



Spatial scale dependence of factors driving climate regulation services in the Americas

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Abstract

Aim: A key hypothesis in macroecology is that the relative importance of factors driving ecological phenomena changes with spatial scale. However, studies on ecosystem services usually ignore this. Here, we test how the importance of factors related to climate regulation services varies with spatial extent (i.e., area of assessment) and how covariation among factors affects scale dependencies.

Location: The Americas.

Time period: Present.

Major taxa studied: Plants.

Methods: We combined a multi-model inference framework with variance partitioning to quantify the importance of factors that could potentially influence climate regulation services (i.e., albedo, evapotranspiration and primary productivity). We quantified abiotic (climate, soil, heterogeneity in soils/topography), biotic (open vegetation, forest area and biomass, plant functional traits) and anthropogenic (forest fragmentation, managed vegetation, non-vegetated surfaces) conditions and tested their importance in relation to climate regulation services at spatial extents ranging from 9×10^3 to 1×10^6 km².

Results: We found that the importance of abiotic factors in relation to climate regulation services increases with spatial extent. However, we found no evidence for a change from primarily biotically to abiotically driven climate regulation services with increasing spatial extent. All spatial extent dependencies were heavily influenced by covariation between abiotic, biotic and anthropogenic factors. After accounting for covariation, we found a primacy of abiotic factors as drivers of climate regulation services across spatial extents. Biotic and anthropogenic factors were less important than abiotic factors, and their independent effects were conserved across spatial extents.

Main conclusions: Our results show that the relative importance of abiotic factors related to climate regulation services depends on spatial extent. Biotic and anthropogenic factors are less important for climate regulation services than abiotic factors, and this hierarchy is scale invariant. Our findings suggest that spatial extent dependence needs to be quantified and assessed in climate-change mitigation projects that focus on ecosystem services.

KEYWORDS

albedo, climate regulation, ecosystem services, evapotranspiration, primary productivity, spatial scale

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1 | INTRODUCTION

The regulation of climate is the most overarching ecosystem service we obtain from nature. All ecosystems on Earth influence climate through exchanges of energy, water and greenhouse gases with the atmosphere. These ecosystem–atmosphere exchanges influence humidity and temperature at local and regional scales, and the concentration of greenhouse gases in the global atmosphere (Anderson-Teixeira et al., 2012). Albedo, evapotranspiration and primary productivity are the main ecosystem properties and processes behind the ecosystem–atmosphere exchanges regulating climate (Anderson-Teixeira et al., 2012; Pielke et al., 1998). The distinct rates and spatial patterns of climate regulation services are thus influenced by abiotic, biotic and anthropogenic factors that drive the underlying ecosystem properties and processes. However, how strongly these factors influence albedo, evapotranspiration and primary productivity at different spatial scales remains largely unexplored despite its importance for international policy targets (Perrings et al., 2010).

Two main features complicate simple answers to the question of how abiotic, biotic and anthropogenic factors influence climate regulation and other services: the spatial extent of assessment (i.e., the area of assessment; Wiens, 1989) and the covariation among different factors (Figure 1). Spatial extent dependency is the effect the area of assessment has on the strength of correlations between ecosystem processes and services and factors such as climate or vegetation. By influencing the magnitude and direction of the effects of driving factors, spatial extent alters how we perceive the mechanisms behind ecosystem processes and services (Figure 1a; Levin, 1992; McGill, 2010; Rahbek, 2005). A common hypothesis based on this spatial extent dependency is that abiotic factors are primarily related to ecological phenomena at spatial extents $> 10^5$ km², whereas biotic factors are more important at spatial extents $< 10^5$ km² (McGill, 2010; Wiens,

1989; see dashed rectangle in Figure 1a). For instance, vegetation–environment interactions, feedbacks within biotic communities and anthropogenic factors, such as habitat fragmentation, might affect ecosystem processes and functioning predominantly at fine spatial scales, such as plot and landscape scales (Laurance, 2004). In contrast, abiotic factors, such as climate, are known to influence ecosystem processes at broad spatial scales, such as North America or the Asian continent (Sitch et al., 2003). However, the consequences of these spatial extent dependencies on ecosystem service quantifications remain largely unexplored.

The second complicating feature influencing the characterization of spatial extent dependencies is that drivers such as abiotic, biotic and anthropogenic factors are not fully independent from each other (Figure 1b). For example, soil, climate, topography and other abiotic factors influence the development and functioning of vegetation (Beer et al., 2010; Reichstein, Papale, et al., 2007; Seddon, Macias-Fauria, Long, Benz, & Willis, 2016). This can result in spatial covariation among abiotic and biotic factors, such as vegetation biomass and climatic conditions (Seddon et al., 2016). Anthropogenic factors can directly affect the density and structure of vegetation (Laurance et al., 2011) and, consequently, have an impact on how ecosystems interact with the abiotic environment (Laurance, 2004). The importance of biotic factors in influencing climate regulation services may thus be confounded with those of abiotic or even anthropogenic factors. These interrelationships directly confound the effects and relative importance of factors driving ecosystem processes and properties, such as albedo, evapotranspiration and primary productivity, across spatial extents. A lack of quantitative evidence on the relative importance of these factors, independent of their covariation, hampers our ability to understand the mechanisms behind climate regulation and many other ecosystem services.

Here, we performed a rigorous quantification of the influence of abiotic, biotic and anthropogenic factors on climate regulation

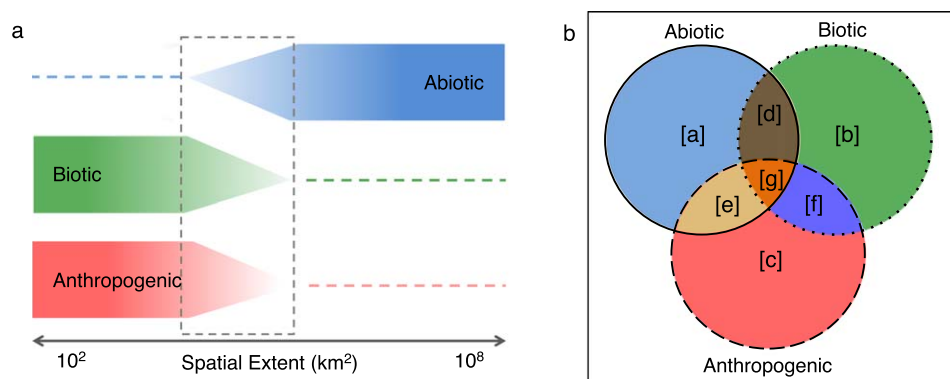


FIGURE 1 Spatial scale dependence and covariation among factors can influence climate regulation services. (a) The importance of abiotic (blue), biotic (green) and anthropogenic (red) factors might change with spatial extent (Levin, 1992), with biotic and anthropogenic factors being more important at the initial spatial extents in our test range and abiotic factors more important at larger spatial extents (McGill, 2010). The dashed rectangle delimits a 'transition zone' where the relative importance of factors decreases or increases. Examples of abiotic, biotic and anthropogenic factors are provided in Table 1. (b) Effects of abiotic, biotic and anthropogenic factors on climate regulation processes might not be fully independent of each other. The variance they explain in climate regulation processes can be partitioned into different fractions (adapted from Legendre & Legendre, 2012). The rectangle represents 100% of the variance in climate regulation processes. The fractions [a], [b] and [c] represent the variation independently explained by abiotic, biotic and anthropogenic factors, respectively. Fractions [d–g] represent the variance inextricably attributed to a combination of factors

TABLE 1 Potential factors driving climate regulation services in the Americas (SD = Standard deviation)

Key factor	Variables	Influence
Abiotic	<i>Climate</i>	Temperature and precipitation mean, range and seasonality determine energy and water availability
	Temperature annual range (°C)	
	Temperature of wettest quarter (°C)	
	Temperature of driest quarter (°C)	
	Precipitation of wettest month (mm)	
	Precipitation of driest month (mm)	
	Precipitation seasonality (coefficient of variation of monthly precipitation)	
	Precipitation of warmest quarter (mm)	
	Precipitation of coldest quarter (mm)	
	<i>Soil</i>	
	Soil pH (in H ₂ O)	
	Bulk density (kg/m ³)	
	Soil organic carbon (SOC; g/kg)	
	Sand content (%)	Variability in soil and topography influence microclimatic and macroclimatic conditions, vegetation and habitat structure
Clay content (%)		
<i>Heterogeneity in soil and topography</i>		
SD of soil pH		
Range of elevation		
SD of elevation		
Biotic	<i>Open vegetation</i>	Distribution of open vegetation types affects rates of climate regulation
	Herbaceous cover (%)	
	Shrub cover (%)	Forest ecosystems tend to have the highest rates of climate regulation and ecosystem processes
	<i>Forest area and biomass</i>	
	Closed-forest area (m ²)	
	Forest carbon density (ton/ha)	
	Tree canopy height (m)	Plant functional traits influence nutrient cycles, reflecting plant growth strategies and successional stages of vegetation
	<i>Plant functional traits</i>	
	Wood density (g/cm ³)	
	Maximum height (m)	
	Seed mass (mg)	
	Leaf nitrogen (%N)	
	Leaf phosphorous (%P)	
Specific leaf area (cm ² /g)		
Anthropogenic	<i>Forest fragmentation</i>	Forest fragmentation has impacts on vegetation distribution and biomass, microclimatic conditions, soil moisture etc.
	Edge area (m ²)	
	Core area (m ²)	
	CAI mean	
	CAI SD	
	Connectivity	
	Number of patches	The cover of managed vegetation reflects the extent of anthropogenic intervention and land use
	<i>Managed vegetation</i>	
	Managed vegetation cover (%)	
	<i>Non-vegetated surfaces</i>	
	Urban cover (%)	
Barren and sparsely vegetated cover (%)	The distribution of barren and urban land cover influences reflectance and microclimatic conditions	

Note. All factors represent spatial data at an equal-area projection and standardized at a continental scale (see Materials and Methods). All individual factors were standardized (mean = 1, standard deviation = 0). Forest fragmentation metrics were calculated at 100 m distance from the forest edge. CAI = core area index.

services by assessing both the spatial extent dependence and the covariation among factors. We focused our assessment on the Americas, where many climate change-mitigation projects are currently in place (<http://www.un-redd.org/>). We represent climate regulation services with albedo and evapotranspiration, net and gross primary productivity. These are the main ecosystem properties and processes providing the service (Anderson-Teixeira et al., 2012). Hereafter, we refer to albedo and evapotranspiration, net and gross primary productivity with the term 'climate regulation process'. As potential drivers, we considered variables representing abiotic, biotic and anthropogenic factors known to relate to climate regulation

processes (Table 1). We combined variance partitioning with a multi-model inference framework to quantify, at each spatial extent, the relative influence of abiotic, biotic and anthropogenic factors on climate regulation processes (Figure 1). We then assessed the covariation among abiotic, biotic and anthropogenic factors by partitioning the total explained variance of each climate regulation process into independent and inextricably shared fractions of abiotic, biotic and anthropogenic factors. We assessed these features of spatial extent dependence across 20 spatial extents ranging from 9×10^3 km² (about the area of Puerto Rico) to 1×10^6 km² (about the area of Colombia). This spatial extent range represents the areas of

assessment most commonly used for ecosystem service assessments (Martínez-Harms & Balvanera, 2012).

We hypothesized that (a) the relative influence of abiotic, biotic and anthropogenic factors will change idiosyncratically across spatial extents because different constraints exist for each climate regulation process [i.e., albedo and surface roughness (Hollinger et al., 2010); evapotranspiration and water supply availability (Mao et al., 2015); and productivity, climate and soil (Seddon et al., 2016)]. Furthermore, we expected that (b) biotic factors influence all climate regulation processes more strongly at spatial extents $< 10^5$ km² because of the local influence of vegetation on surface roughness and resource allocation. For covariation among factors, we expected that (c) the overlap between the biotic and the abiotic influences on the climate regulation process will increase with spatial extent because of the strong correspondence between climatic factors and vegetation density at broad spatial scales (Beer et al., 2010; Seddon et al., 2016).

2 | MATERIALS AND METHODS

2.1 | Data on climate regulation processes

We used data from the Moderate Resolution Imaging Spectroradiometer (MODIS) to represent climate regulation processes: albedo, evapotranspiration, and gross and net primary productivity. We averaged 16-day 1-km² data on black-sky, shortwave albedo to represent land-surface albedo (as a fraction, with no units; Moody, King, Platnick, Schaaf, & Gao, 2005). Black-sky shortwave albedo is a more robust representation of genuine (blue-sky) albedo than white-sky albedo or the average of black- and white-sky albedo estimates (Liu et al., 2009). To represent ecosystem-atmosphere exchanges of water, we used evapotranspiration (ET) and averaged annual evapotranspiration data (in millimetres per year; Mu, Zhao, & Running, 2011). To represent carbon-sequestration potential and, indirectly, respiration, we used MODIS data at 1 km² resolution for both gross primary productivity (GPP) and net primary productivity (NPP) (both in grams of Carbon per square metre; Zhao, Heinsch, Nemani, & Running, 2005). For all analyses, we calculated average estimates of albedo, ET, GPP and NPP for the 2000–2005 period.

2.2 | Factors driving climate regulation processes

To represent abiotic factors, we included 16 variables related to climate, soil and the heterogeneity of soil and topographic conditions (Table 1). Using contemporary global climate normals (1950–2000; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), we calculated eight bioclimatic variables that represent temperature annual range, precipitation and temperature seasonality, and maximum as well as limiting climatic conditions (for details, see Table 1). To deal with strong collinearity among climatic variables, we considered only those with a variance inflation factor < 10 (Dormann et al., 2013).

To represent soil conditions, we included five variables (Table 1), representing the average physical and chemical soil properties in the first metre depth (Hengl et al., 2014): pH (in H₂O), bulk density (in

kilograms per square metre), soil organic carbon (SOC; in grams per kilogram), sand and clay content (expressed as a percentage). To represent heterogeneity in soil and topography, we included three variables (Table 1), namely the standard deviation (SD) of soil pH, the SD of elevation, and the range of elevation (elevation product from Hijmans et al., 2005). The SD of soil pH and SD of elevation were calculated at 100 km² equal-area grid cells resolution using the original 1 km² resolution.

Biotic factors were represented by 11 variables related to open vegetation cover, forest area and biomass, and plant functional traits (Table 1). Open vegetation was represented by herbaceous and shrubland vegetation cover (0–100%) in order to account for changes in surface roughness caused by the densities of different open vegetation types. Herbaceous and shrubland data were obtained from a consensus land-cover gridded product at 1 km² resolution (year 2005; Tuanmu & Jetz, 2014). For forest area and biomass, we included three different variables: closed-forest area, carbon density and tree canopy height (see Table 1). We used 30-m grid-cell resolution tree cover data for the year 2000 (Hansen et al., 2013) to estimate the area of closed forest (in square metres). We defined closed forest as tree cover $\geq 40\%$ and > 0.5 ha in area (Shvidenko, Barber, & Persson, 2005). To approximate the distribution of vegetation biomass, we used data on live above- and belowground carbon density for the year 2000 at 1 km² resolution (in tonnes per hectare; Ruesch & Gibbs, 2008). To approximate forest biomass and structure, we also included data on tree canopy height for the year 2000 at 1 km² (Simard, Pinto, Fisher, & Baccini, 2011). We acknowledge that data on tree canopy height might not entirely reflect biotic factors because it is also related to climatic zones (Zhang, Nielsen, Mao, Chen, & Svenning, 2016) and to semi-natural and agricultural land uses. Data on herbaceous and shrubland cover, forest cover, biomass and canopy height were aggregated from the original 1 km² resolution to 100 km² equal-area grid cells.

We included data on six functional traits of woody plant species: leaf nitrogen [mass percentage of nitrogen (%N)], leaf phosphorus [mass percentage of phosphorus (%P)], specific leaf area (leaf area divided by dry leaf mass; in square centimetres per gram), wood density (in grams per cubic centimetre), maximum height (in metres) and seed mass (in milligrams). These functional traits represent reproductive strategies, growth rates, dominance and structural diversity (Chave et al., 2009; Douma, de Haan, Aerts, Witte, & van Bodegom, 2012; Moles et al., 2009; Reich, Walters, & Ellsworth, 1997). Georeferenced occurrences of woody plant species were obtained from Salvias, the reference centre of environmental information (CRIA, *Centro de Referência em Informação Ambiental*, CRIA, <http://www.cria.org.br/>, accessed in 2009), the Missouri Botanical Garden and New York Botanical Garden, and the Forest Inventory and Analysis National Program database. Occurrences (presence records) of woody plant species were binned into 100 km² equal-area grid cells. For each grid cell, the list of species present was joined to the corresponding matrix of species trait values. Functional trait values were obtained from Swenson and Weiser (2010), Swenson et al. (2011, 2012) and from field collections in the eastern U.S.A. by N.G. Swenson, Y. Iida, A. Wolf and J. Yang. Species and trait data were checked for errors using the

taxonscrubber software (Synthesis and Analysis of Local Vegetation Inventories Across Scales, SALVIAS, Taxon Scrubber 2.0., www.salvias.net/pages/taxonscrubber.html). For all six functional traits, we calculated the mean value across species in each grid cell. We equally weighted the trait values of all species because harmonized species abundance information at continental scales is missing.

To represent anthropogenic factors, we included nine variables related to forest fragmentation, managed vegetation and non-vegetated surfaces variables (Table 1). To calculate variables related to forest fragmentation we considered only closed forests ($\geq 40\%$ in tree cover and > 0.5 ha in area). Closed forests are important storages and sinks of greenhouse gases, and their loss and degradation entail great disruptions in the water–energy balance and emissions of greenhouse gases (Anderson-Teixeira et al., 2012; Laurance, 2004). Using closed-forest cover data, we calculated forest fragmentation variables to represent edge and core areas, core area index, connectivity and the number of forest patches (Table 1). A forest patch was defined here as a spatially contiguous stretch of closed-forest cover (see Supporting Information Appendix S1). To estimate edge and core areas (in square metres), we considered only a distance of 100 m from the forest edge. This is a distance interval at which $> 50\%$ of the documented deleterious edge effects have been found (Broadbent, Asner, Keller, & Knapp, 2008). We also estimated the mean and *SD* of the core area index (CAI) considering 100 m from the forest edge (CAI mean and CAI *SD*, expressed as a percentage). The CAI is the ratio of core area to total area of a patch (Supporting Information Appendix S1). We estimated connectivity between closed-forest patches as the probability that two randomly chosen points in the forest patches of a grid cell are connected (Supporting Information Appendix S1). All forest fragmentation variables represent the year 2000 and were aggregated from 30 m² to a 100 km² equal-area grid-cell resolution, calculating the average of values. Additionally, we represented the percentage of cover of managed vegetation using data on the cover of managed and cultivated vegetation (expressed as a percentage; Tuanmu & Jetz, 2014). Finally, for simplicity, we grouped urban, barren and sparsely vegetated land cover (expressed as a percentage; Tuanmu & Jetz, 2014) at 1 km² grid-cell resolution under a 'non-vegetated surfaces' category.

2.3 | Data processing and spatial extent sampling

All input data span the years 2000–2005. All raster data were projected to a Lambert azimuthal coordinate system and then aggregated into 100 km² equal-area grid cells by calculating the mean values of all pixels with their original resolution (mostly 1 km²). All variables described in the previous section were then standardized for the statistical analyses (mean = 0, *SD* = 1; Supporting Information Appendix S2, Table S2.1). Albedo, ET, GPP and NPP were left untransformed. Raster data were processed in QGIS version 2.8.2-Wien and ArcGIS version 10.1 software (ESRI, Redlands, CA, U.S.A.).

To explore how spatial extent influences the relative importance of abiotic, biotic and anthropogenic factors, we considered 20 area extents from 9×10^3 to 1×10^6 km². This range spans from 'local' to 'regional' spatial extents, which are commonly used scales in ecosystem

service assessments (Martínez-Harms & Balvanera, 2012). The specific extents were defined using logarithmic intervals (that is, 9×10^3 , 12×10^3 , 15×10^3 km², and so on; see Supporting Information Appendix S3), and a total of 1,000 random samples were generated for each of the 20 extents. To generate spatial extent samples, we adapted the spreading-dye algorithm as presented and described by Wang, Rahbek, and Fang (2012). The algorithm: (a) randomly chooses a grid cell on land as a starting point; (b) expands the sample by randomly selecting a new grid cell from the surrounding grid cells; and (c) continues this sampling until the desired spatial extent size is obtained (see also Supporting Information Appendix S3). Owing to the sparse availability of functional trait data (Figure 2b), we set a minimum number of 30 trait observations per spatial extent sample. This decision ensured that sufficient data for each plant functional trait variable were available for the analyses, although it reduced within-biomes representation (Figure 2a). In trials of the sampling algorithm, the selection of the starting grid cell was done using geographically stratified random sampling rather than uniform random sampling. This, however, did not expand on the eco-region representation of our samples (compared with Figure 2a) because of the constraint of the minimum number of trait observations. Nonetheless, our spatial extent samples do cover the main eco-regions in the Americas (Figure 2a).

2.4 | Variance partitioning analyses

To assess the spatial extent dependence and the role of covariation among factors, we used the approach from Legendre and Legendre (2012) and partitioned the variance in climate regulation processes as explained by abiotic, biotic and anthropogenic variables. To deal with collinearity among predictor variables (that is, variables used to fit regression models), we first eliminated individual variables with potentially spurious correlations by fitting bivariate linear regression models between response and predictor variables and discarding those predictor variables with $R^2 \leq 0.05$ (Murray & Conner, 2009). With the remaining predictor variables, we fitted multi-predictor regression models and calculated variance inflation factors (VIFs) to assess collinearity among predictor variables. Discarding collinear predictor variables was an iterative process. At each iteration, we discarded the predictor variable with the highest VIF. This was repeated until all predictor variables met the $VIF < 10$ threshold (Dormann et al., 2013). We then fitted multi-predictor models testing all combinations with one up to five predictor variables and selected those models that had the 5% highest adjusted R^2 (R^2_{adj}) values. This model selection was conducted for abiotic, biotic and anthropogenic variables separately. Variance partitioning analyses were performed using the best 5% abiotic, biotic and anthropogenic models. For simplicity, we refer below to the best 5% models simply as 'models'. The total variance explained by the predictor variables was partitioned for each response variable into independent and inextricably shared fractions, following Legendre and Legendre (2012).

We used the abiotic, biotic and anthropogenic models with highest R^2_{adj} in each sample to evaluate spatial autocorrelation in model residuals. We evaluated spatial autocorrelation using spatial correlograms of Moran's *I* statistics as constructed by the *ncf* library (Bjørnstad, 2013)

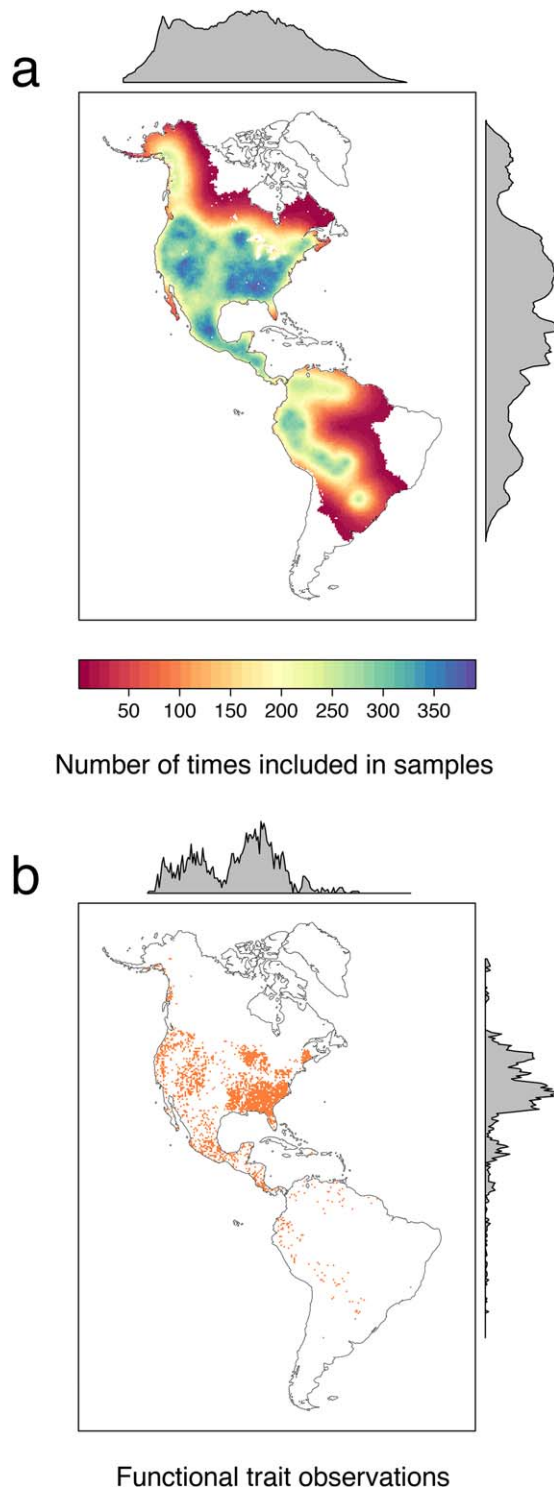


FIGURE 2 Sampling of spatial extent in the Americas. (a) Composite of the total number of times a 100-km² equal-area grid cell was sampled for analysis. Grey areas at the top and right side show the sum of all pixels per latitudinal or longitudinal row/column. (b) Across the Americas, functional trait data for woody plant species are still sparse. To assess and contrast the effects of functional traits in biotic models, the sampling of spatial extents was constrained to include a minimum of 30 trait observations per sample. Samples included in the analyses fall into the majority of eco-regions (see also Supporting Information Appendix S3), but most data are available from North America. Grey areas at the top and right side represent the number of pixels with functional trait data in that latitudinal or longitudinal row/column. The functional trait variables are provided in Table 1. Both panels are in Lambert azimuth equal-area projection

find any systematic bias in the performance of our models explained owing to the increased predictor variance (Supporting Information Appendix S5).

3 | RESULTS

3.1 | Spatial extent dependence of factors driving climate regulation processes

Supporting our first hypothesis, we found that the relative importance of abiotic, biotic and anthropogenic factors related to climate regulation services changes across spatial extents (Figure 3). For albedo, the importance of all three types of factors decreased with spatial extent (Figure 3). In contrast, for ET, GPP and NPP the importance of abiotic and biotic factors increased with spatial extent, whereas anthropogenic factors tended to decrease or remained constant (Figure 3).

Regarding our second hypothesis, we found little evidence that the primacy of abiotic, biotic and anthropogenic factors related to climate regulation processes changes as spatial extent increases (Figure 3). For ET, GPP and NPP, there was a conserved primacy of abiotic factors with increasing spatial extent (Figure 3), with abiotic factors being more important than biotic and anthropogenic factors. For NPP, the primacy of abiotic factors became even more pronounced with increasing spatial extent (i.e., the importance of abiotic factors increased, whereas that of biotic and anthropogenic factors remained relatively constant; Figure 3). For albedo, the influence of anthropogenic factors and biotic factors tended to overlap across spatial extents.

Analyses of spatial autocorrelation in model residuals showed that biotic factors tended to account better for small-scale spatial variation in climate regulation than abiotic or anthropogenic factors (Supporting Information Appendix S4). At larger distance classes (> 1,000 km), abiotic factors accounted well for the large-scale spatial variation in climate regulation. In contrast, biotic and anthropogenic factors showed negative autocorrelation at large distance classes (Supporting Information Appendix S4), indicating that they alone are insufficient to account for spatial variation in climate regulation processes.

for R statistical software version 3.1.2 (R Development Core Team, 2014). Overall, there were only small deviations from zero in the Moran's *I* of residuals of each climate regulation process across spatial extent samples (Supporting Information Appendix S4). Finally, we also tested for any potential biases introduced into our analyses by the increase in predictor variance captured by samples of increasing spatial extent area (Supporting Information Appendix S5). We did not

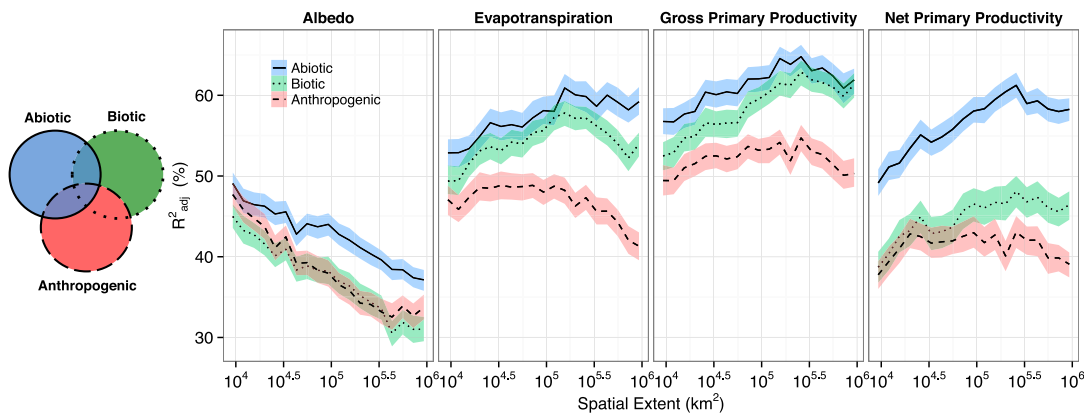


FIGURE 3 Influence of spatial extent on the importance of abiotic, biotic and anthropogenic factors related to climate regulation processes (albedo, evapotranspiration, gross primary productivity and net primary productivity). The importance of abiotic, biotic and anthropogenic factors is quantified here with the percentage of explained variance (R^2_{adj}) in multi-predictor regression models containing the best set of variables for each of these three factors (see Materials and Methods for details). The lines indicate the mean trend across spatial extents. Shaded areas represent the 95% confidence interval

3.2 | Covariation between factors confounds spatial extent dependencies

The results presented above (Figure 3) include fractions of variance in climate regulation explained independently and fractions shared inextricably among factors. This is partly in line with our third expectation; the covariation between factors was a big part of the spatial extent dependence of our models. After partitioning the variance explained by

our models, we found that the independent fractions (see [a] to [c] in Figure 1b) were in all cases $R^2_{adj} < 20\%$ (Figure 4a). This independently explained amount of variance was much smaller than the ‘full influence’ of abiotic, biotic and anthropogenic factors, which ranged from 40 to 70% (see R^2_{adj} in Figure 3). The fraction shared by abiotic and biotic factors showed a moderate increase with spatial extent ([d] in Figure 4b). The shared fraction [g] (i.e., the variation inextricably shared among

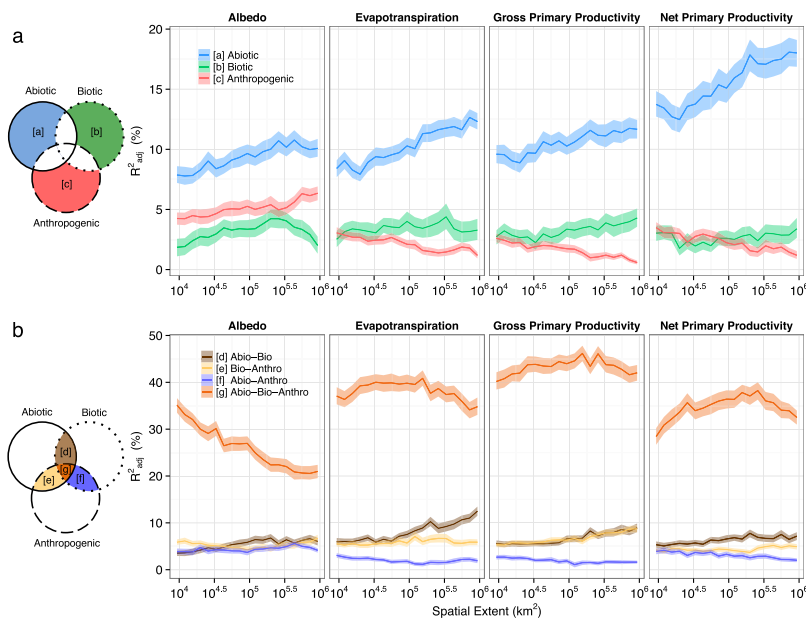


FIGURE 4 Variation in climate regulation services attributed to independent and shared effects of abiotic, biotic and anthropogenic factors. (a) Panels show the amount of variation in climate regulation processes (separately for albedo, evapotranspiration, gross primary productivity and net primary productivity, respectively) that is independently attributed to abiotic, biotic and anthropogenic factors. (b) Variation in climate regulation processes inextricably shared between abiotic, biotic and anthropogenic factors. In all panels, the percentage of explained variance (R^2_{adj} ; %) is derived from multi-predictor regression models after all other independent fractions have been subtracted. The lines indicate the mean trend across spatial extents. Shaded areas represent the 95% confidence interval. The diagrams on the left side illustrate which fractions of variation are quantified using variance partitioning analyses (adapted from Legendre & Legendre, 2012)

abiotic, biotic and anthropogenic factors) represented the largest portion of the overall explained variance ($R_{adj}^2 = 20\text{--}45\%$; Figure 4b). Hence, a large portion of explained variance cannot be attributed solely to abiotic, biotic or anthropogenic factors.

Some of the trends in spatial extent dependencies remained the same after removing the covariation among abiotic, biotic and anthropogenic factors, but others changed (Figure 4a). For instance, the independent fraction explained by abiotic factors increased with spatial extent for all four climate regulation processes ([a] in Figure 4a), confirming the spatial extent dependence for ET, GPP and NPP, but reversing the trend for albedo (compare Figures 3 and 4a). In contrast, the independent fractions of biotic and anthropogenic factors showed conserved changes with spatial extent ([b] and [c] in Figure 4a). Overall, the results of variance partitioning confirmed the conserved primacy of abiotic factors in relating to climate regulation processes from spatial extents 9×10^3 to 1×10^6 km² (Figure 4a), albeit with much lower explanatory power compared with the total explained variance (compare Figures 3 and 4a).

4 | DISCUSSION

Our study quantifies the spatial extent dependence of factors related to climate regulation services across the Americas. To our knowledge, this is the first assessment of spatial scale dependencies of climate regulation services that explicitly takes into account the overlap in correlations between dominant factors. We used spatial extents from 9×10^3 to 1×10^6 km², from 'local' to 'regional', covering the most commonly used scales in ecosystem service assessments (Martínez-Harms & Balvanera, 2012). Our results show how the explained variance by abiotic, biotic and anthropogenic factors related to albedo, evapotranspiration and primary productivity depends on the spatial extent of assessment and how covariation among factors influences such dependencies. However, our expectation that biotic factors are more important than abiotic factors at spatial extents closer to the 'local' (9×10^3 km²) end of our test range was not supported (Figures 3 and 4). Our study is limited by the range of spatial extents tested and by the sparse availability of functional trait data. We cannot assert whether this shift from biotically driven to abiotically driven happens at spatial extents $< 9 \times 10^3$ km². Even so, our results demonstrate that covariation and spatial extent dependence both play a crucial role for assessing how climate, soils, vegetation, forest fragmentation and anthropogenic land use influence climate regulation services.

The spatial extent of assessment has been a central problem in ecology for decades (Levin, 1992). Although spatial extent dependencies have been studied quantitatively for ecological phenomena such as species distributions (McGill, 2010) and large-scale species-richness patterns (Rahbek, 2005), similar quantitative work on ecosystem services is only now emerging (e.g., Lindborg et al., 2017). We performed a spatial extent assessment for climate regulation services and showed that the variance explained by abiotic, biotic and anthropogenic factors often changed with the area of

assessment (Figures 3 and 4). Nevertheless, abiotic factors representing climate, soils and topographic heterogeneity were always the most prominent factors related to albedo, evapotranspiration and primary productivity (see also Supporting Information Appendix S6). This was independent of the spatial extent of assessment. This suggests a dominant role of water and energy availability in addition to nutrient supply in climate regulation processes, such as primary productivity (Beer et al., 2010; Nemani et al., 2003; Reichstein, Ciais, et al., 2007) and evapotranspiration (Jung et al., 2010), and supports the idea that climatic changes, such as global warming and the intensification of the hydrological cycle, will have major consequences for this global ecosystem service. Moreover, given the large fraction of variance shared by the three groups of factors (Figure 4b), our results suggest that biotic and anthropogenic factors might play an important role in combination with abiotic factors. Changes in land use and terrestrial ecosystems can thus strongly affect climate regulation services (Anderson-Teixeira et al., 2012).

Given that the variability and heterogeneity of driving factors change with spatial scale, we also expected a change in the importance of factors related to climate regulation processes, from primarily biotic to primarily abiotic controls as spatial extent increases. Our results did not support such a change for climate regulation processes in the Americas (Figures 3 and 4a): abiotic factors always had the greatest influence on climate regulation services, whereas biotic and anthropogenic factors were always less important. This was contrary of expectations given studies that have provided evidence that biotic factors are strongly related to climate regulation processes at regional extents (e.g., Ruiz-Benito et al., 2014; Serna-Chavez et al., 2017). Nonetheless, we cannot discard that this shift in the primary factors related to climate regulation, in particular, from biotic to abiotic, occurs at spatial extents $< 9 \times 10^3$ km², outside the range we tested. More data at a continental scale, in particular for plant functional traits and vegetation structure, is needed to test this feature systematically in the spatial extent dependencies of climate regulation processes. Furthermore, our results suggest a prevalence of biotic factors over anthropogenic factors, which was conserved across spatial extents in almost all cases (Figures 3 and 4a). For the range of tested spatial extents (9×10^3 to 1×10^6 km²), our results suggest that the relative importance of abiotic, biotic and anthropogenic factors related to albedo, evapotranspiration and primary productivity is relatively scale invariant. Our results provide a first step for the ranking of these factors in terms of their relative importance, and this seems to be rather independent of spatial extent.

A key insight gained after applying the variance partitioning approach from Legendre and Legendre (2012) is that spatial extent dependencies are influenced by the covariation among factors (compare Figures 3 and 4). Although the primacy of abiotic, biotic and anthropogenic factors was often conserved across spatial extents, the explained variance of the independent effects was much smaller ($R_{adj}^2 < 20\%$) than the full influence including covariation with other factors ($R_{adj}^2 = 40\text{--}70\%$). As expected, the variance shared between abiotic and biotic factors did show a slight increase with spatial extent. This is in accordance with existing evidence on the relationship between

climatic factors and vegetation (Beer et al., 2010; Reichstein, Papale, et al., 2007). Moreover, a surprising result is the large proportion of explained variance inextricably shared between all three factors (abiotic, biotic and anthropogenic): $R_{adj}^2 = 20\text{--}45\%$. This share in explained variance attributable to covariation is perhaps expected because of the complex interdependence of factors influencing climate regulation processes. For example, climatic changes such as droughts are known to affect soil moisture and the supply of nutrients to vegetation, thereby impacting vegetation growth, maintenance, reproduction and functional composition (Reichstein, Ciais, et al., 2007; Vicca et al., 2012). Likewise, changes in plant communities from alien invasions or anthropogenic fragmentation can also affect soil conditions and how vegetation interacts with the environment (Briant, Gond, & Laurance, 2010; Chaplin-Kramer et al., 2015; Laurance, 2004). Achieving a deeper understanding of these complex interdependences is fundamental for assessing how abiotic, biotic and anthropogenic factors shape climate regulation or other ecosystem services.

With the increasing application of climate regulation services in international policy targets and society's conservation goals (Perrings et al., 2010), there is an urgent need for better understanding of the spatial scale dependence of the factors influencing the patterns of ecosystem service provision. Our methodological approach offers a quantitative framework for assessing spatial extent dependence and covariation among abiotic, biotic and anthropogenic factors. From our assessment, it is apparent that disregarding the influence of spatial scale can affect the interpretation of the potential underlying mechanisms. However, it also shows that some patterns (e.g., the primacy of abiotic over biotic and anthropogenic factors) are consistent across spatial extents, suggesting that scale-invariant likely mechanisms operate for some climate regulation processes. Our results also show that the different climate regulation processes may have a different spatial extent dependence (for example, albedo deviates from evapotranspiration and productivity), and thus that one cannot rely on a single all-scale, all-purpose monitoring proxy (McAlpine et al., 2010). Further characterization of spatial scale dependencies in other regions, with a comprehensive eco-region representation, will help to guide international policy efforts by deepening our understanding of ecosystem service supply.

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DATA ACCESSIBILITY

All spatial extent samples are available as data tables upon request to Hector Serna Chavez [hmserna@gmail.com]. The algorithm used

for spatial extent sampling can be found in Supporting Information Appendix S3.

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REFERENCES

- Anderson-Teixeira, K. J., Snyder, P. K., Twine, T. E., Cuadra, S. V., Costa, M. H., & Delucia, E. H. (2012). Climate-regulation services of natural and agricultural ecoregions of the Americas. *Nature Climate Change*, 2, 177–181.
- Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., ... Papale, D. (2010). Terrestrial gross carbon dioxide uptake: Global distribution and covariation with climate. *Science*, 329, 834–838.
- Bjornstad, O. N. (2013). Package "ncf": Spatial nonparametric covariance functions (R package version 1.1–5). Retrieved from <https://cran.r-project.org/web/packages/ncf/index.html>
- Briant, G., Gond, V., & Laurance, S. G. W. (2010). Habitat fragmentation and the desiccation of forest canopies: A case study from eastern Amazonia. *Biological Conservation*, 143, 2763–2769.
- Broadbent, E. N., Asner, G. P., Keller, M., & Knapp, D. E. (2008). Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. *Biological Conservation*, 141, 1745–1757.
- Chaplin-Kramer, R., Ramler, I., Sharp, R., Haddad, N. M., Gerber, J. S., West, P. C., ... King, H. (2015). Degradation in carbon stocks near tropical forest edges. *Nature Communications*, 6, 10158.
- Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Zanne, A. E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters*, 12, 351–366.
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., ... Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36, 27–46.
- Douma, J. C., de Haan, M. W. A., Aerts, R., Witte, J.-P. M., & van Bodegom, P. M. (2012). Succession-induced trait shifts across a wide range of NW European ecosystems are driven by light and modulated by initial abiotic conditions. *Journal of Ecology*, 100, 366–380.
- Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., ... Townshend, J. R. G. (2013). High-resolution global maps of 21st-century forest cover change. *Science*, 342, 850–853.
- Hengl, T., de Jesus, J. M., MacMillan, R. A., Batjes, N. H., Heuvelink, G. B. M., Ribeiro, E., ... Gonzalez, M. R. (2014). SoilGrids1km – Global soil information based on automated mapping. *PLoS One*, 9, e105992.
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25, 1965–1978.
- Hollinger, D. Y., Ollinger, S. V., Richardson, A. D., Meyers, T. P., Dail, D. B., Martin, M. E., ... Verma, S. B. (2010). Albedo estimates for land surface models and support for a new paradigm based on foliage nitrogen concentration. *Global Change Biology*, 16, 696–710.
- Jung, M., Reichstein, M., Ciais, P., Seneviratne, S. I., Sheffield, J., Goulden, M. L., ... Zhang, K. (2010). Recent decline in the global land evapotranspiration trend due to limited moisture supply. *Nature*, 467, 951–954.

- Laurance, W. F. (2004). Forest-climate interactions in fragmented tropical landscapes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 359, 345–352.
- Laurance, W. F., Camargo, J., Luizao, R., Laurance, S. G., Pimm, S., Bruna, E. M., ... Lovejoy, T. E. (2011). The fate of Amazonian forest fragments: A 32-year investigation. *Biological Conservation*, 144, 56–67.
- Legendre, P., & Legendre, L. F. (2012). *Numerical ecology*. Amsterdam, The Netherlands: Elsevier.
- Levin, S. (1992). The problem of pattern and scale in ecology. *Ecology*, 73, 1943–1967.
- Lindborg, R., Gordon, L. J., Malinga, R., Bengtsson, J., Peterson, G., Bommarco, R., ... Smith, H. G. (2017). How spatial scale shapes the generation and management of multiple ecosystem services. *Ecosphere*, 8, e01741.
- Liu, J., Schaaf, C., Strahler, A., Jiao, Z., Shuai, Y., Zhang, Q., ... Dutton, E. G. (2009). Validation of Moderate Resolution Imaging Spectroradiometer (MODIS) albedo retrieval algorithm: Dependence of albedo on solar zenith angle. *Journal of Geophysical Research*, 114, D01106.
- Mao, J., Fu, W., Shi, X., Ricciuto, D. M., Fisher, J. B., Dickinson, R. E., ... Zhu, Z. (2015). Disentangling climatic and anthropogenic controls on global terrestrial evapotranspiration trends. *Environmental Research Letters*, 10, 094008.
- Martínez-Harms, M. J., & Balvanera, P. (2012). Methods for mapping ecosystem service supply: A review. *International Journal of Biodiversity Science, Ecosystem Services and Management*, 8, 17–25.
- McAlpine, C., Ryan, J., Seabrook, L., Thomas, S., Dargusch, P., Syktus, J., ... Laurance, W. (2010). More than CO₂: A broader paradigm for managing climate change and variability to avoid ecosystem collapse. *Current Opinion in Environmental Sustainability*, 2, 334–346.
- McGill, B. J. (2010). Matters of scale. *Science*, 328, 575–576.
- Moles, A. T., Warton, D. I., Warman, L., Swenson, N. G., Laffan, S. W., Zanne, A. E., ... Leishman, M. R. (2009). Global patterns in plant height. *Journal of Ecology*, 97, 923–932.
- Moody, E. G., King, M. D., Platnick, S., Schaaf, C. B., & Gao, F. (2005). Spatially complete global spectral surface albedos: Value-added datasets derived from Terra MODIS land products. *IEEE Transactions on Geoscience and Remote Sensing*, 43, 144–158.
- Mu, Q., Zhao, M., & Running, S. W. (2011). Improvements to a MODIS global terrestrial evapotranspiration algorithm. *Remote Sensing of Environment*, 115, 1781–1800.
- Murray, K., & Conner, M. M. (2009). Methods to quantify variable importance: Implications for the analysis of noisy ecological data. *Ecology*, 90, 348–355.
- Nemani, R. R., Keeling, C. D., Hashimoto, H., Jolly, W. M., Piper, S. C., Tucker, C. J., ... Running, S. W. (2003). Climate-driven increases in global terrestrial net primary production from 1982 to 1999. *Science*, 300, 1560–1563.
- Perrings, C., Naeem, S., Ahrestani, F., Bunker, D. E., Burkill, P., Canziani, G., ... Weisser, W. (2010). Ecosystem services for 2020. *Science*, 330, 323–324.
- Pielke, R., Avissar, R., Raupach, M., Dolman, A., Zeng, X., & Denning, A. (1998). Interactions between the atmosphere and terrestrial ecosystems: Influence on weather and climate. *Global Change Biology*, 4, 461–475.
- R Development Core Team. (2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <http://www.R-project.org/>
- Rahbek, C. (2005). The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, 8, 224–239.
- Reich, P. B., Walters, M. B., & Ellsworth, D. S. (1997). From tropics to tundra: Global convergence in plant functioning. *Proceedings of the National Academy of Sciences USA*, 94, 13730–13734.
- Reichstein, M., Ciais, P., Papale, D., Valentini, R., Running, S., Viovy, N., ... Zhao, M. (2007). Reduction of ecosystem productivity and respiration during the European summer 2003 climate anomaly: A joint flux tower, remote sensing and modelling analysis. *Global Change Biology*, 13, 634–651.
- Reichstein, M., Papale, D., Valentini, R., Aubinet, M., Bernhofer, C., Knohl, A., ... Seufert, G. (2007). Determinants of terrestrial ecosystem carbon balance inferred from European eddy covariance flux sites. *Geophysical Research Letters*, 34, L01402, doi: 10.1029/2006GL027880.
- Ruesch, A., & Gibbs, H. K. (2008). *New IPCC tier-1 global biomass carbon map for the year 2000*. Oak Ridge, TN: Oak Ridge National Laboratory, Carbon Dioxide Information Analysis Center. Retrieved from <http://cdiac.ornl.gov>
- Ruiz-Benito, P., Gómez Aparicio, L., Paquette, A., Messier, C., Kattge, J., & Zavala, M. A. (2014). Diversity increases carbon storage and tree productivity in Spanish forests. *Global Ecology and Biogeography*, 23, 311–322.
- Seddon, A. W. R., Macias-Fauria, M., Long, P. R., Benz, D., & Willis, K. J. (2016). Sensitivity of global terrestrial ecosystems to climate variability. *Nature*, 531, 229–232.
- 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, 787–803.
- Shvidenko, A., Barber, C. V., & Persson, R. (2005). Forest and woodland systems. In H. Rashid, R. Scholes, & N. Ash (Eds.), *Ecosystems and human well-being: Current state and trends* (pp. 587–621). Washington, DC: Island Press.
- Simard, M., Pinto, N., Fisher, J. B., & Baccini, A. (2011). Mapping forest canopy height globally with spaceborne lidar. *Journal of Geophysical Research*, 116, G04021.
- Sitch, S., Smith, B., Prentice, I., Arneth, A., Bondeau, A., Cramer, W., ... Venevsky, S. (2003). Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology*, 9, 161–185.
- Swenson, N. G., & Weiser, M. D. (2010). Plant geography upon the basis of functional traits: An example from eastern North American trees. *Ecology*, 91, 2234–2241.
- Swenson, N. G., Enquist, B. J., Pither, J., Kerkhoff, A. J., Boyle, B., Weiser, M. D., ... Nolting, K. M. (2011). The biogeography and filtering of woody plant functional diversity in North and South America. *Global Ecology and Biogeography*, 21, 798–808.
- Swenson, N. G., Erickson, D. L., Mi, X., Bourg, N. A., Forero-Montaña, J., Ge, X., ... Kress, W. J. (2012). Phylogenetic and functional alpha and beta diversity in temperate and tropical tree communities. *Ecology*, 93, S112–S125.
- Tuanmu, M. N., & Jetz, W. (2014). A global 1-km consensus land-cover product for biodiversity and ecosystem modelling. *Global Ecology and Biogeography*, 23, 1031–1045.
- Vicca, S., Luysaert, S., Peñuelas, J., Campioli, M., Chapin, F. S., Ciais, P., ... Janssens, I. A. (2012). Fertile forests produce biomass more efficiently. *Ecology Letters*, 15, 520–526.
- Wang, Z., Rahbek, C., & Fang, J. (2012). Effects of geographical extent on the determinants of woody plant diversity. *Ecography*, 35, 1160–1167.
- Wiens, J. A. (1989). Spatial scaling in ecology. *Functional Ecology*, 3, 385–397.
- Zhang, J., Nielsen, S. E., Mao, L., Chen, S., & Svenning, J.-C. (2016). Regional and historical factors supplement current climate in shaping global forest canopy height. *Journal of Ecology*, 104, 469–478.

Zhao, M. S., Heinsch, F. A., Nemani, R. R., & Running, S. W. (2005). Improvements of the MODIS terrestrial gross and net primary production global data set. *Remote Sensing of Environment*, 95, 164–176.

BIOSKETCH

The author team is broadly interested in understanding the distribution of life on Earth and how humans benefit from services provided by ecosystems. The authors have specific expertise in macro- and community ecology, functional ecology, biogeography, environmental sciences, ecoinformatics, physical geography and geospatial analyses.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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