce the suggestion that water supply and availability affects climate regulation processes [de Deyn *et al.*, 2008; Serna-Chavez *et al.*, 2013]. The influence of soil sand content on AB, on the other hand, may likely be an indirect one, through the effects of barren soil cover and vegetation density: the increase in AB with sand coincided with increases in tree cover (Figure S6).

Moreover, temperature-precipitation interactions, and climatic seasonality and ranges were strongly related to all climate regulation processes, even after accounting for the influence of biotic factors. Temperature annual range was a prominent factor in the abiotic and in the combined model sets (Figures 1 and 3). The influence of temperature annual range on ET, SOC, and productivity likely reflects the limitations imposed by cold temperatures [Boisvenue and Running, 2006; Davidson and Janssens, 2006; Seddon *et al.*, 2016]. In supplementary analyses, minimum temperature of the coldest month had stronger effects on climate regulation processes than maximum temperatures (Figure S7). The influence of temperature annual range on AB may be partly through snow cover and vegetation seasonality. The prominent influence of range and seasonality suggests that the ongoing climatic changes could strongly impact climate regulation processes—albeit differently for each process. The influence of temperature annual range and precipitation seasonality also illustrates the need to account for climatic range and seasonality when analyzing patterns of ecosystem processes and services [cf. Moles *et al.*, 2014].

5. Concluding Remarks

Models using both abiotic and biotic variables explained a considerable amount of the variance in climate regulation processes. The factors with the strongest influences in our models are likely important drivers of the climate-mitigation potential of the temperate forests in the eastern United States. The differences in magnitude and direction of abiotic and biotic influences were not consistent among processes involved in biophysical and biogeochemical fluxes (AB and ET versus GPP, NPP, and SOC). This suggests that even processes behind a single kind of ecosystem-atmosphere flux may react differently to biotic and

environmental changes. We would also like to highlight how forest aboveground carbon, the current indicator for climate regulation services [Bonan, 2008; Jackson *et al.*, 2008], was not strongly related to any of the climate regulation processes considered for this region, for the 2000–2009 time period. The usefulness of any single proxy to monitor climate regulation services will thus be limited. For the climate change-mitigation treaties currently in place, any single proxy must be first validated to avoid suboptimal solutions [Bonan, 2008; Jackson *et al.*, 2008]. Even if treaties continue to focus only in biogeochemical fluxes [Jackson *et al.*, 2008], we need more robust models to monitor climate regulation processes: models that account for differences in the structure and age of biotic communities and for differences in the supply of water to ecosystems.

The heterogeneous patterns of model residuals suggest that the primary abiotic and biotic influences of climate regulation processes likely differ at different landscape-to-local spatial scales, in different areas of the region (Figure 4). Such differences in factors influencing climate regulation processes can result from the interplay of environmental limitations and human interferences. Different local processes or disturbances [Laurance, 2004; Field *et al.*, 2007] likely underlie part of the variance unaccounted for by our models and part of the differences in patterns of model residuals. Characterizing the local influence of, for example, disease outbreaks, historical land use, fragmentation, and other disturbances on climate regulation can help decrease our knowledge gap on the climate-mitigation potential of different forests, in different regions.

The influence of forest structure and successional stage, and temperature-precipitation interactions highlights the need to consider both biotic and abiotic factors in models of climate regulation and, likely, for other services too. For example, forest structure and successional stage likely influence pollination, biological control, and nutrient cycling by providing diverse habitats and substrates [Nilsson and Wardle, 2005]. New remote sensing technologies can improve the characterization of ecosystem attributes like structure, canopy, and leaf physical and chemical properties [Asner *et al.*, 2014; Detto *et al.*, 2015]. Remote sensing, in combination with forest inventory data, can help develop comprehensive data sets on forest structure, successional stage, and density and, hence, help explain patterns of ecosystem processes and services.

The characterization of how abiotic and biotic factors relate to climate regulation, and other ecosystem services, is crucial to increase our understanding of rates and patterns of provision and the impacts of ongoing global change. Our approach of evaluating the statistical relations of abiotic and biotic factors on the main ecosystem properties and processes involved in climate regulation services facilitates the separation of the (partly opposing) influences of functional traits, vegetation structure, succession stage, climate, and the environment. This approach can be useful to understand the underpinnings of other ecosystem services [e.g., Aguirre Gutiérrez *et al.*, 2015]. The characterization of the abiotic and biotic influences of climate regulation services, in other ecological regions and at different spatial and temporal scales, will improve our understanding of current patterns, the impacts of global change, and to formulate hypotheses on the ecological mechanisms behind provision. Ours, and further characterizations of how factors relate to climate regulation services, can help highlight the data need to support climate-mitigation treaties around the world.

Acknowledgments

The Netherlands Organization for Scientific Research (NWO) supported H. Serna-Chavez and M. Davidson (Innovational Research Incentives Scheme, VIDI, grant 276-20-017). N. Swenson was supported by NSF grant DBI-1262475. M. Weiser was supported by NSF grant EF-1065844. H. Serna Chavez thanks Lourens Veen for the help in collecting and processing satellite data. No author has competing interests. Code and data tables are available upon request to the corresponding author, Peter van Bodegom (p.m.van.bodegom@cml.leidenuniv.nl).

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