

# Regional and historical factors supplement current climate in shaping global forest canopy height

Jian Zhang<sup>1,2\*</sup>, Scott E. Nielsen<sup>2</sup>, Lingfeng Mao<sup>3</sup>, Shengbin Chen<sup>4</sup> and Jens-Christian Svenning<sup>1</sup>

<sup>1</sup>Section for Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus University, Ny Munkegade 114, Aarhus C DK-8000, Denmark; <sup>2</sup>Department of Renewable Resources, University of Alberta, Edmonton, Alberta T6G 2H1, Canada; <sup>3</sup>Department of Plant Biology, Michigan State University, East Lansing, MI 48824, USA; and <sup>4</sup>Nanjing Institute of Environmental Sciences, Ministry of Environmental Protection of the People's Republic of China, Nanjing 210042, China

## Summary

1. Canopy height is a key factor that affects carbon storage, vegetation productivity and biodiversity in forests, as well as an indicator of key processes such as biomass allocation. However, global variation in forest canopy height and its determinants are poorly known.

2. We used global data on Light Detection and Ranging-derived maximum forest canopy height ( $H_{\max}$ ) to test hypotheses relating  $H_{\max}$  to current climate (water availability, ambient energy and water–energy dynamics), regional evolutionary and biogeographic history, historical climate change, and human disturbance.

3. We derived  $H_{\max}$  for 32 304 forested 55-km grid cells using 1-km global canopy height data (maximum height of 1-km cells within a 55-km grid). Variation in  $H_{\max}$  was related to latitude and biomes, along with environmental and historical variables. Both spatial and non-spatial linear models were used to assess the relative importance of the different hypothesized factors.

4.  $H_{\max}$  was inversely related to latitude (i.e. tall canopies at the equator), but with high geographical variability. Actual evapotranspiration and annual precipitation were the factors most correlated to  $H_{\max}$  globally, thus supporting the water–energy dynamics hypothesis. However, water limitation emerged as a key factor in tropical and temperate biomes within specific geographic regions, while energy limitation was a more important factor in boreal regions where temperature is more limiting to trees than water.

5.  $H_{\max}$  exhibited strong variation among biogeographic regions, supporting the role of regional evolutionary and biogeographic history in structuring broad-scale patterns in canopy height. Furthermore, there were divergent relationships between climate and  $H_{\max}$  between the Southern and Northern Hemispheres, consistent with historical evolutionary contingencies modulating these relationships. Historical climate change was also related to  $H_{\max}$ , albeit not as strongly, with shorter canopy heights where late-Quaternary climate has been less stable. In contrast, human disturbance was only weakly related to  $H_{\max}$  at the scale (55 km) examined here.

6. *Synthesis.* This study confirms that forest canopy height is strongly controlled by current climate, but also provides evidence for an important supplementary role for regional–historical factors. This highlights the importance of considering evolutionary and biogeographic history for achieving a comprehensive understanding of forest ecosystem properties.

**Key-words:** determinants of plant community diversity and structure, evolutionary history, forest vertical structure, historical contingency, paleoclimate, regional effect, remote sensing, water–energy dynamics

\*Correspondence author. E-mail: jzhang1982@gmail.com

## Introduction

Forest canopy height, as both a product and driver of ecosystem processes, has important effects on biomass allocation and carbon storage (Lefsky *et al.* 2002; Saatchi *et al.* 2011; Slik *et al.* 2013; Zhang *et al.* 2014), forest productivity (Thomas *et al.* 2008; Antonarakis *et al.* 2011), as well as plant and animal diversity (MacArthur & MacArthur 1961; Dudley & DeVries 1990; Zhang, Kissling & He 2013; Gouveia *et al.* 2014; Roll, Geffen & Yom-Tov 2015). Canopy height exhibits strong geographical variability, ranging from over 50 m in Asian dipterocarp (Dipterocarpaceae) forests (Banin *et al.* 2012), Australia's eucalypt (*Eucalyptus*) forests (Givnish *et al.* 2014) and the temperate conifer forests on the North American west coast (Koch *et al.* 2004; Spellenberg, Earle & Nelson 2014) to less than 20 m in many boreal forests (Zhang *et al.* 2014). However, local and regional drivers underlying this variability are not well understood.

Most previous studies have focused on the determinants of the tallest individual trees. For example, Koch *et al.* (2004) analysed the factors limiting tree height in redwoods (*Sequoia sempervirens*) in northern California and concluded that water stress limited growth and height of redwood trees. Moles *et al.* (2009) collected and analysed plant height data from 222 field locations world-wide and found that water availability, measured by precipitation in the wettest month, was an important determinant in maximum plant height, again supporting water stress as a key limiting factor (Ryan, Phillips & Bond 2006). Larjavaara (2014) used a data set of 29 giant trees from across the world, and found that temperature was the most significant determinant of the occurrence of the tallest (>90 m) individual trees, supporting the alternative energy limitation hypothesis.

In contrast to individual maximum tree heights, forest canopy height, which is more directly related to local and regional biomass and productivity, has not attracted as much attention. Banin *et al.* (2012) analysed cross-continental differences in maximum height and allometry using 112 tropical moist forest plots, documenting substantial continental differences in maximum height, partly explained by precipitation seasonality, stand basal area, tree density and wood density. Strong correlations between forest canopy height and biomass has been detected in a number of studies. For example, canopy height explained 73% of the variance in above-ground biomass in tropical forests (Lefsky *et al.* 2005) and 70% of this variance in boreal forests (Zhang *et al.* 2014). Stegen *et al.* (2011) found that climatic variables were poor predictors of forest biomass across the Americas, while Reich *et al.* (2014) found that temperature plays an important role in explaining global variation in forest biomass with water limitation having a weak effect. In addition, evolutionary and biogeographic history (Latham & Ricklefs 1993), historical climate change (McGlone 1996) and human disturbance (Kareiva *et al.* 2007; Ellis *et al.* 2013) could also constrain patterns in canopy height, although these factors have rarely been considered. Overall, the relative importance of environmental and historical factors in explaining regional

and global patterns in forest canopy height remains largely unexplored.

Most previous studies have small sample sizes and geographic biases in sampling. Moles *et al.* (2009) included very few sites in Europe and Asia, especially at high latitudes, while Stegen *et al.* (2011) restricted their analyses to 276 small plots (0.1 ha) across the New World with only ~20 plots located in North America north of Mexico. Sampled sites in many of these studies were non-random in distribution resulting in potential geographic biases. Thus, the lack of sufficient, high-quality and geographically non-biased data has been identified as a barrier to understanding the mechanisms driving broad-scale patterns in forest canopy height (Moles *et al.* 2009).

The development of remote sensing techniques, especially LiDAR (Light Detection and Ranging), provides an expanding source of information for quantifying forest canopy structure (Lefsky *et al.* 2002; Turner *et al.* 2003; Rose *et al.* 2015). At a global scale, Simard *et al.* (2011) produced a global forest canopy height map at 1-km spatial resolution by using the Geoscience Laser Altimeter System (GLAS) estimates that were consistent with field measurements from 66 globally distributed FLUXNET sites. A few recent studies, such as Saatchi *et al.* (2011) in tropical forests and Zhang *et al.* (2014) in boreal forests, have demonstrated the benefits of using LiDAR-derived canopy height data for regional-scale biomass mapping. Gouveia *et al.* (2014) analysed global distribution of non-human primates using LiDAR-derived canopy height as a predictor, finding a strong correlation between primate diversity and canopy height. However, to our knowledge, no study has focused on exploring the mechanisms underlying global-scale forest canopy height patterns using these LiDAR data.

Here, we combined global-scale LiDAR-derived forest canopy height data with environmental and historical variables to quantify the determinants of maximum forest canopy height ( $H_{\max}$ ). Specially, we are interested in testing the following hypotheses:

**1. Current climate:** Previous studies have found clear linkages between current climate and canopy height or biomass, but mixed support for the specific factors involved (Stegen *et al.* 2011; Banin *et al.* 2012). Current climate has been hypothesized to affect canopy height via water- and/or energy-related mechanisms. As trees grow taller, leaf water stress increases due to gravity and path length resistance, ultimately limiting water transport and photosynthesis and thus further growth (Ryan, Phillips & Bond 2006). Given this hydraulic limitation,  $H_{\max}$  should be positively related to water availability (Koch *et al.* 2004). Alternatively, as for biomass accumulation in forest ecosystems (Stegen *et al.* 2011; Larjavaara & Muller-Landau 2012; Reich *et al.* 2014),  $H_{\max}$  could be limited by ambient energy [temperature or potential evapotranspiration (PET)] (Currie 1991; Larjavaara 2014). Tree height may also be limited by the combined effect of water and energy availability (Cramer 2012), resulting in a positive relationship between  $H_{\max}$  and actual evapotranspiration (AET), a combined measure of available water

and environmental energy (Stephenson 1998; Francis & Currie 2003). Since the relative importance of two components of water–energy dynamics may vary along a latitudinal gradient (Hawkins *et al.* 2003), we also predict that energy is the most limiting factor for  $H_{\max}$  at high latitudes, while water limitation should be more important at low latitudes.

**2. Regional evolutionary and biogeographic history:** In addition to current climate, long-term regional evolutionary and biogeographic history may shape broad-scale biodiversity patterns (Ricklefs 1987; Latham & Ricklefs 1993; Kreft & Jetz 2007), including function-related aspects such as the diversity of certain growth forms (Couvreur *et al.* 2015). Effects of evolutionary and biogeographic history on phylogenetic and functional composition may have left imprints on  $H_{\max}$  through long-term evolutionary and dispersal dynamics (Banin *et al.* 2012). We therefore expect idiosyncratic differences in  $H_{\max}$  among biogeographic regions of the world.

**3. Historical climate change:** Past changes in climate over longer time scales have left important legacies in contemporary species distributions and biodiversity patterns (McGlone 1996; Svenning & Skov 2007; Sandel *et al.* 2011), also affecting functional diversity patterns in plants (Ordóñez & Svenning 2015). Such dynamics could also affect  $H_{\max}$ . Specifically, we predict a positive relationship between  $H_{\max}$  and late-Quaternary glacial–interglacial climatic stability due to lower extinction rates and a lower immigration lag.

**4. Human disturbance:** Land use by human populations has dramatically reshaped species distributions and ecosystems (Kareiva *et al.* 2007; Ellis *et al.* 2013; Sandel & Svenning 2013), with potentially strong effects on forest canopy height. Human disturbances such as timber harvesting and agricultural land use conversion have transformed forested lands towards disturbed, early-successional habitats, resulting in shorter forest canopy heights. Hence, past and present human disturbance would be expected to be negatively related to  $H_{\max}$ .

## Materials and methods

### CANOPY HEIGHT DATA FROM SPACEBORNE LIDAR

Maximum forest canopy height ( $H_{\max}$ ) data were extracted from a 1-km resolution global canopy height map (Simard *et al.* 2011). This map was produced from data acquired by the GLAS onboard the Ice, Cloud, and land Elevation Satellite. We aggregated 1-km grid cells into 55-km grid cells with an equal-area Behrmann projection (~30 arc-min at the equator) assigning each cell the maximum of the 1-km cell canopy heights within its extent (maximum of 3025 subsamples). Since our focus were on forest ecosystems and maximum heights, we excluded all 55-km grid cells where maximum canopy height was <10 m. These excluded areas accounted for less than 3% of the total forested area resulting in 32 304 global forested grid cells at the 55-km spatial resolution.

### ENVIRONMENTAL AND HISTORICAL VARIABLES

To test hypotheses related to current climate, we used temperature and precipitation for the period 1950–2000 from the WorldClim data base (Hijmans *et al.* 2005) at a spatial resolution of 10 arc-minute.

These data comprised of 19 biologically relevant climate variables (Table S1). Actual evapotranspiration, PET, latent heat flux, net primary productivity and gross primary productivity were obtained from the Moderate Resolution Imaging Spectrometer global terrestrial data at a 30 arc-s resolution (Running *et al.* 2004; Mu, Zhao & Running 2011). Water deficit was calculated as the difference between PET and AET (Stephenson 1990).

To test the historical climate-change hypothesis, we used the velocity and anomaly for mean annual temperature and annual precipitation between the last glacial maximum (LGM; ~21 000 years ago) and the present (1950–2000) to represent the amplitude of late-Quaternary glacial–interglacial climate change using a resolution of 2.5 arc-min (Sandel *et al.* 2011). Climate velocity was based on estimates of past mean annual temperature and annual precipitation from the Paleoclimate Modelling Intercomparison Project Phase II (Braconnot *et al.* 2007), using the means of the CCSM3 (Collins *et al.* 2006) and MIROC3.2 (K-1 model developers, 2004) simulations.

To test the evolutionary and biogeographic history hypothesis, we tested for differences among biogeographic regions (Region) using definitions from Morrone (2002). Morrone (2002) used information from cladistic and phylogenetic analyses of plant species and plate tectonics to define 12 biogeographic regions: Nearctic, Palearctic, Neotropical, Afrotropical, Oriental, Australotropical, Andean, Cape or Afrotropical, Antarctic, Neoguinean, Australotemperate and Neozelandic regions. We used this classification for the current study.

To test the human disturbance hypothesis, we considered four variables related to current and historical human populations: land use history (the year of first significant use; see below), human population density in AD 1750 (Pop\_1750; persons per km<sup>2</sup>), human population density in AD 2005 (Pop\_2005; persons per km<sup>2</sup>) and change in human population density between AD 1750 and AD 2005 (PopInc). Pop\_1750 represents for historical human activities before the Industrial Revolution, while Pop\_2005 represents the current period. Human population density was derived from the History Database of the Global Environment data base (HYDE 3.1) (Goldewijk *et al.* 2011). Following the approach developed by Ellis *et al.* (2013), we calculated the year of the first substantial land use (>20% land use in area) by comparing all land use layers through all available time periods in the HYDE 3.1 data base.

All these predictor layers were projected and aggregated to the 55-km equal-area grid used for the forest canopy height data. Among the 33 total predictor variables (Table S1), some were highly correlated. To reduce multicollinearity, we removed highly correlated variables using Pearson's correlation coefficients (>|0.7|) and keeping those with clearest biological meaning (Dormann *et al.* 2013). In all, we selected 13 variables for the current analysis (Table 1), including AET, water deficit, annual precipitation (Prep), precipitation seasonality (PrepSeason), annual mean temperature (Temp), Region, LGM-to-present velocity and anomaly for Temp and Prep (Temp\_Velocity, Temp\_Anomaly, Prep\_Velocity, and Prep\_Anomaly), land use history, Pop\_1750, and PopInc. To improve normality and linearity of these variables, we log-transformed AET, WaterDeficit, Prep, Pop\_1750 and PopInc, and square-root-transformed  $H_{\max}$ , Temp, Temp\_Velocity and Prep\_Velocity (Table 1). We did not include soil variables, as a preliminary analysis showed only a weak relation between soil nutrient availability and  $H_{\max}$  (Pearson's  $r = -0.03$ ).

### STATISTICAL ANALYSES

We first used Pearson correlations to analyse pair-wise relationships among the different variables, using Dutilleul's (1993) modified

**Table 1.** The predictor variables and the related hypotheses to explain global patterns of maximum forest canopy height. These 13 variables were selected from 33 environmental variables after considering multicollinearity. The full list and detailed description of all 33 variables can be found in Table S1

Variables	Abbreviation	Hypothesis related	Data transformation
Actual evapotranspiration	AET	Water–energy dynamics	log 10
Water deficit [Potential evapotranspiration (PET) – AET]	WaterDeficit	Water–energy dynamics	log 10
Annual precipitation	Prep	Hydraulic limitation	log 10
Precipitation seasonality (coefficient of variation of the monthly precipitation)	PrepSeason	Hydraulic limitation	N.A.
Annual mean temperature	Temp	Energy limitation	sqrt
Biogeographic regions	Region	Evolutionary and biogeographic history	N.A.
Temperature velocity between LGM and today	Temp_Velocity	Historical climate change	sqrt
Precipitation velocity between LGM and today	Prep_Velocity	Historical climate change	sqrt
Temperature anomaly between LGM and today	Temp_Anomaly	Historical climate change	N.A.
Precipitation anomaly between LGM and today	Prep_Anomaly	Historical climate change	N.A.
Land use history (the years of first substantial land use)	LandUseHistory	Human disturbance	N.A.
Human population density in 1750	Pop_1750	Human disturbance	log 10
Increase of human population density between 1750 and 2005	PopInc	Human disturbance	log 10

*t*-test to calculate statistical significance accounting for spatial autocorrelation.

Both non-spatial multiple regression models (ordinary least squares) and spatial linear models (SLM) were used to evaluate the relative importance of the predictor variables in determining patterns in forest canopy height (Mauricio Bini *et al.* 2009). For SLM, spatial simultaneous autoregressive error models (SARs) were used, which allow the inclusion of residual spatial autocorrelation in data (Kissling & Carl 2008). We then used the ‘LMG’ approach to evaluate the relative importance of each predictor on global patterns in canopy height. The ‘LMG’ approach, named after Lindeman, Merenda & Gold (1980), yields ‘natural’ decompositions of the model  $R^2$  in linear regression models (Grömping 2015). This computer-intensive approach has been recently recommended after comparing other importance metrics (Johnson & Lebreton 2004; Grömping 2006), since it clearly identifies a variable’s contribution by itself and in combination with all other predictors (Johnson & Lebreton 2004).

To avoid multicollinearity problems, we divided our analyses into eight models by excluding highly correlated variables (AET and Prep; Temp\_Velocity and Temp\_Anomaly) (Table S2) from the same models. Averages and variances of the relative importance of all models were used for reporting results. To calculate the relative importance of variables in SLM, we first fit a SLM and then removed the spatial component of fitted values by entering  $H_{\max}$ , excluding the spatial component as a new response variable in the  $R^2$  partitioning procedure (Belmaker & Jetz 2011). These analyses were conducted for the whole data set and separate data sets for each of the seven forest biomes (Olson *et al.* 2001) and for both the Southern and Northern Hemispheres. The seven forest biomes assessed were (i) tropical and subtropical moist broadleaf forests, (ii) tropical and subtropical dry broadleaf forests, (iii) tropical and subtropical coniferous forests, (iv) Mediterranean forests, woodlands and scrub, (v) temperate broadleaf and mixed forests, (vi) temperate coniferous forests and (vii) boreal forests (Olson *et al.* 2001).

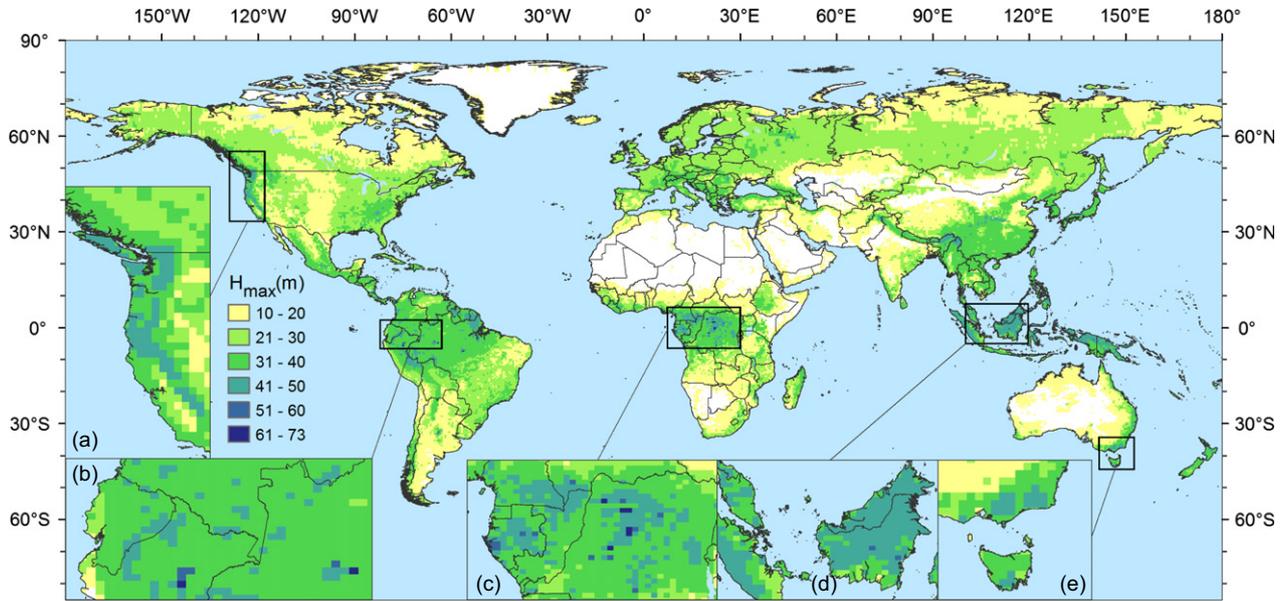
All statistical analyses were carried out using R 3.1.2 software (R Core Team 2014). Pearson correlation coefficients after accounting for spatial autocorrelation were calculated with the R package ‘SPATIALPACK 0.2-3’ (Osorio & Vallejos 2014), and Moran’s *I* values and SARs were calculated using the R library SPDEP 0.5-88. The spatial weight matrices of the SARs and the Moran’s *I* values were calculated with the nearest neighbour and a row-standardized coding style

(Kissling & Carl 2008). Since computing SARs for large data sets is computationally demanding, we randomly selected 7000 grid cells for our analyses using both the global extent and individual hemispheres. For the analyses for forest biomes, we used all available data. For the SAR analyses including the categorical variable ‘Region’, a dummy-coded variable was automatically generated in R. Relative importance of the predictor variables was calculated using the R package ‘RELAIMPO 2.2-2’ (Grömping 2006).

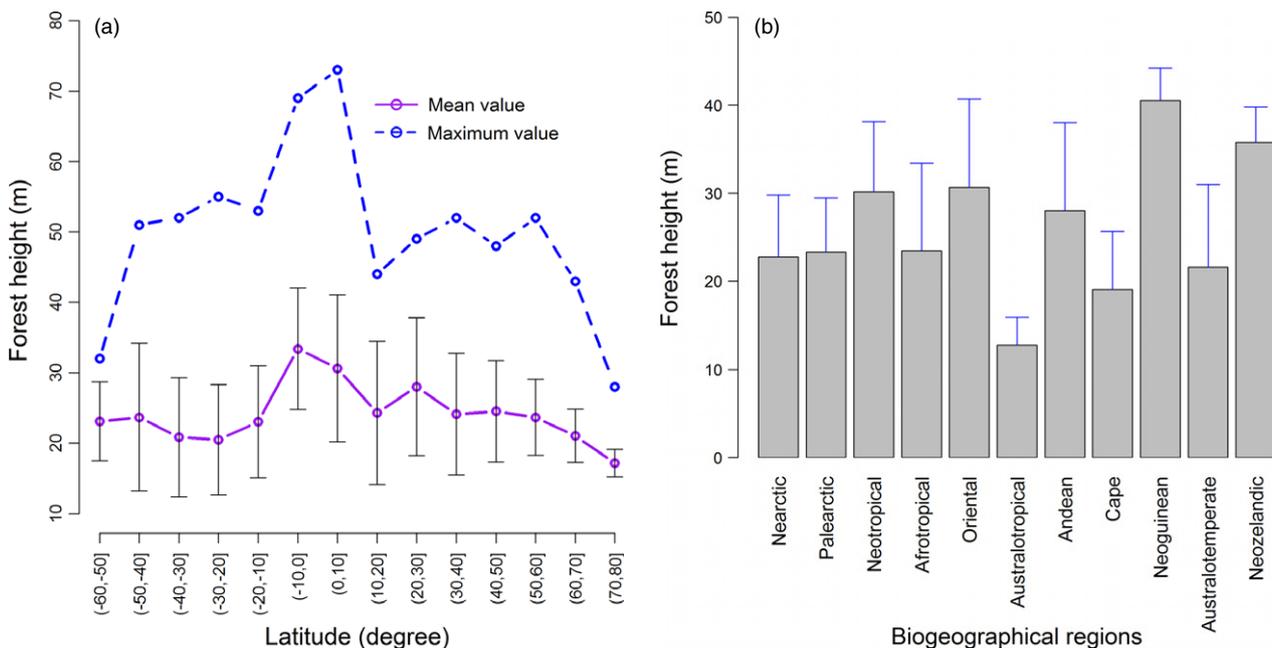
## Results

Maximum canopy height ( $H_{\max}$ ) within 55-km forest grid cells exhibit strong geographic variation (Fig. 1) with an inverse latitudinal gradient evident with the highest heights close to equator and the lowest heights at high latitudes (Fig. 2a). The tallest forest canopy was 73 m and located at  $\sim 1.7^\circ\text{N}$ , with the cells with the 10 tallest canopies all located between  $7^\circ\text{S}$  and  $4^\circ\text{N}$ . Further, the majority of grid cells with  $>40$  m canopy height were distributed in the Indo-Malayan region (Fig. 1). Outside the tropics, certain smaller areas such as in the North American Pacific Northwest and south-east Australia also have many grid cells with  $>40$  m canopy height (Fig. 1). Among 11 other biogeographic regions, the Neoguinean and Neozelandic regions had relatively high average  $H_{\max}$ , while the Australotropical region had the lowest average  $H_{\max}$  (Fig. 2b). Across seven forest biomes, tropical and subtropical moist broadleaf forests and tropical and subtropical coniferous forests had the highest  $H_{\max}$  (mean  $\pm$  SD:  $35.3 \pm 6.9$  and  $34.1 \pm 4.8$  m, respectively). Boreal forests and Mediterranean forests, woodlands and scrub had the lowest average  $H_{\max}$  (mean  $\pm$  SD:  $22.4 \pm 4.4$  and  $22.0 \pm 7.9$  m, respectively).

At the global scale, our spatial models explained  $>55\%$  of the variation in  $H_{\max}$  (Table S3). The water-related current climate variables of AET and Prep were the most correlated with patterns in forest canopy height, following by biogeographic region, water deficit, PrepSeason and Temp (Fig. 3 and Table S2 in Supporting Information). Two historical



**Fig. 1.** Global pattern of maximum forest canopy height ( $H_{\max}$ ). Maximum canopy height within 55-km equal-area grid cells is shown, including only cells with  $\geq 10$  m canopy height. The inset maps highlight geographical variation in  $H_{\max}$  for five selected regions: (a) Pacific north-west, (b) western Amazonia, (c) central Africa, (d) western Malesia, and (e) south-east Australia.



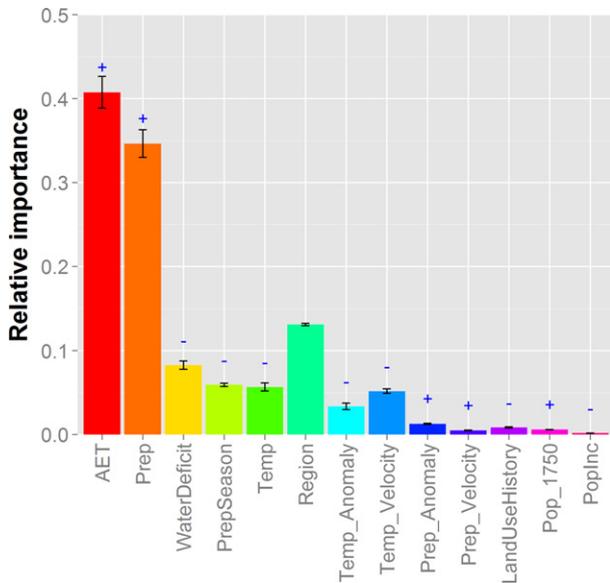
**Fig. 2.** Variations of maximum forest canopy height ( $H_{\max}$ ) (a) along latitudinal gradient and (b) among biogeographic regions. (a) Maximum values of  $H_{\max}$  for the 55-km grid cells in each  $10^\circ$  latitude interval are shown in blue. Mean values of  $H_{\max}$  are shown in pink and standard deviation in black. (b) Mean values ( $\pm$ SD) of  $H_{\max}$  within each biogeographic region are shown. The classification of biogeographic regions is based on Morrone (2002).

climate variables, Temp\_Velocity and Temp\_Anomaly, were also related to canopy height, with the expected negative effects (Fig. 3 and Table S2). Variables related to human disturbance contributed little to explaining global patterns in maximum canopy height at this spatial grain (55 km cells).

The water-related current climate variables AET and Prep were also important variables within most forest biomes

(Figs 4, S1 and S2). There was, however, variation among the biomes in the importance of specific climate variables. For example, Prep showed a much stronger effect on maximum canopy height in two temperate biomes, but had little effect in the boreal zone, where Temp was the most important variable.

Biogeographic region was the most important history-related variable for tropical and subtropical coniferous forests



**Fig. 3.** Relative importance of environmental and historical variables for explaining geographic variation in maximum forest height. Relative importance was derived from spatial linear models. To avoid multicollinearity effects, we divided our analyses into eight separate models by excluding highly correlated variables (AET and Prep, and Temp\_Velocity and Temp\_Anomaly) from the same models. The relative importance of a given variable was then estimated as the average of its relative importance in all models that included it. The blue signs '+' and '-' at the top of each bar represent for positive and negative effects on average, and the variable 'Region' does not have a sign since it is categorical. Variable abbreviations are explained in Table 1.

and also ranked high in boreal, Mediterranean, and tropical and subtropical dry broadleaf forests (Fig. 4). Considering the four historical climate variables, Temp\_Anomaly was the second most important determinant of patterns in canopy height in the boreal biome, but had much weaker explanatory power elsewhere, while the other historical climate variables never had high importance (Fig. 4).

Land use history (human disturbance) also contributed little to explaining patterns in canopy height within biomes. Pop\_1750 and PopInc had moderate explanatory power in tropical and boreal biomes, but not in the temperate biome.

In comparisons with Southern and Northern Hemispheres, AET and Prep were the most significant determinants of  $H_{\max}$  in both hemispheres (Fig. 5). In contrast, water deficit was much more important in the Southern Hemisphere than in the Northern Hemisphere. Biogeographic region was also an important factor in both hemispheres, while the influence of the other variables was relatively weak.

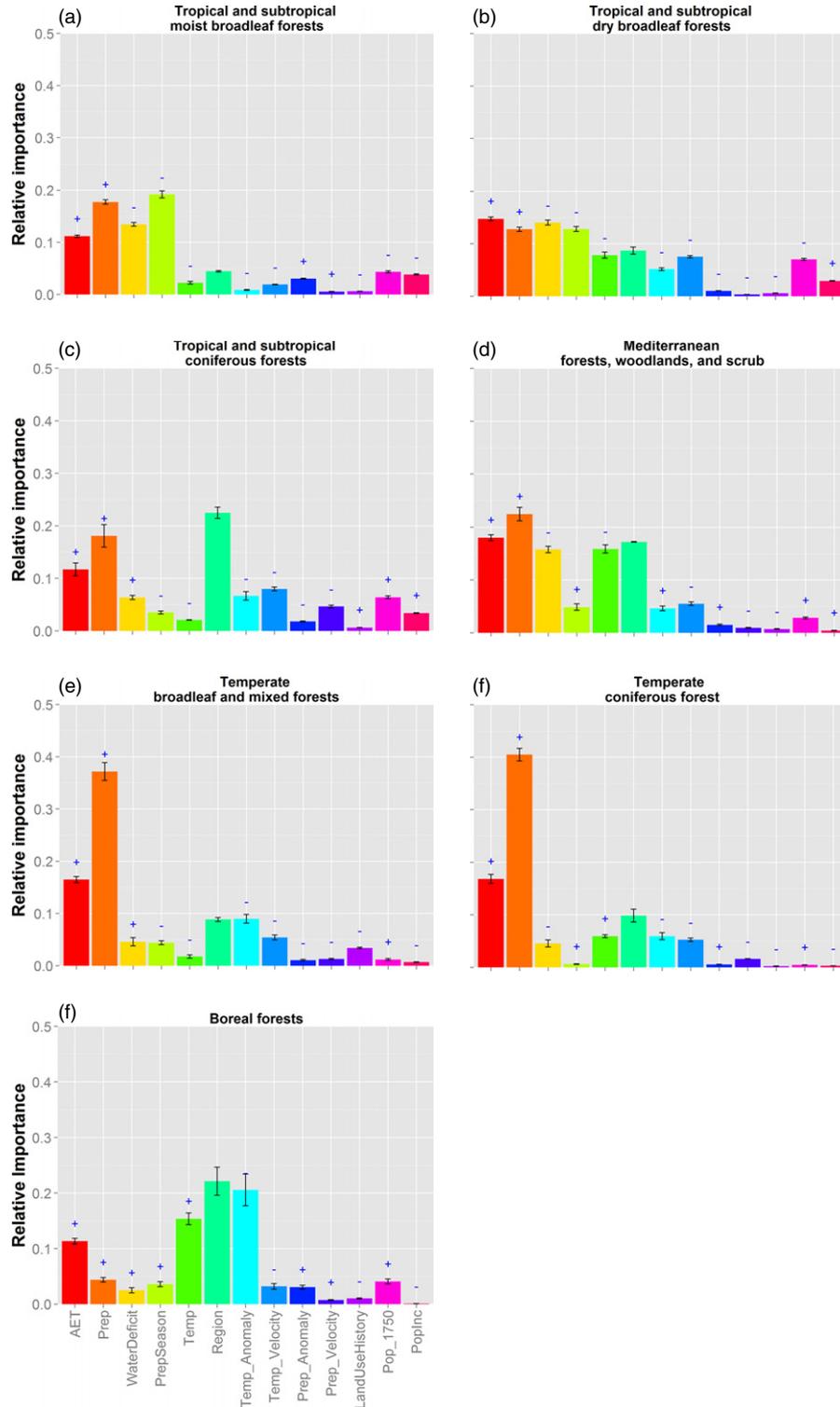
## Discussion

Understanding world-wide geographic variability in forest canopy height is essential to accurately quantifying and predicting dynamics in forest carbon stocks, carbon cycles and biodiversity. To this end, we here combined global-scale LiDAR-derived forest canopy height data with data on potential environmental and historical drivers to assess the relative

importance of current climate, regional evolutionary and biogeographic history, historical climate change and human disturbance for global patterns in maximum forest canopy height ( $H_{\max}$ ). We documented that forests with the highest canopy height mostly occur near the equator, although with much geographic variability (Simard *et al.* 2011). Indo-Malayan forests have higher canopy heights compared to African and South American tropical forests. These findings are not entirely consistent with that of the analyses on the tallest individual trees (>70 or 90 m in height) (see fig. 1 in Tng *et al.* 2012 and fig. 2 in Larjavaara 2014), which identified that trees with >90 m heights are located in California and South Australia. Regions with higher values of  $H_{\max}$  also matched well with previously reported hotspots of biomass carbon storage (Ruesch & Gibbs 2008) and biodiversity (Myers *et al.* 2000). Therefore, our comprehensive analysis of canopy height patterns sheds more insight into our understanding of broad-scale patterns and dynamics of carbon storage and biodiversity.

Our results support the hypotheses that AET (a measure of water–energy balance) and mean annual precipitation (Prep) are the most important global drivers of  $H_{\max}$ . The relative importance of AET, mean annual precipitation, precipitation seasonality and water deficit varied among different forest biomes, although the water–energy dynamics hypothesis was also consistently supported (Stephenson 1998; Cramer 2012). Water limitation emerged as a key factor of canopy height patterns in tropical and temperate regions in our study, while energy limitation was especially dominant in the boreal region where water is less limiting than temperature. Water limitations at low latitudes were also supported in studies of giant trees (Koch *et al.* 2004; Ryan, Phillips & Bond 2006; Moles *et al.* 2009; Slik *et al.* 2013; Givnish *et al.* 2014).

Our analysis also identified regional evolutionary and biogeographic history (described by the biogeographic regions) on broad-scale patterns in canopy height, although with varying importance among the forest biomes. The role of evolutionary and biogeographic history in constraining species richness patterns has been much debated and has received varying levels of support (Latham & Ricklefs 1993; Francis & Currie 2003; Kreft & Jetz 2007), but has been rarely tested for other ecosystem properties (Couvreur *et al.* 2015). Banin *et al.* (2012) compared differences in forest architecture using 112 tropical moist forest plots in Asia, Africa, Australia and South America and documented a continental difference in maximum height, with taller canopies in Asia. This is thought to be due to the dominance of Dipterocarpaceae trees in this region (Dudley & DeVries 1990; Banin *et al.* 2014). The canopy height differences among the biogeographic regions, controlling for current climate and other drivers, confirmed this pattern, but also highlighted differences in other biomes. These are likely also related to differences in species composition driven by long-term regional evolutionary and biogeographic dynamics, for example regional extinctions (Eiserhardt *et al.* 2015) and dispersal constraints (Ricklefs 1987; Mao *et al.* 2012). We note that there may be a tendency for regions with particularly tall-canopied forests to be

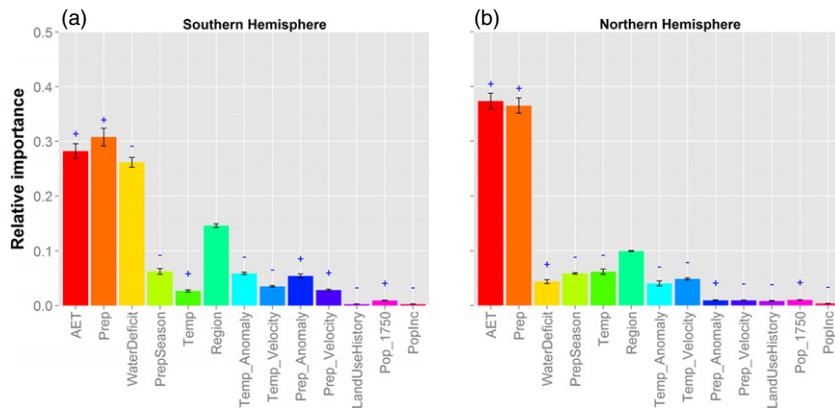


**Fig. 4.** Relative importance of environmental and historical variables for explaining geographic variation in maximum forest height within seven forest biomes. Variable abbreviations are explained in Table 1. Methods are as explained in Fig. 3.

dominated by ectomycorrhizal tree clades, for example Dipterocarpaceae in the Indo-Malayan region. This is consistent with findings that tall-growing tree species are disproportionately ectomycorrhizal (Slik *et al.* 2013), perhaps reflecting enhanced water and nutrient uptake (Halling 2001). In sum-

mary, our study highlighted the importance of evolutionary and biogeographic history towards a comprehensive understanding of canopy height and other forest properties.

Quaternary glacial–interglacial climate change, as measured by the velocity and anomaly of temperature and precipitation



**Fig. 5.** Relative importance of environmental and historical variables in explaining geographic variation in maximum forest height within the Southern and Northern Hemispheres. Variable abbreviations are explained in Table 1. Methods are as explained in Fig. 3.

between the LGM and the present, had consistent, but moderate relationships to  $H_{\max}$ . Notably,  $H_{\max}$  were negatively related to glacial–interglacial temperature instability, potentially explainable by extinction-driven losses of tall-growing tree taxa. The Quaternary glacial–interglacial oscillations have caused dramatic changes on species distribution and vegetation composition (Harrison & Prentice 2003), leaving important legacies in species distribution, species diversity and functional diversity patterns for plants, especially in Europe (Svenning & Skov 2007; Normand *et al.* 2011; Ordonez & Svenning 2015). Notably, the Pleistocene glaciations resulted in the extinction from Europe of several tall-growing genera such as *Sequoia*, *Liriodendron* and *Pseudotsuga* (Svenning 2003; Eiserhardt *et al.* 2015).

Surprisingly, despite the well-known historical and ongoing human impacts on land cover at a global scale (Ellis *et al.* 2013), past and present human disturbance contributed little to global patterns of  $H_{\max}$ . However, this does not imply that there is no influence of historical and current human activities on forest ecosystems. There are two possible reasons for this. First, the influence of human disturbance is scale-dependent (Hill & Hamer 2004). Our analysis was relatively coarse in scale (nearly  $0.5^\circ$ ) and therefore may not be able to capture local effects of human disturbances. Secondly, our focus is only on maximum canopy height (maximum height of all 1-km cells within a 55-km grid), meaning that the persistence of small undisturbed areas will obscure human impacts on the average vegetation structure. Variance in canopy height might therefore be a better indicator of the strength of human disturbance. Hence, further studies are needed to more fully assess the importance of human-induced changes in forest canopy height patterns across the world.

Our study highlights the importance and potential value of remote sensing data for understanding broad-scale research questions (Turner *et al.* 2003; Rose *et al.* 2015), although some potential limitations on the accuracy and resolution of remote sensing data still exist. Relating to the space borne LiDAR canopy height data used in the current study, the raw data at 1-km resolution (Simard *et al.* 2011) may not be able to capture local-scale variation in forest vertical structure. However, the influence of data accuracy on those studies at regional and global scales (e.g. Saatchi *et al.* 2011; Roll, Gefen & Yom-Tov 2015 and this study) should be weak. Previ-

ous assessment on the accuracy of canopy height data also showed good agreement with FLUXNET sites distributed globally (Simard *et al.* 2011) and airborne LiDAR data with 25-m resolution in Canada (Bolton, Coops & Wulder 2013). Further improvements in accuracy of ecological properties may be expected from the increasing availability of higher-resolution remote sensing data coupled with further advances in data processing techniques.

In conclusion, our study provides the first quantification of the current and historical drivers of global variation in forest canopy height. As a fundamental property of forest ecosystems, canopy height is strongly linked to other important ecosystem properties such as carbon storage and biodiversity. Our study shows that current climate, together with regional and historical factors, shapes forest canopy height globally. Thus, our findings are important in the context of biodiversity conservation and global change. Notably, the importance of regional and historical factors mean that we should not expect forests around the world to respond identically to future changes in climate or anthropogenic disturbance regimes. Furthermore, the potential link of part of the regional effects to past climate-induced extinctions suggest that future tree diversity losses could have very long-term effects on forest ecosystem structure and functioning. A number of trends unfortunately show that the risk of such losses is becoming higher. Recent studies on large trees and climate change have shown a declining trend in large trees that are related to recent climate change (Lindenmayer, Laurance & Franklin 2012; McIntyre *et al.* 2015). Drought-induced tree mortality (Allen *et al.* 2010; McIntyre *et al.* 2015), climate-change-related forest dynamics (Mora *et al.* 2015; Zhang, Huang & He 2015), competition with invasive plants (Hellmann *et al.* 2008) and logging and urbanization (Foley *et al.* 2005) pose threats to natural forest ecosystems across the world. Continued investigation of forest canopy changes over space and time is needed for achieving a better understanding of climatic and anthropogenic impacts on forests today and in the future.

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## Data accessibility

Global 1-km forest Canopy height data is publically available from the original study (Simard *et al.* 2011).

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## Supporting Information

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

**Figure S1.** Bivariate plots of actual evapotranspiration (AET) and maximum forest canopy height in different biomes.

**Figure S2.** Bivariate plots of mean annual precipitation (Prep) and maximum forest canopy height in different biomes.

**Table S1.** All environmental variables we considered.

**Table S2.** Pearson correlations among selected predictors.

**Table S3.** Summary of non-spatial and spatial regression models with maximum forest canopy height as a response variable, and environmental and historical variables as predictor variables.