













The relationship of woody plant size and leaf nutrient content to large-scale productivity for forests across the Americas

Irena Šímová^{1,2}  | Brody Sandel³  | Brian J. Enquist^{4,5}  | Sean T. Michaletz^{4,6}  |
Jens Kattge^{7,8} | Cyrille Violle⁹  | Brian J. McGill¹⁰ | Benjamin Blonder^{11,12}  |
Kristine Engemann^{13,14}  | Robert K. Peet¹⁵  | Susan K. Wiser¹⁶  |
Naia Morueta-Holme¹⁷  | Brad Boyle^{4,18}  | Nathan J. B. Kraft¹⁹ |
Jens-Christian Svenning^{13,14} 

¹Center for Theoretical Study, Charles University and The Czech Academy of Sciences, Praha, Czech Republic; ²Department of Ecology, Charles University, Praha, Czech Republic; ³Department of Biology, Santa Clara University, Santa Clara, California; ⁴Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona; ⁵The Santa Fe Institute, Santa Fe, New Mexico; ⁶Department of Botany and Biodiversity Research Centre, University of British Columbia, Vancouver, Canada; ⁷Max Planck Institute for Biogeochemistry, Jena, Germany; ⁸German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany; ⁹Centre d'Ecologie Fonctionnelle et Evolutive (UMR 5175, CNRS - Université de Montpellier - Université Paul-Valéry, Montpellier, France; ¹⁰School of Biology and Ecology / Sustainability Solutions Initiative, University of Maine, Orono, Maine; ¹¹Environmental Change Institute, University of Oxford, Oxford, Great Britain; ¹²School of Life Sciences, Arizona State University, Tempe, Arizona; ¹³Section for Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus University, Aarhus C, Denmark; ¹⁴Center for Biodiversity Dynamics in a Changing World (BIOCHANGE), Department of Bioscience, Aarhus University, Aarhus C, Denmark; ¹⁵Department of Biology, University of North Carolina, Chapel Hill, North Carolina; ¹⁶Manaaki Whenua - Landcare Research, Lincoln, New Zealand; ¹⁷Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark; ¹⁸Hardner & Gullison Associates, LLC, Amherst, New Hampshire and ¹⁹Department of Ecology and Evolutionary Biology, University of California, Los Angeles, California

Correspondence

Irena Šímová

Email: simova@cts.cuni.cz

Funding information

Grantová Agentura České Republiky, Grant/Award Number: 16-26369S; H2020 European Research Council, Grant/Award Number: ERC-2012-StG-310886-HISTFUNC and ERC-StG-2014-639706-CONSTRAINTS; Maine Agricultural and Forest Experiment Station, Grant/Award Number: 1011538; Villum Fonden, Grant/Award Number: 16549; National Science Foundation, Grant/Award Number: ABI-1660000, DBI-0735191, DEB-1457812, EF-1065844 and EF-0553768

Handling Editor: Andy Hector

Abstract

1. Ecosystem processes are driven by both environmental variables and the attributes of component species. The extent to which these effects are independent and/or dependent upon each other has remained unclear. We assess the extent to which climate affects net primary productivity (NPP) both directly and indirectly via its effect on plant size and leaf functional traits.
2. Using species occurrences and functional trait databases for North and South America, we describe the upper limit of woody plant height within 200 × 200 km grid-cells. In addition to maximum tree height, we quantify grid-cell means of three leaf traits (specific leaf area, and leaf nitrogen and phosphorus concentration) also hypothesized to influence productivity. Using structural equation modelling, we test the direct and indirect effects of environment and plant traits on remotely sensed MODIS-derived estimates of NPP, using plant size (satellite-measured canopy height and potential maximum tree height), leaf traits, growing season length, soil nutrients, climate and disturbances as explanatory variables.
3. Our results show that climate affects NPP directly as well as indirectly via plant size in both tropical and temperate forests. In tropical forests NPP further increases with leaf phosphorus concentration, whereas in temperate forests it increases with leaf nitrogen concentration. In boreal forests, NPP most strongly

increases with increasing temperature and neither plant size nor leaf traits have a significant influence.

4. *Synthesis*. Our results suggest that at large spatial scales plant size and leaf nutrient traits can improve predictions of forest productivity over those based on climate alone. However, at higher latitudes their role is overridden by stressful climate. Our results provide independent empirical evidence for where and how global vegetation models predicting carbon fluxes could benefit from including effects of plant size and leaf stoichiometry.

KEYWORDS

BIEN database, biogeography and macroecology, biomass production, ecosystem function and services, leaf nitrogen, leaf phosphorous, MODIS, TRY database

1 | INTRODUCTION

The composition of plant species assemblages is often cited as a significant driver of key ecosystem functions, such as carbon, nutrient and water cycles, and of the resulting ecosystem processes such as evapotranspiration, decomposition and biomass production (Cornwell et al., 2008; Grime, 1997; Lavorel & Garnier, 2002). As such, a key challenge for improving our ability to predict the ecological impacts of global climate change lies in understanding how environmental and land-use changes alter the composition of plant assemblages and how this in turn affects ecosystem processes (Chapin et al., 2000). Plant functional traits are increasingly emphasized as a way to link species composition to ecosystem function. For example, at the organismal and community scale, several studies have documented that variation in functional traits drives variation in ecosystem functions such as carbon or water cycles (Michaletz, Cheng, Kerkhoff, & Enquist, 2014; Reich, Walters, & Ellsworth, 1997; Stephenson et al., 2014; Violle et al., 2007). Nevertheless, how such relationships scale up from larger landscapes to continental scales remains unresolved. A way forward is to combine maps of functional traits of species assemblages with maps of ecosystem processes (e.g. satellite-derived productivity data) to allow the importance of plant traits in driving ecosystem processes at large spatial scales to be evaluated (Díaz et al., 2007; Lavorel et al., 2013).

Perhaps the most important trait affecting variation in ecosystem carbon, water and nutrient fluxes is plant size, which is often measured as height or stem diameter (Chapin, Bret-Harte, Hobbie, & Zhong, 1996; Niklas & Enquist, 2001; Stephenson et al., 2014). Metabolic scaling theory (MST) for forest structure and dynamics predicts that whole-stand resource use (e.g. carbon flux) should be proportional to the size of the largest individual present at the stand (Enquist, West, & Brown, 2009; West, Enquist, & Brown, 2009):

$$B_{\text{tot}} \propto (M_{\text{tot}})^b \propto r_m,$$

where B_{tot} is the whole-stand metabolic rate or resource flux (e.g. carbon or water), M_{tot} is the total biomass of the stand, b is a mass-scaling exponent (which depends on the size structure of the stand, the scaling of resource use with plant size and the scaling of stem radius

and plant biomass) and r_m is the size (measured as stem radius) of the largest individual in the stand. MST predicts that the largest individual in the stand should be a central if not the primary predictor of variation in B_{tot} and M_{tot} . In agreement with theory, there is evidence that stand biomass of tropical and temperate forest plots, primarily determined by the size of the largest tree (Stegen et al., 2011), is one of the major drivers of forest productivity (Michaletz et al., 2014; Michaletz, Kerkhoff, & Enquist, 2018). Furthermore, given that tall trees sequester carbon at higher absolute rates compared to smaller trees (Stephenson et al., 2014), they are often strong contributors to the whole-stand carbon flux (Fauset et al., 2015; Gholz, 1982; but see Ligot et al., 2018). These theoretical predictions, however, are expected to be modified by human land-use or natural disturbances (Kerkhoff & Enquist, 2007; McDowell et al., 2018; see also Coomes, Holdaway, Kobe, Lines, & Allen, 2012; Muller-Landau et al., 2006).

Although some studies claim that variation in forest productivity is primarily determined by the direct effects of climate (Raich, Russell, Kitayama, Parton, & Vitousek, 2006; Sankaran et al., 2005; Schuur, 2003), others suggest an indirect role of climate acting via local adaptations, soil nutrients or regional land-use history mirrored in stand biomass (Chapin, Matson, & Vitousek, 2011; Michaletz et al., 2014, 2018) or a combination of these (Chu et al., 2016). Therefore, the unique contribution of stand biomass to rates of carbon flux, carbon sequestration and productivity relative to factors such as climate, disturbances and land-use intensity still needs to be evaluated.

Here, we test whether climate affects net primary productivity (NPP) directly or indirectly via its effect on tree size, a surrogate of stand biomass, as measured by maximum tree height, in 200×200 km grid cells. As an NPP estimate, we used MODIS (Moderate Resolution Imaging Spectroradiometer) derived NPP (Running et al., 2004), defined as the total carbon that plants gain during photosynthesis minus the carbon lost by respiration. Our analyses utilized and compared two different measures of maximum tree height: (a) maximum canopy height per cell ("canopy height" hereafter), derived from remote sensing using a Geoscience Laser Altimeter System (GLAS), and (b) potential maximum tree height of all co-occurring plant species per cell, obtained by intersecting species occurrence records from that cell and species trait data.

The relationship between tree height, climate and NPP can be supplemented or modified by other factors such as leaf traits that drive photosynthetic and whole plant growth rates (Enquist et al., 2015; Lavorel & Garnier, 2002; Reich, Walters, & Ellsworth, 1992; Reich et al., 1997; Violle et al., 2007) or intensity of disturbances. To reflect these influences, we have included fire frequency, human land-use, specific leaf area, leaf nitrogen concentration and leaf phosphorus concentration in our evaluation.

Building on the recent theoretical expectations and empirical evidence (Enquist et al., 2015; Michaletz et al., 2014), we predict that climate and other environmental variables such as fire frequency and human land-use (disturbances) affect NPP primarily *indirectly* via their effects on tree height (Prediction P1; see Figure 1 for a conceptual schema) (McDowell et al., 2018). Specifically, we predict that tree height is limited by water availability. Larger trees are closer to hydraulic limits that are defined by local precipitation and temperature (Bennett, McDowell, Allen, & Anderson-Teixeira, 2015; Gholz, 1982; McDowell & Allen, 2015; Ryan & Yoder, 1997). The basic tenet of the “hydraulic limitation hypothesis” is that taller trees exhibit increased stomatal closure due to an increase in hydraulic resistance with tree height combined with the need to maintain a minimum leaf water potential to avoid catastrophic embolism (Ryan & Yoder, 1997).

The derived values of potential maximum tree height for a cell may or may not be realized due to disturbance, climate stress, etc. Therefore, we predict (P2) that potential maximum tree height affects NPP indirectly, via its influence on canopy height, and that climate (P1a) and disturbances (P1b) and their interaction affect NPP indirectly by constraining the degree to which canopy height is a realization of potential tree height. Climate can also affect potential maximum tree height as an environmental filter that prevents establishment of species not adapted to local conditions.

Finally, we predict (P3) NPP to be affected by leaf traits that are driven by climate or soil nutrient concentration. Specifically, NPP should increase with increasing specific leaf area and leaf nitrogen concentration as these influence rates of photosynthesis and whole plant growth (Enquist et al., 2015; Reich et al., 1997; Violle et al.,

2007; Wright et al., 2004). NPP should also increase with increasing leaf phosphorus concentration, particularly in tropical forests (Mercado et al., 2011; Tanner, Vitousek, & Cuevas, 1998). Leaf nitrogen and phosphorus concentration should be driven by the concentrations of these nutrients in the soil, which can be partly driven by climate (Hedin, 2004; Reich & Oleksyn, 2004). Specifically, we predict soil phosphorus availability to decrease with increasing precipitation because of higher leaching rates. Soil nitrogen availability should increase with increasing temperature due to the temperature-dependence of the forest nitrogen cycle (Brookshire, Gerber, Webster, Vose, & Swank, 2011). As for maximum potential tree height, climate can also affect leaf traits directly via environmental filtering.

To disentangle the relative importance of climate, disturbances, functional traits and soil properties in controlling large-scale forest productivity and to evaluate the interactions among these factors, we apply a path analysis framework (see Figure 1a for a conceptual schema). Given the possibly different drivers of NPP in different forest biomes, we test the above-mentioned predictions for all forests together and for individual biomes separately.

2 | MATERIALS AND METHODS

2.1 | Species and trait data

We extracted species occurrence records from the BIEN 3.0 database (<http://bien.nceas.ucsb.edu/bien/>). Most of these data are publicly available via the *BIEN* R package (Maitner, 2017) with some exceptions such as endangered species and private records (see Maitner et al., 2018 for details). We included all plant occurrence records having their coordinates georeferenced within the mainland areas of the Americas, excluding occurrence data of cultivated species. We overlaid the occurrences with a 200 × 200 km grid (projection was Lambert Azimuthal Equal Area) to obtain a list of species for each grid cell. We included only cells with more than 80% of their area on land. We restricted our analyses to woody species following

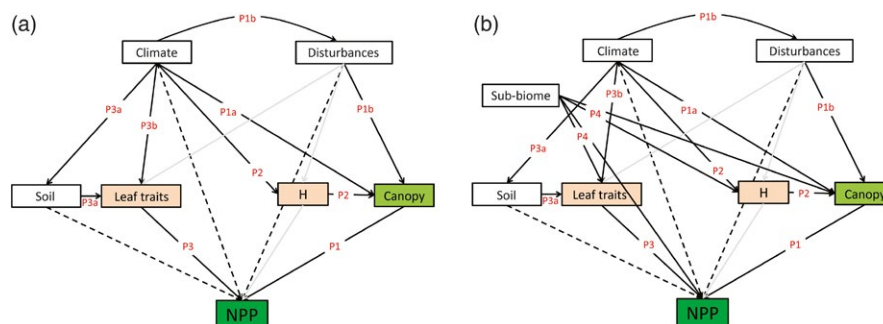


FIGURE 1 The conceptual path diagram for the structural equation modelling demonstrating the hypothesized causal relationships of climate, disturbances, canopy height (“Canopy”), potential maximum tree height (“H”), leaf traits, and soil nutrient concentration (“Soil”) in explaining net primary productivity (“NPP”) of forest assemblages. Solid black lines represent our predictions about the indirect effect of climate, disturbances and soil nutrient concentration on NPP via tree size and leaf traits, whereas dashed lines represent alternative direct effects of these variables on NPP. We further tested for the possible missing paths in the model, highlighted in grey. Besides the original model (a), we added an effect of sub-biome (b), separating tropical and subtropical moist broadleaf forests from tropical and subtropical dry broadleaf forests and temperate broadleaf and mixed forests from temperate coniferous forests

Engemann et al. (2016) (angiosperm and gymnosperm trees, shrubs and lianas; 6,107 species in total).

We obtained plant maximum height, specific leaf area, leaf nitrogen concentration and phosphorus concentration data for woody species from both the BIEN and TRY (Kattge et al., 2011) databases, resulting in 14,451 species-level trait values. We assigned the trait values to the species occurrences resulting in values for maximum height for 2,583 species, specific leaf area for 2,408 species, leaf nitrogen concentration for 2,615 species and leaf phosphorus concentration for 1,754 species (see Figure S1 in Appendix S2 for maps of showing spatial the distribution of trait values). MST predicts that the size (height) of the largest individual is a key predictor of whole-stand productivity. Therefore, to calculate potential maximum tree height, we estimated the per-cell 95th percentile of maximum tree height. We chose the 95th percentile over the maximum value as it reduces the possible effect of outliers. We

used the mean of per-cell values of the specific leaf area (SLA), leaf nitrogen concentration (leaf N) and leaf phosphorus concentration (leaf P) (Figure 2a–d) to characterize assemblage strategies (Enquist et al., 2015; Garnier et al., 2004). Due to the low number of species with known trait values at some grid cells (mostly boreal forests; Figure S1) we retained only those cells with >3 species with known values of each trait.

2.2 | Canopy height

We used the canopy height map derived from the Geoscience Laser Altimeter System (GLAS) from collection periods between 2003 and 2007 (Lefsky, 2010). The map applies to forest patches identified with MODIS imagery. Although a more recent map of canopy vegetation height has been developed spanning a larger spatial extent including non-forest areas (Simard, Pinto, Fisher, & Baccini, 2011), it

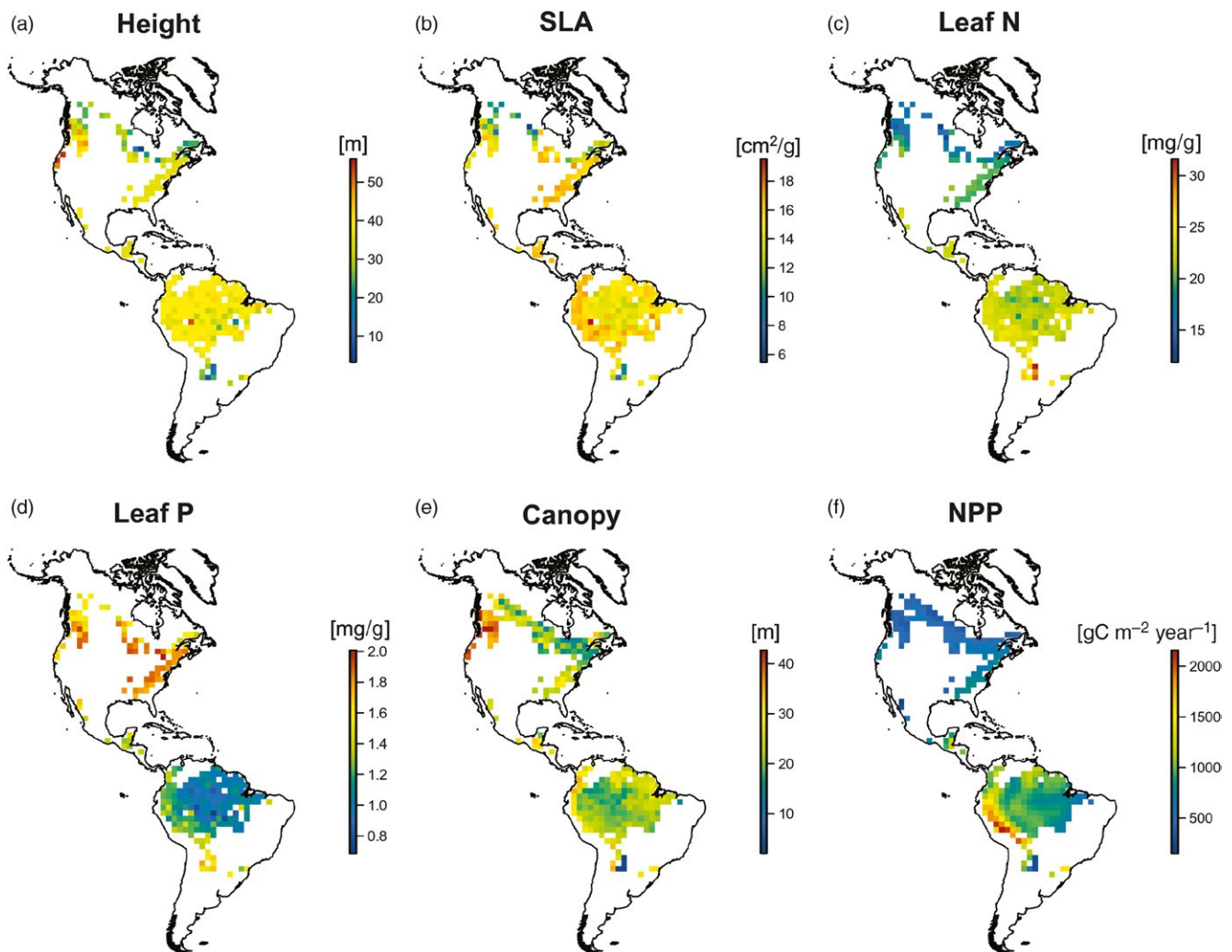


FIGURE 2 Maps of the productivity, canopy height and assemblage functional trait values of the forest biomes estimated over the 200×200 km grid-cells. (a) Potential maximum tree height ("Height"), (b) specific leaf area ("SLA"), (c–d) leaf nitrogen and phosphorus concentration ("Leaf N" and "Leaf P") estimated from woody species occurrences, (e) canopy height ("Canopy") estimated from the Geoscience Laser Altimeter System and (f) net primary productivity ("NPP") derived from the MODIS data. Note that panels a–d show only those cells with >3 species with known values of all four traits and with at least 50% of forest coverage whereas cells on panels e–f are restricted only to at least 50% of forest coverage (see also Figure S1 in Appendix S2 for the sampling coverage). See Figure S3 in Appendix S2 for maps of all variables used in our models

models canopy height using both GLAS measurements and climate variables (mean annual temperature, annual precipitation and their seasonality), and therefore is not appropriate for regression models incorporating those same climate variables (see also Tao, Guo, Li, Wang, & Fang, 2016). In this map, about 1/4 of all forest patches have direct measurements. Those were assigned a value equal to the 90th percentile of the GLAS-based canopy height estimate (Lefsky, 2010). Canopy height of patches without direct measurements were estimated by statistical modeling using the values from the surrounding patches (Lefsky, 2010). We restricted our analyses to cells where >50% of cell area was assigned with non-null canopy height values (i.e. cells with forest coverage >50%). To estimate the canopy height variable, we used these non-null canopy height values to calculate per-cell 95th percentile (Figure 2e).

2.3 | Net primary productivity

NPP is a product of the MODIS sensor (Running et al., 2004). It is calculated as gross primary productivity (GPP) minus autotrophic respiration. GPP is modelled as a function of photosynthetically active radiation (PAR), the fraction of PAR absorbed by plants, biome-specific light-use efficiency, daily minimum temperature and vapour pressure deficit (Zhao, Heinsch, Nemani, & Running, 2005; Zhao & Running, 2010). Respiration combines maintenance respiration (a function of the daily average air temperature and leaf area index) and growth respiration (estimated as a constant proportion of total NPP). We averaged the NPP layer (available via <http://www.ntsg.umd.edu/>) over the years 2000–2012 and over each grid cell (Figure 2f).

2.4 | Environmental data

We included mean annual temperature and annual precipitation (1960–1990 means) extracted from the Worldclim database (version 1.4; www.worldclim.org; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). We selected these variables as both temperature (incorporated into potential evapotranspiration) and precipitation have been identified as strong predictors of forest canopy height (Tao et al., 2016), and temperature has been found to be the best predictor of mean height of woody species assemblages in 200 × 200 km grid squares in the Americas (Šímová et al., 2018). To reflect water limitation of plant growth, we included the yearly average of the fraction of soil water content available for evapotranspiration process ("soil water content" hereafter) obtained from CGIAR-CSI GeoPortal (<http://www.cgiar-csi.org/data>; Trabucco & Zomer, 2010). This variable is calculated as a difference between effective precipitation, actual evapotranspiration and water runoff where effective precipitation represents the total precipitation minus the precipitation intercepted by vegetation. We also included growing season length as another potentially important factor limiting forest NPP (Chapin et al., 2011; Michaletz et al., 2018) obtained from FAO (The Food and Agriculture Organization; <http://www.fao.org/geonetwork/srv/en/main.home>). This variable is defined as the period during the year when average temperatures are

greater than or equal to 5°C and precipitation plus moisture stored in the soil exceed half the potential evapotranspiration and the values are grouped into 16 zones.

As our first disturbance measure, we obtained fire frequency from Tansey et al. (2008), and averaged this variable over years 2000–2007. As a second disturbance measure, we quantified human land use from the GlobCover 2009 land cover database (http://due.esrin.esa.int/page_globcover.php). We chose the year 2009 to match the period of NPP data measurements (years 2000–2012) and canopy height measurements (years 2003–2007). We used the area covered by urban areas and all types of croplands (post-flooding or irrigated croplands, rain fed croplands, mosaic cropland and mosaic vegetation/cropland) in each grid cell as a measure of the intensity of human land use. We obtained soils data from ORNL DAAC (<https://daac.ornl.gov/>). We retrieved total soil phosphorus and organic soil phosphorus content from the Global Gridded Soil Phosphorus Distribution Maps (Yang, Post, Thornton, & Jain, 2014) and used these as surrogates of phosphorus available to plants. We retrieved topsoil organic carbon content from the Regrided Harmonized World Soil Database (Wieder, Boehnert, Bonan, & Langseth, 2014) and used this as a negative surrogate for nitrogen available to plants. We calculated the mean of climate variables, fire frequency and soil variables at 200 × 200 km grid cell size using the package *raster* (Hijmans et al., 2016) in R (R Development Core Team, 2017). See Figure S3 in Appendix S2 for maps and units of all variables.

2.5 | Forest biomes

For the grid cells with >50% of forest coverage we assigned the forest biomes according to the following protocol. First, we grouped the major habitat types recognized by the WWF (World Wildlife Foundation; www.worldwildlife.org) and obtained from The Nature Conservancy (http://maps.tnc.org/gis_data.html) into three main biomes: (a) tropical forests (defined as area covered by tropical and subtropical moist broadleaf forests, Tropical and subtropical dry broadleaf forests or tropical and subtropical coniferous forests), (b) temperate forests (area covered by temperate broadleaf and mixed forests or temperate coniferous forest) and (c) boreal forests (defined as boreal forests/Taiga). Second, for each grid cell, we considered the biome covering the largest area as the dominant biome (Figure S2 in Appendix S2). Given the variability in canopy height values within tropical and temperate forest biomes, we further define four sub-biomes based on the WWF classification. These are (a) temperate broadleaf and mixed forests, (b) temperate coniferous forests, (c) tropical and subtropical moist broadleaf forests and (d) tropical and subtropical dry broadleaf forests. We omitted the tropical and subtropical coniferous forests sub-biome due to its limited spatial extent (four grid cells).

2.6 | Data analyses

We fit structural equation models (package "lavaan" in R) (Rosseel, 2012) to assess the distinct effects of potential maximum tree height, leaf traits, canopy height, length of the growing season,

temperature, precipitation, human land-use and fire frequency on NPP. We \log_e -transformed human land-use and fire frequency to improve normality. We checked for collinearity among variables using the variance inflation factor (VIF) where small VIF values indicate a low degree of collinearity. Some researchers recommend that the VIF of each variable entering the model be lower than 10 (Dormann et al., 2013), and others recommend VIF less than 5 (Hair, Ringle, & Sarstedt, 2011), or under ideal conditions even less than 3 (Hair, Risher, Sarstedt, & Ringle, 2018). In tropical forests all variables had VIF <10 and most of them had VIF <5. To meet similar VIF levels in temperate and boreal forests and across all forests we fit separate models using either temperature and water deficit (results presented in the main text) or precipitation and length of the growing season (results presented in Appendix S3). Although not all variables were perfectly independent of each other, all of them were theoretically motivated and we aimed to avoid too many alternative models.

We first ran the model with all solid black and dashed links as presented in Figure 1a. Here, solid black lines represent our predictions (P1–P4) about the indirect effect of climate, human land-use and fire on NPP via tree size and leaf traits. Dashed lines represent alternative direct effects of climate, human land-use and fire. To obtain the best-fit model we took a stepwise approach and removed weak and non-significant links and evaluated the model parameters at each step. Specifically, we aimed to (a) identify non-significant *p*-values of the Chi-squared test reflecting the probability of failing to reject the model given the data, (b) minimize the BIC_c (sample size-adjusted Bayesian Information Criterion) and the Root Mean Square Error of Approximation (RMSEA) and (c) maximize the Comparative Fit Index (CFI) and Tucker-Lewis Index (TLI) (Bollen, Harden, Ray, & Zavisca, 2014). We also checked for possible missing paths in the model according to the modification indices (μ) that represent the reduction in the Chi-squared value after adding the missing path; paths with $\mu > 3.84$ (corresponding to the Chi-square statistic value of $p = 0.05$) were retained. We tested for missing paths between traits and disturbances (fire frequency, human land-use). These two predictors were not included in our original model because of mismatched temporal scales; plant species occurrence records were collected over a much longer time period than were the data underpinning the disturbance layers. Also, given that satellite data estimate of canopy height can be biased (Mitchard et al., 2014), we additionally explored a direct effect of potential maximum tree height on NPP acting independently of canopy height. We performed these analyses for all forests and then for tropical, temperate and boreal forest biomes individually.

In analyses focused on tropical and temperate forests, we accounted for a sub-biome effect (moist and dry tropical forests, coniferous and deciduous temperate forests). We predict (P4) the sub-biome to mirror climate effects, in part, and to also reflect differences in evolutionary history, topography or edaphic conditions that can affect NPP directly or indirectly via their effects on canopy height or the traits of species assemblages (Figure 1b).

3 | RESULTS

Across all forest biomes (Figure 3a, see also Figure S4 in Appendix S3), NPP increased with increasing canopy height (in accordance with P1). Also, potential maximum tree height affected NPP indirectly via canopy height (in accordance with P2) and there was a positive link between potential maximum tree height and both soil water content (P2) and temperature. Still, the strongest NPP determinant was leaf N (in accordance with P3), while both temperature (with positive effect) and soil water content (with negative effect) affected NPP indirectly via leaf N (P3b). Unexpectedly (P3a), we did not find a support for a link between leaf N and soil nutrients. NPP further increased with increasing soil water content and temperature. When growing season length and precipitation were substituted for temperature and soil water content (Figure S5a in Appendix S3), the growing season length became the strongest predictor of NPP (with positive effect) and of canopy height (with negative effect). Also, precipitation became the strongest determinant of potential maximum tree height (in accordance with P2) and there was a new negative link between topsoil organic carbon content and leaf N (in accordance with P3a). Other relationships were consistent with the first model.

In tropical forests (Figure 3c, Figure S6 in Appendix S3), NPP increased with increasing canopy height (in accordance with P1), and also, potential maximum tree height affected NPP indirectly via canopy height (in accordance with P2). NPP further increased with increasing leaf P (in accordance with P3). As predicted (P1, P2 and P3b), climate had an indirect effect on NPP via plant traits. Specifically, potential maximum tree height increased with increasing soil water content, leaf P increased with decreasing precipitation, and both canopy height and leaf P increased with decreasing temperature. Leaf P further increased with increasing total soil phosphorus concentration (in accordance with P3a). Still, besides the indirect effect of climate, NPP of tropical forests strongly increased with increasing soil water content and growing season length while it also decreased with increasing precipitation. After accounting for moist and dry tropical sub-biome, sub-biome became an important predictor of NPP, canopy height, potential maximum tree height and leaf P as expected (P4) and the link between NPP and growing season length disappeared (Figure 3d); otherwise relationships were consistent with the first model.

When analysed across temperate forests (Figure 3e, see also S7 in Appendix S3), we did not find support for our prediction of the positive link between NPP and canopy height (P1). Also, the effect of leaf traits on NPP was unimportant. Instead, NPP increased with increasing temperature and soil water content. Lack of support for P1, however, was largely driven by the difference between broadleaf and coniferous sub-biome. Support for P1 was observed after controlling for the effect of sub-biome, when we found a significant positive missing path between NPP and potential maximum tree height (Figure 3f). The non-significant effect of canopy height on NPP was largely driven by coniferous sub-biome (Figure S7) where canopy height often exceeded potential maximum tree height (Figure S8 in Appendix S3) possibly due to the increasing uncertainty of

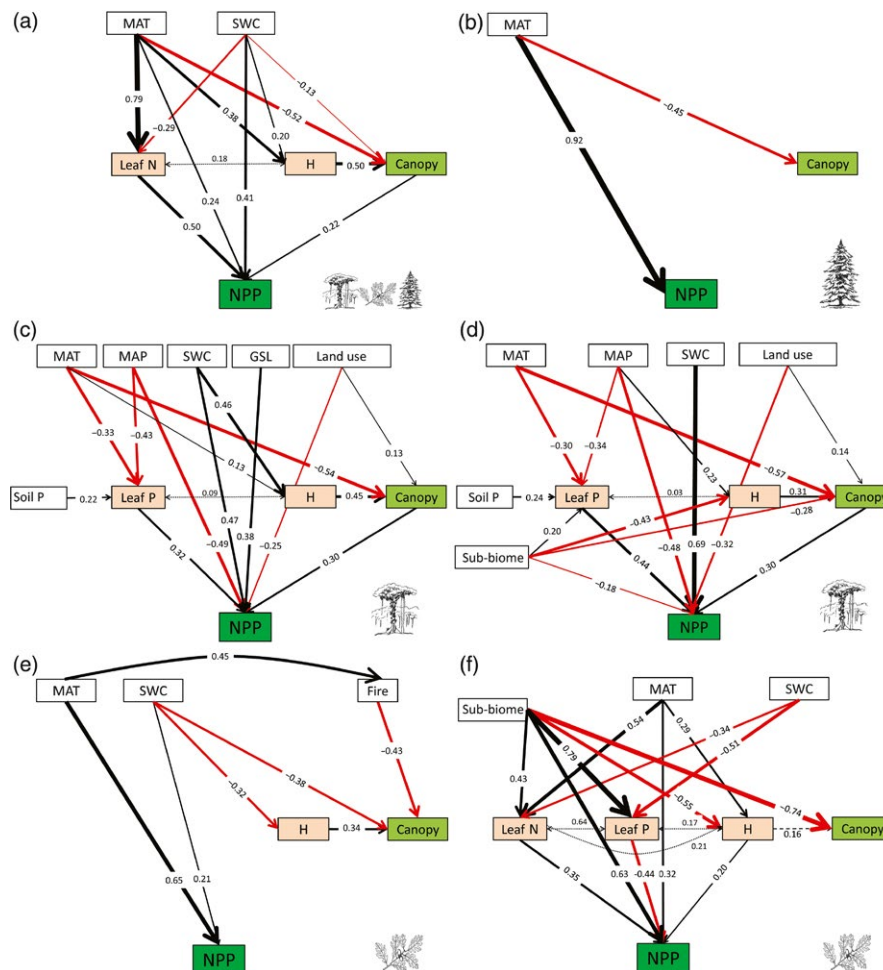


FIGURE 3 Structural equation models representing connections between productivity, canopy height and assemblage functional traits values for all forests together (a), boreal forests (b), tropical forests without (c) or with (d) sub-biomes included, and temperate forests without (e) or with (f) sub-biomes included. “MAT” is temperature, “MAP” is precipitation, “SWC” is soil water content, “GSL” is growing season length, “Land-use” is human land-use, “Fire” is fire frequency, “Canopy” is canopy height, “H” is potential maximum tree height, “Leaf N” is leaf nitrogen concentration, “Leaf P” is leaf phosphorus concentration, “Soil P” is total soil phosphorus concentration and “NPP” is net primary productivity. Sub-biome is coded as 0/1 for moist/dry tropical forests and for coniferous/broadleaf temperate forests respectively. Significant links are represented by solid arrows, non-significant links ($p > 0.05$) are represented by dashed arrows and error covariance is represented by dotted arrows. Positive links are black, negative links are red. The numbers next to each arrow are standardized coefficients. See Table 1 for the model results summary and Figure S4, S6–7, S9 for bi-variate relationships of each variable plotted against NPP. See also Figure S5 for models with growing season length and precipitation instead of temperature and soil water content

satellite-based canopy height measurements with increasing terrain rugosity (Lefsky, 2010). Furthermore, both leaf N (with positive effect) and leaf P (with negative effect) became important predictors of NPP in temperate forests, and climate had an indirect effect on NPP via these traits (P3b). Specifically, leaf N increased with increasing temperature and both leaf N and leaf P decreased with increasing soil water content. Contrary to our expectation (P3a), soil variables had no significant effects on leaf traits. Still, sub-biome became the strongest determinant of NPP, canopy height and potential maximum tree height. When using growing season length and precipitation instead of temperature and soil water content, precipitation became an important predictor of leaf N, leaf P and potential maximum tree height (Figure S5c–d); otherwise results remained qualitatively similar to the first model.

In boreal forests, temperature was the only predictor of both NPP (with positive effect) and canopy height (with negative effect) (Figure 3b, see also Figure S9 in Appendix S3) and none of our predictions concerning plant traits (P1, P2 and P3) were supported. These results could be affected by the low sample size ($n = 25$) caused by the low number of cells with >3 species with known values of all traits. Therefore, we repeated the analysis without traits using all grid cells with boreal forest cover $>50\%$ ($n = 58$). Still, the results remained qualitatively similar, except that NPP also increased with increasing total soil phosphorus concentration (Figure S10a in Appendix S3). When growing season length and precipitation were substituted for temperature and soil water content, NPP strongly increased with increasing growing season length. It also weakly increased with increasing precipitation (Figures S5b and Figure S10b).

TABLE 1 Results from the structural equation models for different forest biomes and for all forests together

Biome	Sub-biome	Chi-sq	df	p-value (Chi)	CFI	TLI	RMSEA	K	n	r^2_{NPP}	r^2_{Canopy}	r^2_{H}	$r^2_{\text{Leaf P}}$	$r^2_{\text{Leaf N}}$	r^2_{Fire}
All forests	0	1.54	2	0.46	1.00	1.00	0.00	16	258	0.50	0.31	0.19	—	0.70	—
Tropical	0	14.66	15	0.48	1.00	1.00	0.00	19	181	0.44	0.44	0.26	0.57	—	—
Tropical	1	17.36	13	0.18	0.99	0.98	0.04	21	177	0.50	0.51	0.36	0.58	—	—
Temperate	0	6.52	6	0.37	0.99	0.99	0.04	12	52	0.49	0.55	0.11	—	—	0.20
Temperate	1	5.02	7	0.66	1.00	1.03	0.00	23	52	0.70	0.69	0.28	0.44	0.56	—
Boreal	0	0.00	0	0.00	1.00	1.00	0.00	5	25	0.84	0.20	—	—	—	—

Note. "Sub-biome" indicates whether the variable sub-biome is included in the model (1) or not (0). Chi-square contains the values of the Chi-square statistics, p-value (Chi) is the p-value of the Chi-square test, CFI is Comparative Fit Index, TLI is Tucker-Lewis Index, RMSEA is Root Mean Square Error of Approximation, BICc is sample-size-adjusted Bayesian Information Criterion, K is the number of free parameters, n is number of samples (grid cells) and r^2_{NPP} , r^2_{Canopy} , r^2_{H} , $r^2_{\text{Leaf P}}$, $r^2_{\text{Leaf N}}$, r^2_{Fire} show variation explained for NPP, Canopy height, Potential maximum tree height (H), leaf phosphorus and nitrogen concentration (Leaf P, Leaf N) and fire frequency. See Figure 3 for the model diagrams.

To evaluate whether models including traits improve predictions of NPP over those based on climate alone, we additionally compared three sets of models: (a) Partial mediation models where climate affects NPP both directly and indirectly via functional traits, (b) No mediation models where traits do not explain the association between climate and NPP, and (c) Complete mediation models where traits completely explain the variation in NPP and climate has only indirect effect (see Figure S11 as an example). We performed this analysis only for those biomes where traits were selected as important productivity predictors, specifically where Partial mediation models were selected by the model evaluation procedure (Figures 3a,c–d,f, S5a,d). For the No mediation model we used the Partial mediation model structure and set all parameters between traits and NPP to zero. To build the Complete mediation models we removed all direct links between climate (temperature, precipitation, soil water concentration and growing season length) and NPP. We compared the model fit according to the AIC and Chi-square statistics. In all cases Partial mediation models provided the best explanation of the data (Table S3).

4 | DISCUSSION

We found that productivity of American tropical and temperate forests is jointly affected by climate, plant size and leaf nutrient traits, but through differing direct and indirect paths. In boreal forests neither tree size nor leaf traits appeared as important predictors of productivity. Instead, productivity in boreal forests was driven by a direct role of temperature. Together, these results are largely consistent with theoretical expectations and recent empirical evidence (Enquist et al., 2015; Michaletz et al., 2014) where tree size is a central trait affecting carbon flux and biomass production in mature forests. Our results further underscore that more stressful climates likely modify these theoretical predictions at higher latitudes. Our results also agree with recent evidence of nutrient availability as another important regulator of forest carbon flux (Fernández-Martínez et al., 2014).

The finding that productivity of tropical forests increased with the height of the tallest trees is consistent with the previous observations that tree size is an important predictor of biomass production in this biome (Bastin et al., 2015; Fauset et al., 2015; Finegan et al., 2015). Our findings also agree with Michaletz et al. (2014), Michaletz et al. (2018) who concluded that climate affects productivity of forest plots indirectly, acting via stand biomass (see also Enquist, 2011). Here, we found a positive indirect link between water availability (expressed as precipitation and soil water content) and productivity acting via potential maximum tree height, and a negative indirect link between temperature and productivity acting via canopy height. This is consistent with the hydraulic limitation hypothesis (Ryan & Yoder, 1997) as decreasing water availability and increasing temperature increase the probability of drought embolism in tree hydraulic pathways (McDowell & Allen, 2015).

Our results indicate that tropical forest productivity is strongly influenced by water availability. Soil water content had a direct

positive effect on tropical productivity and this link was stronger than the indirect path via plant size. In addition to the role of tree size and soil water content, tropical productivity increased with increasing leaf phosphorus concentration, driven by both climate and soil phosphorus concentration. This agrees with our prediction and with evidence of phosphorus as a key nutrient influencing productivity in warm and wet tropical lowland forests (Quesada et al., 2012; Vitousek, 1984). Unexpectedly, productivity of tropical forests further decreased with increasing precipitation. This relationship is, however, largely driven by the sites of high precipitation (>3 m) that are not the most productive (Figure S6). The highest precipitation occurs in northern part of the Amazon (Figure S3) whereas the most productive sites are in the foothills of the Andes (Figure 2). Such NPP patterns could result from the lower plant respiration rates caused by the lower temperature in higher altitudes. Lower productivity at sites of highest rainfall can also result from higher rates of soil weathering and nutrient leaching (Quesada et al., 2012). At the same time, higher tree mortality and turnover rates may lead to higher rates of carbon flux at sites with lower rainfall as a result of higher soil disturbances and episodic drought (Malhi et al., 2015; Quesada et al., 2012). Still, the variation explained in productivity of tropical forests was rather low compared to temperate and boreal forests, suggesting that we were missing some other important factor such as climatic or topographic heterogeneity, climate velocity or the effect of tree plantations.

In temperate forests, we found support for our prediction that tree size positively affects productivity only when we accounted for coniferous and deciduous sub-biomes. Still, whereas productivity increased with increasing potential maximum tree height, the link between canopy height and productivity was unexpectedly not significant. It is, therefore, possible that other factors than realized tree height, such as past land-use legacies, leaf area index or nutrient limitation play, important role in carbon cycle of temperate forests (Coomes et al., 2012; Waring, 1983).

Consistent with the observation that nitrogen limitation on productivity is more pronounced in temperate than tropical regions (but see LeBauer & Treseder, 2008; Reich & Oleksyn, 2004), we found a strong positive link between leaf nitrogen concentration and temperate forest productivity. Our finding that leaf nitrogen concentration strongly increased with increasing temperature is consistent with the temperature-dependence of the forest nitrogen cycle (Brookshire et al., 2011). In contrast to tropical forests, productivity of temperate forests decreased with increasing leaf phosphorus, a relation largely driven by the deciduous sub-biome (Figure S7). Although phosphorus availability certainly limits plant growth in temperate forests (Wardle, Walker, & Bardgett, 2004), this finding can be interpreted as an adaptive response of plants to selection on fast growth rate (thus on high phosphorus demand) during the short vegetation season at high latitudes and altitudes (Kerkhoff, Enquist, Elser, & Fagan, 2005) where the productivity is generally low (Figure 2f). Also, younger soils of temperate forests are richer in phosphorus relative to nitrogen available to plants, with the consequence that nitrogen availability generally drives production

in this sub-biome (Vitousek, Porder, Houlton, & Chadwick, 2010; Walker & Syers, 1976). Alternatively, this finding could result from an indirect effect of precipitation leaching soil phosphorus on older soils at lower latitudes (see also Šímová, Rueda, & Hawkins, 2017). Besides the indirect effect of climate (acting via potential maximum tree height and leaf traits), productivity of temperate forests also increased with increasing mean annual temperature, suggesting the direct effect of stressful climate on photosynthetic rates. Still, the strongest productivity predictor was the effect of the sub-biome. This indicates that coniferous forests are on average less productive, given their canopy height, in comparison to deciduous forests (except of the relatively small area of highly productive forests of the North American pacific coast), which also corresponds to their relatively low carbon-use efficiency (DeLucia, Drake, Thomas, & Gonzalez-Meler, 2007).

In contrast to tropical and temperate forests, temperature was the only productivity determinant in boreal forests and we did not find any evidence for the effect of plant size or leaf traits. This finding deviates from a previous plot-based study showing that biomass production increases with the stand biomass, particularly in low-productivity boreal and montane forests (Keeling & Phillips, 2007). We suspect that the correlation between stand biomass and productivity of boreal forests observed by other studies (Jenkins, 2015; Keeling & Phillips, 2007) may be only indirect and could result from the effect of temperature limiting both these variables, but more studies are needed to confirm this hypothesis.

Despite the comprehensive datasets, our results may be affected by several important potential biases. First, our study is based on relatively coarse spatial grain leading to the relatively low number of cells with at least 50% forest coverage, in turn resulting in omitting some forest areas such as Rocky Mountains and Sierra Nevada in USA and Sierra Madre in Mexico. Also, at such spatial grain we cannot capture fine-scale influences, such as topography and forest development stages, which are key determinants of productivity (e.g. Michaletz et al., 2014). Nevertheless, this resolution avoids the false absence problem caused by the clumped distribution of species occurrence data and is generally recommended in macroecological studies (Hurlbert & Jetz, 2007).

A second potential issue is sampling bias; there were gaps in spatial coverage of tree occurrences in both the Amazon Basin and Canada (Figure S1), which may have generated some of the outlying values in grid-cell 95th percentile and average of trait values. A possible solution to avoid the sampling bias would be to use modelled species range maps. Nevertheless, the disadvantage of species range maps is that they are modelled in part using climate variables (Goldsmith et al., 2016), which could generate some level of circularity in analyses with climate as an explanatory variable. Also, for trait values, we were missing many records, especially from the Amazon Basin, which could also have biased our results. Still, as we showed in a previous study (Šímová et al., 2018), the trait-climate correlations of woody species are robust to this sampling bias. Some uncertainty also concerns canopy height due to the necessary extrapolation of the spatially separated point

measurements (Tao et al., 2016), and also due to its inaccurate estimate with increasing terrain rugosity (Lefsky, 2010; Simard et al., 2011). Moreover, the ability of satellite-based canopy height in predicting above ground biomass (and thus also NPP) may be biased due to missing information of variation in wood density and tree allometry (Mitchard et al., 2014).

We suggest that our findings should be reexamined when better, large-scale trait and canopy data become available. Similar problems may also affect the MODIS-based productivity estimate, which is modelled based on remote sensing, solar radiation, temperature and water vapour deficit (Running et al., 2004; Zhao et al., 2005), potentially leading to some circularity in analyses with climate. Moreover, the MODIS-based productivity model does not explicitly account for the effect of soil nutrients as one of the factors limiting plant growth, which leads to some uncertainty of the productivity estimates, especially in tropical regions (Cleveland et al., 2015; Šímová & Storch, 2017). Large-scale soil data also can be problematic as they are generated with relatively high uncertainty (Yang, Post, Thornton, & Jain, 2013), which can be responsible for the overall weak support for the links between leaf and soil nutrients. Another potential problem concerns the data analysis. Although structural equation modelling (SEM) is a powerful data-analytic technique, selecting the model that best fits the data can result in some degree of selection uncertainty (Whittingham, Stephens, Bradbury, & Freckleton, 2006). This is due to the dependency of model rankings on sample size (Preacher & Merkle, 2012). Consequently, it is important that our results be reevaluated when more data are available, especially from other parts of the world. Lastly, as our study is restricted to forests, we recommend future studies explore the link between plant functional traits and large-scale ecosystem processes in non-forest biomes.

In summary, our results point to the importance of tree size as a driver of forest productivity. We found that water availability limits productivity of tropical and temperate forests, both directly and indirectly via the maximum size to which tree species can grow. This finding agrees with the Metabolic Scaling Theory (West et al., 2009) and with recent evidence for tall trees as important drivers of forest carbon flux (Fauset et al., 2015; Stephenson et al., 2014). Furthermore, we found that productivity of tropical and temperate forests strongly depends on the leaf nutrient concentration, which is also largely driven by climate. Our results support recent attempts to include information on plant functional traits in models predicting dynamics of the global carbon cycle (Reichstein, Bahn, Mahecha, Kattge, & Baldocchi, 2014). Nevertheless, the importance of plant traits is not universal, or is at least context dependent, as different processes matter more in different environmental contexts.

ACKNOWLEDGEMENT

This work was conducted as a part of the Botanical Information and Ecology Network (BIEN) Working Group (PIs BJE, Richard Condit, BBoyle, SD, RKP) supported by the National Center for Ecological Analysis and Synthesis (funded by NSF Grant

#EF-0553768), the University of California, Santa Barbara, and the State of California. The BIEN Working Group was also supported by iPlant (NSF #DBI-0735191; URL: www.iplantcollaborative.org). This study has also been supported by the TRY initiative on plant traits (<http://www.try-db.org>). The TRY initiative and database is hosted at the Max Planck Institute for Biogeochemistry, Jena, Germany, and is currently supported by DIVERSITAS/Future Earth, the EU BACI project (#640176) and the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig. I.S. was funded by grant #16-26369S from the Grant Agency of The Czech Republic and by Charles University Research Centre program No. 204069. B.J.E. was supported by NSF awards (#DEB1457812 and #EF1065844). J.-C.S. was supported by the European Research Council (#ERC-2012-StG-310886-HISTFUNC) and also considers this work a contribution to his VILLUM Investigator project funded by VILLUM FONDEN (grant #16549). B.J.M. was supported by USDA Hatch grant to MAFES #1011538 and NSF ABI grant #1660000. N.M.-H. was supported by the Carlsberg Foundation and acknowledges the Danish National Research Foundation for support to the Center for Macroecology, Evolution and Climate. S.K.W. was supported by Core funding for Crown Research Institutes from the New Zealand Ministry of Business, Innovation and Employment's Science and Innovation Group. C.V. was supported by the European Research Council (ERC) Starting Grant Project 'Ecophysiological and biophysical constraints on domestication of crop plants' (#ERC-StG-2014-639706-CONSTRAINTS). B.B. was supported by the UK Natural Environment Research Council (NERC) (#NE/M019160/1). We thank Marco Giardello for the useful comments on the structural equation models.

AUTHORS' CONTRIBUTIONS











I.S., J.-C.S., B.S. and B.J.E. conceived the study; I.S. analysed the data and led the writing with major contributions from J.-C.S., B.S. and S.T.M.; B.J.E., R.K.P., B. Boyle, J.-C.S., S.K.W., C.V., N.J.B.K., N.M.-H. and B.J.M. developed the BIEN database (<http://bien.nceas.ucsb.edu/bien/>), J.K. provided the TRY database. All authors discussed and commented on the manuscript.

DATA ACCESSIBILITY

The reference list for BIEN and TRY data is available in Appendix S1. The species occurrence table and raster maps of mean leaf traits are available via Šímová et al. (2018). The raster map of maximum plant height and aggregated data frame is available online at TRY file archive (<https://www.try-db.org/TryWeb/Data.php#20>). Trait data are available via the BIEN package (Maitner, 2017) and TRY (www.try-db.org).

ORCID

Irena Šímová  <https://orcid.org/0000-0002-9474-569X>

Brody Sandel  <https://orcid.org/0000-0003-2162-6902>
 Brian J. Enquist  <https://orcid.org/0000-0002-6124-7096>
 Sean T. Michaletz  <https://orcid.org/0000-0003-2158-6525>
 Cyrille Violle  <https://orcid.org/0000-0002-2471-9226>
 Benjamin Blonder  <https://orcid.org/0000-0002-5061-2385>
 Kristine Engemann  <https://orcid.org/0000-0003-1431-1726>
 Robert K. Peet  <https://orcid.org/0000-0003-2823-6587>
 Susan K. Wiser  <https://orcid.org/0000-0002-8938-8181>
 Naia Morueta-Holme  <https://orcid.org/0000-0002-0776-4092>
 Brad Boyle  <https://orcid.org/0000-0002-9934-6655>
 Jens-Christian Svenning  <https://orcid.org/0000-0002-3415-0862>

REFERENCES

- Bastin, J.-f., Barbier, N., Réjou-Méchain, M., Fayolle, A., Gourlet-Fleury, S., Maniatis, D., ... Bogaert, J. (2015). Seeing Central African forests through their largest trees. *Scientific Reports*, 5, 13156. <https://doi.org/10.1038/srep13156>
- Bennett, A. C., McDowell, N. G., Allen, C. D., & Anderson-Teixeira, K. J. (2015). Larger trees suffer most during drought in forests worldwide. *Nature Plants*, 1(10), 15139. <https://doi.org/10.1038/NPLANTS.2015.139>
- Bollen, K. A., Harden, J. J., Ray, S., & Zavisca, J. (2014). BIC and alternative Bayesian information criteria in the selection of structural equation models. *Structural Equation Modeling: A Multidisciplinary Journal*, 21(1), 1–19. <https://doi.org/10.1080/10705511.2014.856691>
- Chapin, F. S. III, Bret-Harte, M. S., Hobbie, S. E., & Zhong, H. (1996). Plant functional types as predictors of transient responses of arctic vegetation to global change. *Journal of Vegetation Science*, 7(3), 347–358. <https://doi.org/10.2307/3236278>
- Chapin, F. S. III, Matson, P. A., & Vitousek, P. (2011). *Principles of terrestrial ecosystem ecology* (2nd ed.). New York: Springer-Verlag.
- Chapin III, F. S., Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., ... Díaz, S. (2000). Consequences of changing biodiversity. *Nature*, 405(6783), 234–242. <https://doi.org/10.1038/35012241>
- Chu, C., Bartlett, M., Wang, Y., He, F., Weiner, J., Chave, J., & Sack, L. (2016). Does climate directly influence NPP globally? *Global Change Biology*, 22(1), 12–24. <https://doi.org/10.1111/gcb.13079>
- Cleveland, C. C., Taylor, P., Chadwick, K. D., Dahlin, K., Doughty, C. E., Malhi, Y., ... Townsend, A. R. (2015). A comparison of plot-based, satellite and Earth system model estimates of tropical forest net primary production. *Global Biogeochemical Cycles*, 29(5), 626–644. <https://doi.org/10.1002/2014GB005022>
- Coomes, D. A., Holdaway, R. J., Kobe, R. K., Lines, E. R., & Allen, R. B. (2012). A general integrative framework for modelling woody biomass production and carbon sequestration rates in forests. *Journal of Ecology*, 100(1), 42–64. <https://doi.org/10.1111/j.1365-2745.2011.01920.x>
- Cornwell, W. K., Cornelissen, J. H. C., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., ... Westoby, M. (2008). Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters*, 11(10), 1065–1071. <https://doi.org/10.1111/j.1461-0248.2008.01219.x>
- DeLucia, E. H., Drake, J. E., Thomas, R. B., & Gonzalez-Meler, M. (2007). Forest carbon use efficiency: Is respiration a constant fraction of gross primary production? *Global Change Biology*, 13(6), 1157–1167.
- Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K., & Robson, T. M. (2007). Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences*, 104(52), 20684–20689. <https://doi.org/10.1073/pnas.0704716104>
- 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(1), 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>
- Engemann, K., Sandel, B., Boyle, B., Enquist, B. J., Jørgensen, P. M., Kattge, J., ... Svenning, J.-C. (2016). A plant growth form dataset for the New World. *Ecology*, 97(11), 3243–3243. <https://doi.org/10.1002/ecy.1569>
- Enquist, B. J. (2011). Forest annual carbon cost: comment. *Ecology*, 92(10), 1994–1998. <https://doi.org/10.1890/10-1912.1>
- Enquist, B. J., Norberg, J., Bonser, S. P., Violle, C., Webb, C. T., Henderson, A., ... Savage, V. M. (2015). Scaling from traits to ecosystems: Developing a general Trait Driver Theory via integrating trait-based and metabolic scaling theories. *Advances in Ecological Research*, 52, 249–318. <https://doi.org/10.1016/b.s.aecr.2015.02.001>
- Enquist, B. J., West, G. B., & Brown, J. H. (2009). Extensions and evaluations of a general quantitative theory of forest structure and dynamics. *Proceedings of the National Academy of Sciences*, 106(17), 7046–7051. <https://doi.org/10.1073/pnas.0812303106>
- Fauset, S., Johnson, M. O., Gloor, M., Baker, T. R., Monteagudo M., A., Brien, R. J. W., ... Phillips, O. L. (2015). Hyperdominance in Amazonian forest carbon cycling. *Nature Communications*, 6, 6857. <https://doi.org/10.1038/ncomms7857>
- Fernández-Martínez, M., Vicca, S., Janssens, I. a., Sardans, J., Luyssaert, S., Campioli, M., ... Peñuelas, J. (2014). Nutrient availability as the key regulator of global forest carbon balance. *Nature Climate Change*, 4(6), 471–476. <https://doi.org/10.1038/nclimate2177>
- Finegan, B., Peña-Claros, M., de Oliveira, A., Ascarrunz, N., Bret-Harte, M. S., Carreño-Rocabado, G., ... Poorter, L. (2015). Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses. *Journal of Ecology*, 103(1), 191–201. <https://doi.org/10.1111/1365-2745.12346>
- Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., ... Toussaint, J.-P. (2004). Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, 85(9), 2630–2637. <https://doi.org/10.1890/03-0799>
- Gholz, H. L. (1982). Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. *Ecology*, 63(2), 469–481. <https://doi.org/10.2307/1938964>
- Goldsmith, G. R., Morueta-Holme, N., Sandel, B., Fitz, E. D., Fitz, S. D., Boyle, B., ... Kraft, N. J. (2016). Plant-O-Matic: A dynamic and mobile guide to all plants of the Americas. *Methods in Ecology and Evolution*, 7(8), 960–965. <https://doi.org/10.1111/2041-210X.12548>
- Grime, J. P. (1997). Biodiversity and ecosystem function: The debate deepens. *Science*, 277(5330), 1260–1261. <https://doi.org/10.1126/science.277.5330.1260>
- Hair, J. F., Ringle, C. M., & Sarstedt, M. (2011). PLS-SEM: Indeed a silver bullet. *Journal of Marketing Theory and Practice*, 19(2), 139–152. <https://doi.org/10.2753/MTP1069-6679190202>
- Hair, J. F., Risher, J. J., Sarstedt, M., & Ringle, C. M. (2018). When to use and how to report the results of PLS-SEM. *European Business Review*, 31(1), <https://doi.org/10.1108/EBR-11-2018-0203>
- Hedin, L. O. (2004). Global organization of terrestrial plant–nutrient interactions. *Proceedings of the National Academy of Sciences*, 101(30), 10849–10850. <https://doi.org/10.1073/pnas.0404222101>
- 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(15), 1965–1978. <https://doi.org/10.1002/joc.1276>
- Hijmans, R. J., van Etten, J., Cheng, J., Mattiuzzi, M., Sumner, M., Greenberg, J. A., Shortridge, A. (2016). raster: Geographic Data Analysis and Modeling version 2.5-8. (Version 2.5-8). Retrieved from <http://cran.r-project.org/package=raster><https://cran.r-project.org/web/packages/raster/index.html>
- Hurlbert, A. H., & Jetz, W. (2007). Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proceedings of the National Academy of Sciences*, 104(33), 13384–13389. <https://doi.org/10.1073/pnas.0704469104>
- Jack Brookshire, E. N., Gerber, S., Webster, J. R., Vose, J. M., & Swank, W. T. (2011). Direct effects of temperature on forest nitrogen cycling revealed through analysis of long-term watershed records. *Global Change Biology*, 17(1), 297–308. <https://doi.org/10.1111/j.1365-2486.2010.02245.x>
- Jenkins, D. G. (2015). Estimating ecological production from biomass. *Ecosphere*, 6(4), art49. <https://doi.org/10.1890/ES14-00409.1>
- Kattge, J., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönsch, G., ... Wirth, C. (2011). TRY – A global database of plant traits. *Global Change Biology*, 17(9), 2905–2935. <https://doi.org/10.1111/j.1365-2486.2011.02451.x>
- Keeling, H. C., & Phillips, O. L. (2007). The global relationship between forest productivity and biomass. *Global Ecology and Biogeography*, 16(5), 618–631. <https://doi.org/10.1111/j.1466-8238.2007.00314.x>
- Kerkhoff, A. J., & Enquist, B. J. (2007). The implications of scaling approaches for understanding resilience and reorganization in ecosystems. *AIBS Bulletin*, 57(6), 489–499. <https://doi.org/10.1641/B570606>
- Kerkhoff, A. J., Enquist, B. J., Elser, J. J., & Fagan, W. F. (2005). Plant allometry, stoichiometry and the temperature-dependence of primary productivity. *Global Ecology and Biogeography*, 14(6), 585–598. <https://doi.org/10.1111/j.1466-822X.2005.00187.x>
- Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology*, 16(5), 545–556. <https://doi.org/10.1046/j.1365-2435.2002.00664.x>
- Lavorel, S., Storkey, J., Bardgett, R. D., de Bello, F., Berg, M. P., Le Roux, X., ... Harrington, R. (2013). A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. *Journal of Vegetation Science*, 24(5), 942–948. <https://doi.org/10.1111/jvs.12083>
- LeBauer, D. S., & Treseder, K. K. (2008). Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology*, 89(2), 371–379. <https://doi.org/10.1890/06-2057.1>
- Lefsky, M. A. (2010). A global forest canopy height map from the Moderate Resolution Imaging Spectroradiometer and the Geoscience Laser Altimeter System. *Geophysical Research Letters*, 37(15), L15401. <https://doi.org/10.1029/2010GL043622>
- Ligot, G., Gourlet-Fleury, S., Ouedraogo, D.-Y., Morin, X., Bauwens, S., Baya, F., ... Fayolle, A. (2018). The limited contribution of large trees to annual biomass production in an old-growth tropical forest. *Ecological Applications*, 28(5), 1273–1281. <https://doi.org/10.1002/eap.1726>
- Maitner, B. (2017). BIEN: Tools for Accessing the Botanical Information and Ecology Network Database version 1.1.0. (Version 1.1.0). Retrieved from <https://CRAN.R-project.org/package=BIEN>
- Maitner, B. S., Boyle, B., Casler, N., Condit, R., Donoghue, J., Durán, S. M., ... Kraft, N. J. (2018). The bien r package: A tool to access the Botanical Information and Ecology Network (BIEN) database. *Methods in Ecology and Evolution*, 9(2), 373–379. <https://doi.org/10.1111/2041-210X.12861>
- Malhi, Y., Doughty, C. E., Goldsmith, G. R., Metcalfe, D. B., Girardin, C. A. J., Marthews, T. R., ... Phillips, O. L. (2015). The linkages between photosynthesis, productivity, growth and biomass in lowland Amazonian forests. *Global Change Biology*, 21(6), 2283–2295. <https://doi.org/10.1111/gcb.12859>
- McDowell, N. G., & Allen, C. D. (2015). Darcy's law predicts widespread forest mortality under climate warming. *Nature Climate Change*, 5(7), 669–672. <https://doi.org/10.1038/nclimate2641>
- McDowell, N. G., Michaletz, S. T., Bennett, K. E., Solander, K. C., Xu, C., Maxwell, R. M., & Middleton, R. S. (2018). Predicting chronic climate-driven disturbances and their mitigation. *Trends in Ecology & Evolution*, 33(1), 15–27. <https://doi.org/10.1016/j.tree.2017.10.002>
- Mercado, L. M., Patino, S., Domingues, T. F., Fyllas, N. M., Weedon, G. P., Sitch, S., ... Lloyd, J. (2011). Variations in Amazon forest productivity correlated with foliar nutrients and modelled rates of photosynthetic carbon supply. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 366(1582), 3316–3329. <https://doi.org/10.1098/rstb.2011.0045>
- Michaletz, S. T., Cheng, D., Kerkhoff, A. J., & Enquist, B. J. (2014). Convergence of terrestrial plant production across global climate gradients. *Nature*, 215, 39–43. <https://doi.org/10.1038/nature13470>
- Michaletz, S. T., Kerkhoff, A. J., & Enquist, B. J. (2018). Drivers of terrestrial plant production across broad geographical gradients. *Global Ecology and Biogeography*, 27(2), 166–174. <https://doi.org/10.1111/geb.12685>
- Mitchard, E. T. A., Feldpausch, T. R., Brien, R. J. W., Lopez-Gonzalez, G., Monteagudo, A., Baker, T. R., ... Phillips, O. L. (2014). Markedly divergent estimates of Amazon forest carbon density from ground plots and satellites. *Global Ecology and Biogeography*, 23(8), 935–946. <https://doi.org/10.1111/geb.12168>
- Muller-Landau, H. C., Condit, R. S., Chave, J., Thomas, S. C., Bohlman, S. A., Bunyavejchewin, S., ... Ashton, P. (2006). Testing metabolic ecology theory for allometric scaling of tree size, growth and mortality in tropical forests. *Ecology Letters*, 9(5), 575–588. <https://doi.org/10.1111/j.1461-0248.2006.00904.x>
- Niklas, K. J., & Enquist, B. J. (2001). Invariant scaling relationships for interspecific plant biomass production rates and body size. *Proceedings of the National Academy of Sciences*, 98(5), 2922–2927. <https://doi.org/10.1073/pnas.041590298>
- Preacher, K. J., & Merkle, E. C. (2012). The problem of model selection uncertainty in structural equation modeling. *Psychological Methods*, 17(1), 1. <https://doi.org/10.1037/a0026804>
- Quesada, C. A., Phillips, O. L., Schwarz, M., Czimczik, C. I., Baker, T. R., Patiño, S., ... Lloyd, J. (2012). Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. *Biogeosciences*, 9(6), 2203–2246. <https://doi.org/10.5194/bg-9-2203-2012>
- R Development Core Team (2017). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
- Raich, J. W., Russell, A. E., Kitayama, K., Parton, W. J., & Vitousek, P. M. (2006). Temperature influences carbon accumulation in moist tropical forests. *Ecology*, 87(1), 76–87. <https://doi.org/10.1890/05-0023>
- Reich, P. B., & Oleksyn, J. (2004). Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences of the United States of America*, 101(30), 11001–11006. <https://doi.org/10.1073/pnas.0403588101>
- Reich, P. B., Walters, M. B., & Ellsworth, D. S. (1992). Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs*, 62(3), 365–392. <https://doi.org/10.2307/2937116>
- 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*, 94(25), 13730–13734. <https://doi.org/10.1073/pnas.94.25.13730>
- Reichstein, M., Bahn, M., Mahecha, M. D., Kattge, J., & Baldocchi, D. D. (2014). Linking plant and ecosystem functional biogeography.

- Proceedings of the National Academy of Sciences*, 111(38), 13697–13702. <https://doi.org/10.1073/pnas.1216065111>
- Rosseel, Y. (2012). lavaan: An R package for structural equation modeling. *Journal of Statistical Software*, 48(2), 1–36.
- Running, S. W., Nemani, R. R., Heinsch, F. A., Zhao, M., Reeves, M., & Hashimoto, H. (2004). A continuous satellite-derived measure of global terrestrial primary production. *BioScience*, 54(6), 547–560. [https://doi.org/10.1641/0006-3568\(2004\)054\[0547:ACSMOG\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054[0547:ACSMOG]2.0.CO;2)
- Ryan, M. G., & Yoder, B. J. (1997). Hydraulic limits to tree height and tree growth. *BioScience*, 47(4), 235–242. <https://doi.org/10.2307/1313077>
- Sankaran, M., Hanan, N. P., Scholes, R. J., Ratnam, J., Augustine, D. J., Cade, B. S., ... Zambatis, N. (2005). Determinants of woody cover in African savannas. *Nature*, 438(7069), 846–849. <https://doi.org/10.1038/nature04070>
- Schuur, E. A. G. (2003). Productivity and global climate revisited: The sensitivity of tropical forest growth to precipitation. *Ecology*, 84(5), 1165–1170. [https://doi.org/10.1890/0012-9658\(2003\)084\[1165:PAGCRT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[1165:PAGCRT]2.0.CO;2)
- Simard, M., Pinto, N., Fisher, J. B., & Baccini, A. (2011). Mapping forest canopy height globally with spaceborne lidar. *Journal of Geophysical Research: Biogeosciences*, 116(G4), G04021. <https://doi.org/10.1029/2011JG001708>
- Šímová, I., Rueda, M., & Hawkins, B. A. (2017). Stress from cold and drought as drivers of functional trait spectra in North American angiosperm tree assemblages. *Ecology and Evolution*, 7(18), 7548–7559. <https://doi.org/10.1002/ece3.3297>
- Šímová, I., & Storch, D. (2017). The enigma of terrestrial primary productivity: Measurements, models, scales and the diversity–productivity relationship. *Ecography*, 40(2), 239–252. <https://doi.org/10.1111/ecog.02482>
- Šímová, I., Violle, C., Svenning, J.-C., Kattge, J., Engemann, K., Sandel, B., ... Enquist, B. J. (2018). Spatial patterns and climate relationships of major plant traits in the New World differ between woody and herbaceous species. *Journal of Biogeography*, 45(2), 895–916. <https://doi.org/10.1111/jbi.13171>
- Stegen, J. C., Swenson, N. G., Enquist, B. J., White, E. P., Phillips, O. L., Jørgensen, P. M., ... Núñez Vargas, P. (2011). Variation in above-ground forest biomass across broad climatic gradients. *Global Ecology and Biogeography*, 20(5), 744–754. <https://doi.org/10.1111/j.1466-8238.2010.00645.x>
- Stephenson, N. I., Das, A. J., Condit, R., Russo, S. E., Baker, P. J., Beckman, N. G., ... Zavala, M. A. (2014). Rate of tree carbon accumulation increases continuously with tree size. *Nature*, 507(7490), 90–93. <https://doi.org/10.1038/nature12914>
- Tanner, E. V. J., Vitousek, P. M., & Cuevas, E. (1998). Experimental investigation of nutrient limitation of forest growth on wet tropical mountains. *Ecology*, 79(1), 10–22. [https://doi.org/10.1890/0012-9658\(1998\)079\[0010:EIONLO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[0010:EIONLO]2.0.CO;2)
- Tansey, K., Grégoire, J.-M., Defourny, P., Leigh, R., Pekel, J.-F., van Bogaert, E., & Bartholomé, E. (2008). A new, global, multi-annual (2000–2007) burnt area product at 1 km resolution. *Geophysical Research Letters*, 35(1), L01401. <https://doi.org/10.1029/2007GL031567>
- Tao, S., Guo, Q., Li, C., Wang, Z., & Fang, J. (2016). Global patterns and determinants of forest canopy height. *Ecology*, 97(12), 3265–3270. <https://doi.org/10.1002/ecy.1580>
- Trabucco, A., & Zomer, R. J. (2010). Global soil water balance geospatial database. CGIAR Consortium for Spatial Information. Retrieved from CGIAR-CSI GeoPortal at <http://www.Cgiar-Csi.Org>
- Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional!. *Oikos*, 116(5), 882–892. <https://doi.org/10.1111/j.2007.0030-1299.15559.x>
- Vitousek, P. M. (1984). Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology*, 65(1), 285–298. <https://doi.org/10.2307/1939481>
- Vitousek, P. M., Porder, S., Houlton, B. Z., & Chadwick, O. A. (2010). Terrestrial phosphorus limitation: Mechanisms, implications, and nitrogen–phosphorus interactions. *Ecological Applications*, 20(1), 5–15. <https://doi.org/10.1890/08-0127.1>
- Walker, T. W., & Syers, J. K. (1976). The fate of phosphorus during pedogenesis. *Geoderma*, 15(1), 1–19. [https://doi.org/10.1016/0016-7061\(76\)90066-5](https://doi.org/10.1016/0016-7061(76)90066-5)
- Wardle, D. A., Walker, L. R., & Bardgett, R. D. (2004). Ecosystem properties and forest decline in contrasting long-term chronosequences. *Science*, 305(5683), 509–513.
- Waring, R. H. (1983). Estimating forest growth and efficiency in relation to canopy leaf area. In A. MacFadyen, & E. D. Ford (Eds.), *Advances in ecological research* (Vol. 13, pp. 327–354). Cambridge, MA: Academic Press. [https://doi.org/10.1016/S0065-2504\(08\)60111-7](https://doi.org/10.1016/S0065-2504(08)60111-7)
- West, G. B., Enquist, B. J., & Brown, J. H. (2009). A general quantitative theory of forest structure and dynamics. *Proceedings of the National Academy of Sciences*, 106(17), 7040–7045. <https://doi.org/10.1073/pnas.0812294106>
- Whittingham, M. J., Stephens, P. A., Bradbury, R. B., & Freckleton, R. P. (2006). Why do we still use stepwise modelling in ecology and behaviour? *Journal of Animal Ecology*, 75(5), 1182–1189. <https://doi.org/10.1111/j.1365-2656.2006.01141.x>
- Wieder, W. R., Boehnert, J., Bonan, G. B., & Langseth, M. (2014). RegridDED Harmonized World Soil Database v1.2. ORNL DAAC. <https://doi.org/10.3334/ORNLDAAAC/1247>
- Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., ... Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, 428(6985), 821–827. <https://doi.org/10.1038/nature02403>
- Yang, X., Post, W. M., Thornton, P. E., & Jain, A. (2013). The distribution of soil phosphorus for global biogeochemical modeling. *Biogeosciences*, 10(4), 2525–2537. <https://doi.org/10.5194/bg-10-2525-2013>
- Yang, X., Post, W. M., Thornton, P. E., & Jain, A. K. (2014). Global Gridded Soil Phosphorus Distribution Maps at 0.5-degree Resolution. ORNL DAAC. <https://doi.org/10.3334/ORNLDAAAC/1223>
- Zhao, M., 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(2), 164–176. <https://doi.org/10.1016/j.rse.2004.12.011>
- Zhao, M., & Running, S. W. (2010). Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. *Science*, 329(5994), 940–943. <https://doi.org/10.1126/science.1192666>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Šímová I, Sandel B, Enquist BJ, et al. The relationship of woody plant size and leaf nutrient content to large-scale productivity for forests across the Americas. *J Ecol.* 2019;00:1–13. <https://doi.org/10.1111/1365-2745.13163>