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Tropical forest canopies and their relationships with climate and disturbance: results from a global dataset of consistent field-based measurements

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Abstract

Background: Canopy structure, defined by leaf area index (LAI), fractional vegetation cover (FCover) and fraction of absorbed photosynthetically active radiation (fAPAR), regulates a wide range of forest functions and ecosystem services. Spatially consistent field-measurements of canopy structure are however lacking, particularly for the tropics.

Methods: Here, we introduce the Global LAI database: a global dataset of field-based canopy structure measurements spanning tropical forests in four continents (Africa, Asia, Australia and the Americas). We use these measurements to test for climate dependencies within and across continents, and to test for the potential of anthropogenic disturbance and forest protection to modulate those dependences.

Results: Using data collected from 887 tropical forest plots, we show that maximum water deficit, defined across the most arid months of the year, is an important predictor of canopy structure, with all three canopy attributes declining significantly with increasing water deficit. Canopy attributes also increase with minimum temperature, and with the protection of forests according to both active (within protected areas) and passive measures (through topography). Once protection and continent effects are accounted for, other anthropogenic measures (e.g. human population) do not improve the model.

Conclusions: We conclude that canopy structure in the tropics is primarily a consequence of forest adaptation to the maximum water deficits historically experienced within a given region. Climate change, and in particular changes in drought regimes may thus affect forest structure and function, but forest protection may offer some resilience against this effect.

Keywords: Leaf area index, Fractional vegetation cover, Fraction of absorbed photosynthetically active radiation, Human population pressure, Protected areas, Drought, Climate change

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Background

Because of their functional representation of terrestrial ecosystems (Ozanne et al. 2003), canopy structure variables characterise key land surface attributes in models of the climate system (Masson et al. 2003), the earth system (Brovkin et al. 2006; IPCC 2013), ecosystem productivity (Nemani et al. 2003; Zhao and Running 2010; Potter et al. 2012), and landscape hydrology (Thyer et al. 2004). However, characterising canopy structure variables, their dependencies on climate, and the covariation of both across biogeographic regions (Reich 2012) in such models is challenging due to deficiencies in long-term and spatially consistent measurements of the structure of forest canopies, which are particularly lacking for the tropics (Pfeifer et al. 2014).

Canopy structure can be described by leaf area index (LAI, in m^2m^{-2}), the fraction of absorbed photosynthetically active radiation (fAPAR), and fractional canopy cover (FCover, in %). Thereby, LAI is typically defined as one half the total leaf area per unit of horizontal ground surface area (Chen and Black 1992; Weiss et al. 2004; Gonsamo and Pellikka 2008), whereas fAPAR refers to the fraction of photosynthetically active radiation (PAR: 400–700 nm) that is absorbed by vegetation canopy. Both canopy attributes tend to be highly inter-correlated in individual studies (Steven et al., 2015). LAI and fAPAR, in turn, are implicitly related to FCover, defined as the proportion of horizontal vegetated area occupied by the vertical projection of canopy elements (Gonsamo et al. 2013).

Canopy attributes of vegetation have been measured primarily using direct techniques and indirect optical techniques (reviewed in Jonckheere et al. 2004). Direct techniques involve collecting leaves (e.g. through destructive harvesting or collecting leaf litter), measuring leaf area (e.g. using planimetric or gravimetric approaches), and upscaling estimates to stand level assuming stand homogeneity (Jonckheere et al. 2004). Whilst being the most accurate, their usefulness for assessing canopy structure at stand level is limited due to time requirements but also due to their limited representativeness for heterogeneous canopies typically for natural forests. Indirect optical techniques infer canopy structure from radiation transmission through vegetation canopies (e.g. LAI-2000, hemispherical photography, Sunscan-LAI instrument) and are thus faster, non-destructive and can be implemented at larger spatial scales (Jonckheere et al. 2004). However, the maximum measurable LAI is lower compared to direct assessments due to saturation of light interception as LAI approaches 5–6 (Gower et al. 1999). Nevertheless, hemispherical photography has been demonstrated to be a cost-effective tool, which combined with image thresholding using the Ridler method on the blue band of images to separate sky from vegetation (Jonckheere et al. 2005)

and a clumping algorithm to account for non-randomness of leaf distribution at sub-canopy level (Jonckheere et al. 2006) can provide representative measurements of forest canopy structure in the field.

LAI and fAPAR are essential climate variables (Baret et al. 2013) and the main controls over water, energy, gas and momentum fluxes (Asner et al. 2003) and hence the primary productivity of terrestrial ecosystems (i.e., gross and net primary productivities) (Field et al. 1995), microclimates (Hardwick et al. 2015), as well as their water balances (Calder 2002; Silva et al. 2017). Forest canopies create vertical light gradients within forests and buffer the effects of temperature and precipitation, thereby regulating forest-dependent biodiversity (Valverde and Silvertown 1997; Pringle et al. 2003; Dáttilo and Dyer 2014; Nakamura et al. 2017). Through exchanges of water, energy, carbon dioxide and other chemical components including volatile organic compounds, forest canopies regulate the climate system, both locally and through global carbon budgets (Dixon et al. 1994; Bonan 2008; Luyssaert et al. 2008). Of an estimated global stock of 861 ± 66 Pg C, tropical forests store about 55%, of which more than half is stored in biomass. Even when taking into account forest degradation and forest die-back due to drought, tropical forests overall still represent a persistent global gross carbon sink (Pan et al. 2011). Recent key climate change mitigation policies, agreed at COP21 in Paris, recognise the central role that forests play for climate solutions (United Nations 2015), with the global climate change mitigation mechanism REDD+ (Reducing carbon Emissions from Deforestation and forest Degradation in developing countries and sustainable forest management) given particular prominence (Turnhout et al. 2017).

Studies on net primary productivity (NPP) of tropical forests suggest positive trends of forest productivity with increasing temperatures and hump-backed productivity relationships with measures of water availability (Clark et al. 2001; Nemani et al. 2003). The latter is echoed by canopy structure data on natural forests, which are largely from temperate regions (Iio et al. 2014), but also by data from tropical East Africa (Pfeifer et al. 2014). This suggests that canopy LAI is limited by water availability at the lower end of the rainfall spectrum and by cloud cover variability at the upper end, the latter regulating incident solar radiation on forest canopies and, hence, constraining vegetation productivity (Nemani et al. 2003). Within the context of limited water availability, forest stands are believed to adopt a strategy that maximises carbon gain under water stress. They do so by reducing water loss from leaves and allowing lower stomatal conductance where stomatal regulation is adapted to the xylem pressures that are within the tolerance of the hydraulic system of the tree species (Choat et al. 2012).

Intensifying global change, particularly changes in climate system, radiative transfer through the atmosphere, deposition of pollutants and atmospheric CO₂ concentrations, is expected to alter forest structural components, thereby impacting forest functioning and gas exchange (Wright 2005). For example, modelling and experimental studies suggest that while increasing atmospheric CO₂ concentrations will increase LAI (Kergoat et al. 2002; McGrath et al. 2010), rainfall anomalies and in particular droughts can increase tree mortality and cause canopy dieback resulting in reductions in canopy leaf area (Nepstad et al. 2004) of up to 30% (Meir et al. 2008) and an overall decrease in forest carbon storage (Gatti et al. 2014; Rowland et al. 2015). Field and earth observation studies show that logging has contributed to widespread tropical forest degradation and fragmentation (Pereira et al. 2002; Hansen et al. 2013; Souza Jr et al. 2013), in particular outside protected areas (Joppa et al. 2008). Selective logging, for example, alters the biophysical structure of forests in the landscape, opening forest canopies and reducing LAI (Pfeifer et al. 2012, 2016). Droughts are interacting with forest degradation and fragmentation in positive feedbacks to further modify forest canopy structure and functioning (Laurance and Bruce Williamson 2001) reducing canopy coverage and aboveground biomass (Brando et al. 2014). In order to project future global change in tropical canopy structure variables, a benchmark database for contemporary climates is needed. Although there are large and increasing databases for Northern hemisphere temperate and boreal ecosystems (Iio et al. 2014), measurements of key forest canopy variables for tropical regions are underrepresented (Pfeifer et al. 2014).

Here, we analyse a large global dataset on canopy structure variables, acquired for tropical natural forests using hemispherical photography (including one dataset from subtropical South Africa). We particularly concentrate on the role climate plays in shaping forest canopies at regional and global scales, under the hypothesis that forests adapt to local climate leading to an equilibrium

in canopy structure variables (Kergoat et al. 2002). Using this dataset, we test two hypotheses. **First**, that tropical forest canopy attributes differ among continents (Australasia, Africa, Americas, Asia) reflecting regional differences in water availability, temperature and radiation (Nemani et al. 2003). In particular, we hypothesise LAI, FCover and fAPAR to be lower in Africa and Australia, both continents encompassing forests ecosystems that are water-limited as opposed to radiation-limited (Nemani et al. 2003). We use high resolution climate data (Fick and Hijmans 2017) to identify the climate-dependencies of canopy structure variables within and across continents, paying particular attention to annual and seasonal long-term averages in water availability. **Second**, we test the hypothesis that protected tropical forests yield significantly higher LAI, fAPAR and FCover compared to unprotected forests, because of reduced anthropogenic disturbance. We use measures of passive (landscape topography) and active (forests within protected areas) protection, in combination with measures of human population pressure to test whether anthropogenic disturbance has already modulated climate dependencies of tropical forest canopies.

Methods

We used linear mixed effects models to compare variation of canopy attributes of tropical forests within and across continents sampled with hemispherical images for the Global LAI project. We related canopy attributes to environmental predictors to test for climate dependencies of tropical canopies and additional impacts of anthropogenic pressure on climate – canopy structure relationships.

The global LAI database

The Global LAI database is an international researcher network measuring and compiling canopy structure data, with particular emphasis on the tropics. For this study, we focussed on tropical forest plots, which were located in Africa, Asia, Australasia and the Americas (Fig. 1).

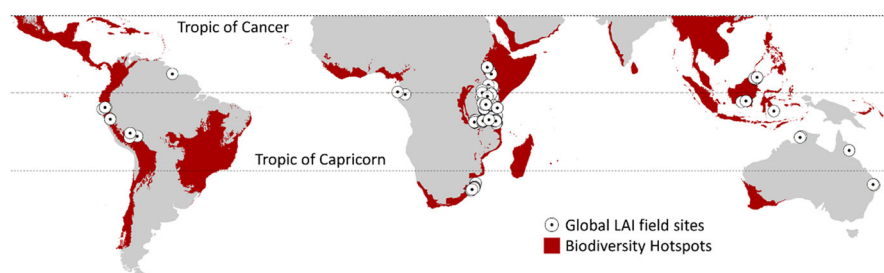


Fig. 1 Location of the 887 forest and woodland plots for which canopy structure estimates have been sampled using hemispherical photography. The map shows the distribution of plots with regard to the locations of global biodiversity hotspots (Mittermeier et al. 2004)

Canopy measurements followed a standardised sampling design, described in the protocol of the Global LAI project (Pfeifer 2015). The first step involved the acquisition of upward-looking hemispherical images using a digital camera equipped with a fisheye lens, with the camera held at one meter above ground and sampling points within a plot set up to match the sampling scheme of Validation of Land European Remote Sensing Instruments (<http://w3.avignon.inra.fr/valeri/>). Second, we used an in-house algorithm to pre-process each image, first extracting the blue-channel pixel brightness values from each image and then applying a thresholding algorithm on the blue band channel to generate a binary sky - vegetation image (Jonckheere et al. 2005). Third, we analysed these binary images to indirectly estimate canopy structure attributes using the free canopy analysis software CAN-EYE v6.3.8 (Baret et al. 2010) with the field of view of the lens limited to values between 0° and 60° to avoid mixed pixels. We avoided masking plants (which aims to keep only visible leaves) as this could lead to large underestimations of the actual canopy structure variables depending on the way leaves are grouped with other parts of the plant (Baret et al. 2010).

True LAI (a dimensionless quantity), which accounts for clumping of vegetation elements at the scale of plants and canopies, was estimated as one half of the total leaf area (m^2) in a canopy per unit ground surface area (m^2). The CAN-EYE software quantifies LAI as plant area index (PAI), an indirect estimate that includes materials such as stems, branches and plant reproductive parts (Bréda et al. 2003). Black-sky fAPAR was estimated as the fraction of the incoming solar radiation that is absorbed by the green and alive leaves for photosynthesis. FCover was defined as the fraction of the soil covered by vegetation canopies as viewed in the nadir direction. Thereby, true LAI and fAPAR are plot-level estimates while FCover is calculated as the average of FCover estimates acquired for at each sampling point within a plot (Pfeifer et al. 2014; Hardwick et al. 2015). These estimates were stored together with the geographic coordinates for each plot (Geographic Latitude Longitude World Geodetic System 1984), a land use identifier (e.g. forest, woodland) and additional information on habitats if available (e.g. main plant species, degradation status).

We identified all plots that were measured in vegetation identified as either natural forest or natural woodland (not intensively managed for timber in recent times but potentially used by local people) and that were sampled using at least eight sample points per plot (mean \pm standard error: 17 ± 0.50 , maximum: 66). The final dataset included 887 plots, of which 516 were located on the African continent, 94 in America, 250 in Asia, and 27 in Australasia (Fig. 1). Plots (ranging in size

from 0.025 ha to 1 ha) were sampled during 37 field campaigns implemented between 2003 and 2016 (Additional file 1: Table S1).

Environmental predictors of canopy structure attributes

All climate predictors were derived from WorldClim version 2 climate data, downloaded from <http://worldclim.org/version2>. These are 30 arc-second (~ 1 km) gridded climate surfaces for global land areas developed from monthly climate station data, which were spatially interpolated using elevation, distance to the coast and MODIS derived maximum and minimum land surface temperatures, and cloud cover as covariates (Fick and Hijmans 2017).

We focussed on five climatic predictors that we expected to influence forest functioning in the tropical realms: mean minimum temperature of the coldest month (**MinT**, in °C), mean annual rainfall (**MAP**, in mm), the coefficient of variation in annual rainfall (**CovP**) as a measure of rainfall seasonality, an annual moisture index (**AMI**) as an estimate of precipitation availability over atmospheric water demand (Zomer et al. 2008), and maximum water deficit (**MWD**, in mm) as a measure of dry season water stress (Platts et al. 2010). We directly downloaded three of these: BIO6 (MinT), BIO12, (MAP) and BIO15 (CovP). We computed AMI, a dimensionless measure, as the ratio of mean annual precipitation to mean annual potential evapotranspiration (PET), the latter estimated according to the Hargreaves method (Hargreaves and Allen 2003, Eq. 1):

$$PET = 0.0023 \times RA \times (T_{av} + 17.8) \times TD^{0.5}, \quad (1)$$

where RA is extra-terrestrial radiation, T_{av} is mean temperature and TD as daily temperature range. Values of AMI < 0.2 are indicative of an arid or hyper-arid environment, 0.2–0.5 semi-arid, 0.5–0.65 dry sub-humid, and > 0.65 humid (UNEP 1997). We computed MWD across consecutive months that experience rainfall < monthly PET, over which the shortfall in rain was accumulated. In cases where there is more than one dry season, we recorded the maximum deficit experienced throughout the year.

To capture large-scale effects of anthropogenic disturbance, we used maps of human population density (**Popden**) and human population pressure (**Poppress**) in the landscape. For Africa, Asia and the Americas, we obtained gridded population data from WorldPop Version 2.0 (<http://www.worldpop.org.uk/>) at 30 arc-sec resolution (WGS84 coordinate reference system). The reference year is 2015, adjusted to match UN national estimates. We pre-processed these grids to convert pixel values from people/pixel to people/km², before projecting to the Sinusoidal coordinate system. This allows for

accurate area calculations globally, with minimal shape distortion near to the equator and central meridian. For Australia, we obtained gridded population data from the Australian Bureau of statistics, presenting people per 1 km² pixel using the GDA1995 Albers coordinate reference system (<http://www.abs.gov.au/AUSSTATS/abs@.nsf/Lookup/1270.0.55.007Main+Features12011>). Given the distance of Australia from the central meridian, this local coordinate system was preferred to the Sinusoidal.

Population pressure grids accrue to a particular point in space, the pressure exerted by all persons across a landscape. We calculated pressure grids using a range of sigma values ($\sigma = 5, 15, 25, 50$), providing scope for capturing human-driven pressures at a variety of spatial scales. We imposed a maximum distance of 100 km, beyond which no pressure is exerted. The pressure on location i increases linearly according the number of persons (p) in a remote location j . The weight (w) given to a particular remote population decreases exponentially with distance (d), according to a half-normal decay (Eq. 2):

$$Poppress_i = \sum_{j=1}^N p_j w_{ij}, \quad w_{ij} = \exp\left(-\left(d_{ij}/\sigma\right)^2\right), \quad (2)$$

where N is the number of locations across which pressure accumulates (Platts 2012). Modifying the value of sigma changes the shape of the curve, such that higher values increase the weight given to distant populations (Additional file 1: Figure S1).

Landscape topography can determine forest accessibility, with forests on steep slopes and at higher elevation being less likely to be disturbed compared to lowland tropical forests (Pfeifer et al. 2012). We therefore used minimum elevation (**Ele_Min**) and mean slope (**Slope**) calculated for plots within the 1 km grid cell as additional proxies for anthropogenic disturbance. We derived both variables from Shuttle Radar Topography Mission V4 digital elevation data (~90 m pixel resolution, produced by NASA), which we downloaded from <http://srtm.csi.cgiar.org/> (accessed 13/06/2017) (Jarvis et al. 2008).

Protected areas can be an effective tool to stop forest clearance and to reduce forest degradation activities such as logging, fire or grazing (Bruner et al., 2001; Pfeifer et al. 2012), but their effectiveness in doing so varies within and across continents (Gaveau et al. 2007; Laurance et al. 2012). We analysed climate and disturbance dependencies of tropical forest canopies distinguishing between protected and unprotected plots (**Protection**). We downloaded the World Database on Protected Areas (<https://protectedplanet.net/>, accessed 01/01/2016) and extracted for each plot its protection status, considering all types protected areas as equally important including IUCN protected areas (summarised in Leroux et al. 2010).

Statistical analyses

For each plot, we extracted values for all climatic (MinT, MAP, CovP, AMI, MWD) and disturbance predictors (Popden, Poppres, Ele_Min, Slope, Protection) described above. We aggregated plot attributes including canopy structure variables and disturbance - related predictors to match the resolution of the climate grids.

Because the assumptions of normality distribution in the data were violated (Shapiro-Wilk test, $p < 0.001$) and variances were not homogeneous (Fligner-Killeen test, $p < 0.001$), we used non-parametric pairwise Wilcoxon comparison with Bonferroni adjustment of p values to test for significant differences in canopy attributes, climatic environments of plots and human population pressure on plots among continents.

We used linear mixed-effects models implemented in the R statistical software package *lme4* (Bates et al. 2012) to predict canopy structure attributes from the environmental predictors described above. We bounded the three canopy attributes for this modelling: FCover (bounded between 0 and 100), fAPAR (bounded between 0 and 1) and LAI (bounded between 0 and 10). We computed Spearman's rho correlation to test for inter-correlations between predictors and excluded highly inter-correlated predictors from subsequent global models ($r > 0.6$). Rainfall-dependent climatic predictors were highly inter-correlated, and so were MinT and mean elevation of plots as well as human population density and human population pressure (Table 1). Because the correlation was strongest between MWD and each canopy structure variable (Fig. 4), we excluded AMI, CovP and MAP from subsequent multiple

Table 1 Inter-correlation among environmental predictors quantified using Spearman's Rho for correlations among numeric predictors, with r - values > 0.6 indicating high inter-correlation among predictors

	AMI	CovP	Elev	MAP	MinT	MWD	Popd	Popp	Slope
AMI	1								
CovP	-0.66	1							
Elev	-0.23	0.42	1						
MAP	0.93	-0.62	-0.41	1					
MinT	0.41	-0.48	-0.78	0.55	1				
MWD	-0.91	0.76	0.15	-0.77	-0.33	1			
Popd	-0.22	0.22	0.29	-0.28	-0.40	0.14	1		
Popp	-0.14	0.24	0.35	-0.21	-0.43	0.1	0.81	1	
Slope	0.22	-0.14	0.41	0.03	-0.24	-0.35	0.16	0.13	1

AMI annual moisture index, CovP coefficient of variation in annual precipitation, Elev minimum elevation of plots measured in a 1 km grid cell (m above sea level), MAP mean annual precipitation (mm), MinT minimum temperature of the coldest month (°C), MWD maximum water deficit (mm), Popd human population density, Popp human population pressure with sigma set to 5, Slope mean slope of plots measured in a 1 km grid cell [°]. Numbers in bold indicate highly inter-correlated predictor variables

predictor models. Similarly, the correlation was stronger between MinT and LAI and between MinT and FCover compared to elevation, and we excluded elevation from multiple predictor models for both canopy structure variables. For models predicting fAPAR, we excluded MinT instead of elevation because Elevation showed a stronger correlation with fAPAR. We used human population pressure instead of human population density in each model. We used the scale function in R to standardise the predictor variables used in the model, so that they have a mean of zero and standard deviation of one, which ensures that the estimated coefficients are all on the same scale making it easier to compare effect sizes. As fixed effects, we entered predictors and interaction terms of each predictor with the 'Protection' variable into the model. As random effects, we entered intercepts for continent (geographic location) as well as by-continent status random slopes for the effect of MWD as fixed effect predictor: e.g. $\text{LAI_bounded} \sim \text{scale(MWD)*Protection} + (1 + \text{scale(MWD)})|\text{Continent}$.

We fitted multiple predictor models using automated model selection via information theoretic approaches and multi-model averaging using maximum likelihood. We included a spatial autocorrelation term in each global model (plot Latitude \times plot Longitude). For each of the three global models, we used the dredge function in the R MuMIn package v1.10.5 (Barton 2014), which constructs models using all possible combinations of the predictor variables supplied in each global model. These models were ranked, relative to the best model, based on the change in the Akaike Information Criterion (delta AIC). A multi-model average (final model) was calculated across all models with delta AIC < 2.

Results

Comparing canopy structure and plot environments between continents

We found considerable variation in canopy attributes both within and between continents (Fig. 3). Australasian forests consisted of native dry, open canopy Eucalypt forests to humid rainforests. African forests consisted of dry deciduous broadleaved woodlands of varying species compositions (e.g. *Acacia* woodlands in Kenya and Ethiopia, Miombo woodlands in Tanzania), coastal forests and mangroves, and broadleaved semi-deciduous to moist evergreen forests in the lowlands and at higher altitudes. Forests in Asia and the Americas ranged from lowland humid forests to high elevation cloud forests.

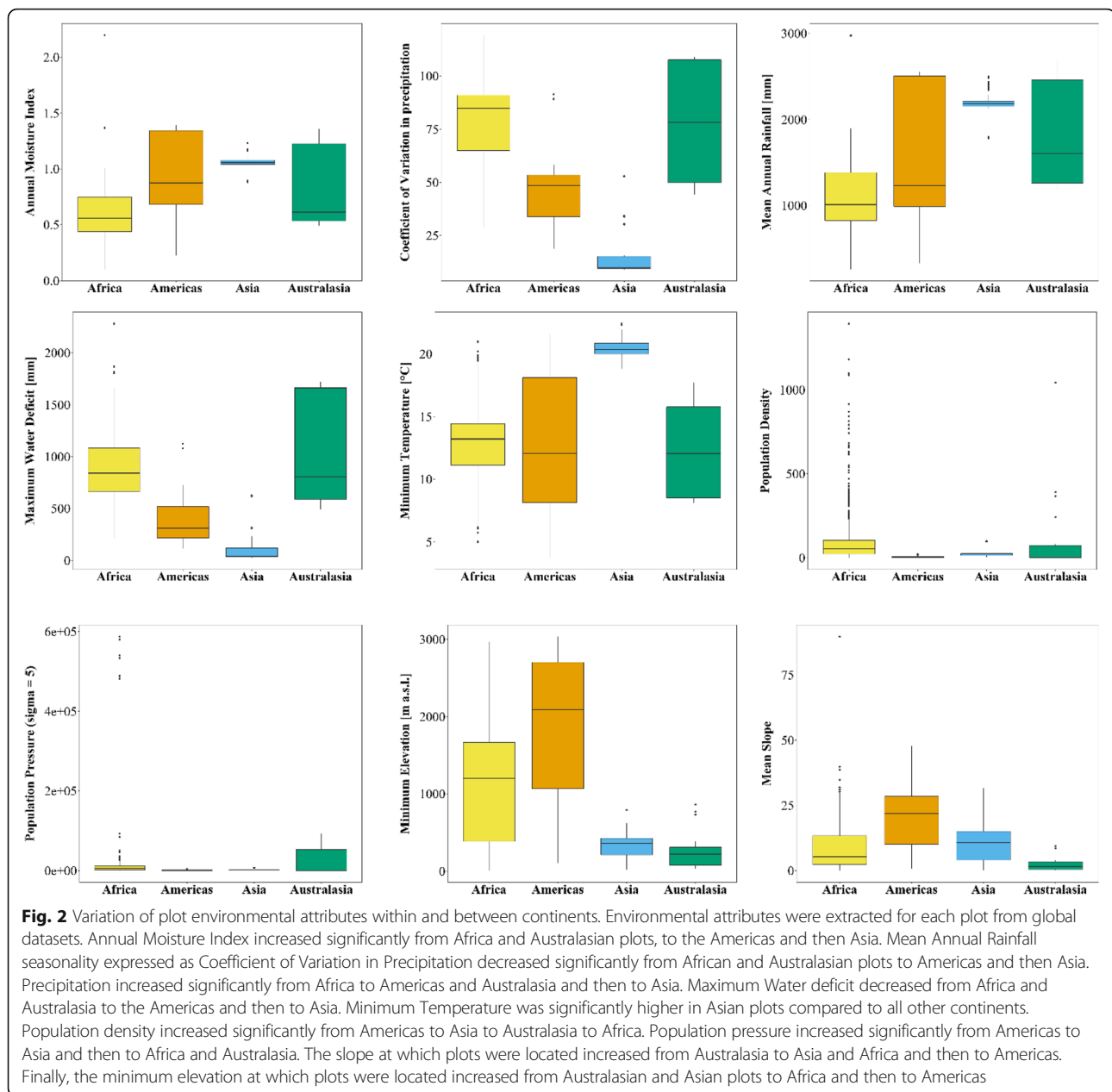
Forest canopies differed significantly in their structure between continents (pairwise Wilcoxon test, Bonferroni adjusted: $p < 0.001$). Continents also differed in climatic and disturbance predictors described above. In particular, MWD decreased significantly from African and Australian plots to American and then to Asian plots,

and the coefficient of variation in rainfall was most pronounced in African and Australian plots decreasing to plots in America, and then to plots in Asia (Fig. 2). Asian plots also had significantly higher minimum temperature compared to all other plots.

MWD had significant and strong correlations with LAI, FCover and fAPAR, supporting our first hypothesis that forest canopy attributes differ among continents reflecting regional differences in water availability (Fig. 4). Visual inspections of residual plots did not reveal obvious deviations from data normality. MWD lowered canopy attributes with the slope of this effect being steeper for Australasian and African plots and the intercept for this effect being higher for plots in the Americas compared to plots in other geographic regions (Fig. 4).

Observed inter-regional differences in canopy structure variables were driven by protection status of forests in Africa and Australia, which supported our second hypothesis (Fig. 3). Unprotected forests in Africa, for example, featured canopies with significantly reduced LAI, FCover and fAPAR compared to protected forests in Africa and protected as well as unprotected forests in Asia and the Americas. Australian forests, for which data availability was lowest, featured highly variable forest canopy structure: unprotected forests had significantly lower LAI and more open canopies compared with protected forests in Africa, Asia and the Americas (Fig. 3). Our second hypothesis, on the importance of protection, is corroborated by evidence that human population density was highest for African plots decreasing to Australian to Asian and then to American plots (although population pressure showed more complex regional patterns). Slopes, a measure of terrain topography that indicates forest accessibility, were steepest for plots in America, decreasing significantly to Asia and Africa and then to Australia.

Multiple predictor models predicting canopy attributes from climatic and disturbance predictors suggested that whilst climate, and in particular MWD, was the main driver of variability in canopy structure across plots, climate interacted with the protection status of a forest in determining forest canopy structure. Model averaging resulted in final models for LAI and FCover that encompassed four important predictors (Table 2): MWD, MinT, Protection and the interaction between Protection and MWD. For fAPAR the final model encompassed Protection, Ele_Min, Slope, MWD and the interaction between Protection and MWD. Overall, protection status of a forest and higher minimum temperatures had positive effects and MWD had negative effects on canopy LAI and FCover. Protection and terrain slope had positive effects on fAPAR, while the minimum elevation of plots and MWD had negative effects. The interaction

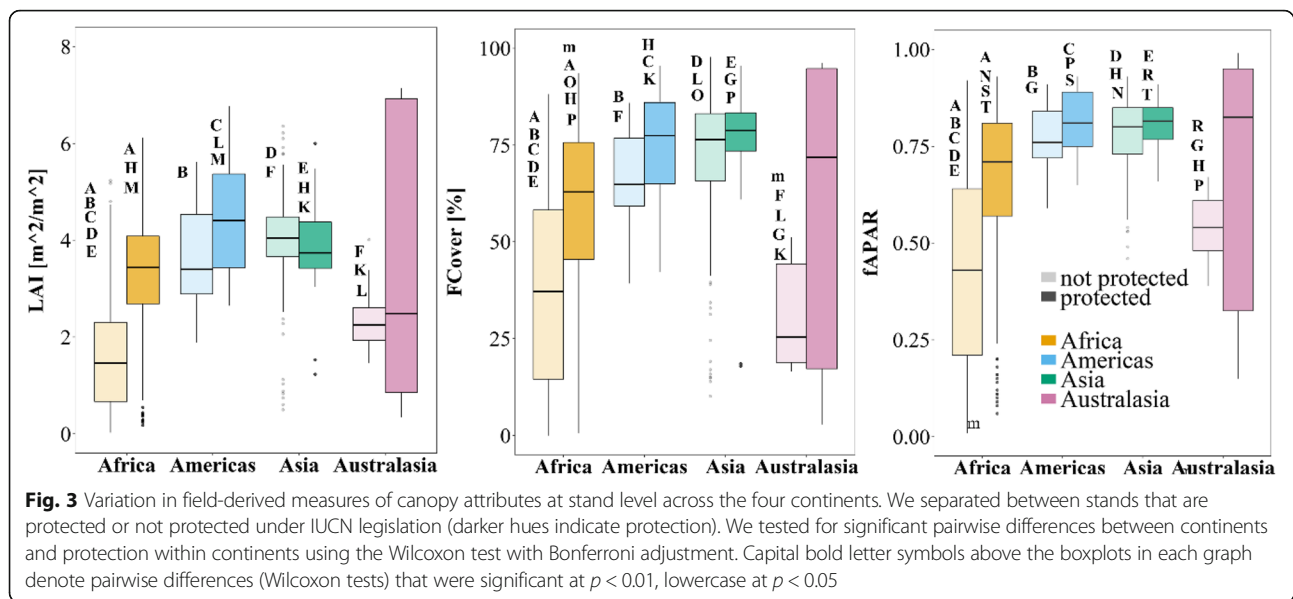


term between protection and MWD was positive in all three final models. The spatial autocorrelation term did not play a significant part in the models predicting LAI and fAPAR, but had a negative effect in the model predicting FCover (Table 2).

To quantify whether predictors identified as important in above multiple-predictor models improved the conditional R^2 of MWD based models (see Fig. 4 for details), we directly added MinT to the models predicting LAI and FCover from MWD and we added Ele_Min and Slope to the MWD based model predicting fAPAR. The conditional R^2 of the models improved from 76% to 83% for LAI, from 64% to 85% for FCover and from 64% to 80% for fAPAR.

Discussion

Our analyses demonstrate significant differences between continents with regard to forest canopy attributes that play a key role in forest ecosystem processes. These differences are significantly correlated with intercontinental variation in water availability throughout the year, as shown in the relationship of canopy attributes with MWD, with additional beneficial impacts of forest protection. In particular, the maximum water deficit in a region - which forest stands experience and thus evolve to adapt to (Kergoat et al. 2002) - had the strongest relationship with canopy structure variation across plots and continents, with canopy LAI, fAPAR and FCover



declining significantly with increasing long-term averages of maximum water deficits. We also show that steeper slopes, likely characterising reduced forest accessibility rather than optimal forest growth conditions, and warmer minimum temperatures co-vary with higher forest fAPAR and LAI/FCover respectively. Contrary to our expectations, human population densities and pressure grids did not aid in explaining canopy structure variability once effects of climate, protection and topography were accounted for. While it is likely that both provide only proximate measures for human impacts on forest structure at local scales, it may also suggest that climate and legal protection are by far the most important controls on forest canopy structure and functioning.

Forest canopies and climate

Our analyses suggest that forests canopy structure is shaped by long-term regional climate, and in particular to the maximum water deficit experienced annually in a region. This would imply that short-term increases in water deficits that fall outside the range typically experienced by forests could push trees outside the tolerance of their hydraulic strategies, increasing mortality with detrimental impacts on forest canopies and forest functioning. Evidence from the literature supports this interpretation of our results. Prolonged droughts in the Amazon for example have been implicated in forest die-back resulting in larger canopy gaps (Malhi et al. 2009; Asner and Alencar 2010). Similar observations have been reported for tropical moist forest in Uganda, cedar forests in Algeria, mountain forests in Zimbabwe and tropical moist forests in Malaysian and Indonesian Borneo (reviewed in Allen et al. 2010). Drought impacts may be stronger in moist forests of the humid tropics,

which may be less adapted to cope with decreasing water availability given their canopy structure variation in our dataset. While global analyses have so far found little difference in drought induced mortality between angiosperms and gymnosperms, or between evergreen and deciduous species (Greenwood et al. 2017), the same study did find evidence for tree species with lower wood density and high specific leaf area (implying a higher potential for leaf water loss) being more susceptible to drought-induced mortality than species with lower specific leaf area (Greenwood et al. 2017).

In addition to water deficits experienced by forests, we found that higher minimum temperatures were also linked to increased canopy leaf area and canopy closure. This suggests a potentially positive response of forest functioning to global warming and is in line with observed increases in productivity of tropical forests in recent decades (Nemani et al. 2003). Yet, we emphasize that water stress was the primary constraining factor in our analyses: structural changes in tropical forests in response to warming will need to be balanced by the trees demand for water, especially as the majority of trees operate within narrow hydraulic margins irrespective of biome (Choat et al. 2012).

Previous studies focussing on temperate natural forests and forest plantations (Iio et al. 2014) and tropical forests in East Africa (Pfeifer et al. 2014) have found a decline in canopy LAI in regions with very high levels of rainfall and water availability. This is in line with studies showing a decline in NPP of humid tropical forests under high rainfall regimes, with NPP peaking at around 2500 mm mean annual rainfall, with subsequent declines linked to decreased radiation inputs (high cloud cover), increased nutrient leaching, or reduced soil oxygen

Table 2 Linear mixed effect models used to model variation in canopy structure attributes as a function of climate and disturbance predictors. We scaled the continuous predictors in each model

A) LAI (bounded between 0 and 10), Linear mixed effects model	
Global model	MWD * Protection + Poppress * Protection + MinT * Protection + Slope * Protection + LatLong + (1 + MWD Continent)
N final models	2
Model importance and sign of coefficient estimates (conditional model-average)	Intercept: + 0.342 Protection = 1: 1, + 0.117 MinT: 1, + 0.036 MWD: 0.72, - 0.073 Protection: MWD: 0.72, + 0.046
B) FCover (bounded between 0 and 100), Linear mixed effects model	
Global model	MWD * Protection + Poppress * Protection + MinT * Protection + Slope * Protection + LatLong + (1 + MWD Continent)
N final models	1
Model importance and sign of coefficient estimates	Only one final model, so all predictors equally important. Intercept: + 0.409 Protection = 1: + 0.179 MinT: 1, + 0.063 MWD: 1, - 0.197 Protection: MWD: 1, + 0.085 LatLong: 1, - 0.068
C) FAPAR (bounded between 0 and 1), Linear mixed effects model	
Global model	MWD * Protection + Poppress * Protection + Ele_Min * Protection + Slope * Protection + LatLong + (1 + MWD Continent)
N final models	2
Model importance and sign and of coefficient estimates	Intercept: P+ 0.597 Protection = 1: 1, + 0.165 Ele_Min: 1, - 0.092 MWD: 1, - 0.142 Protection: MWD: 1, + 0.091 Slope: 0.42, + 0.027

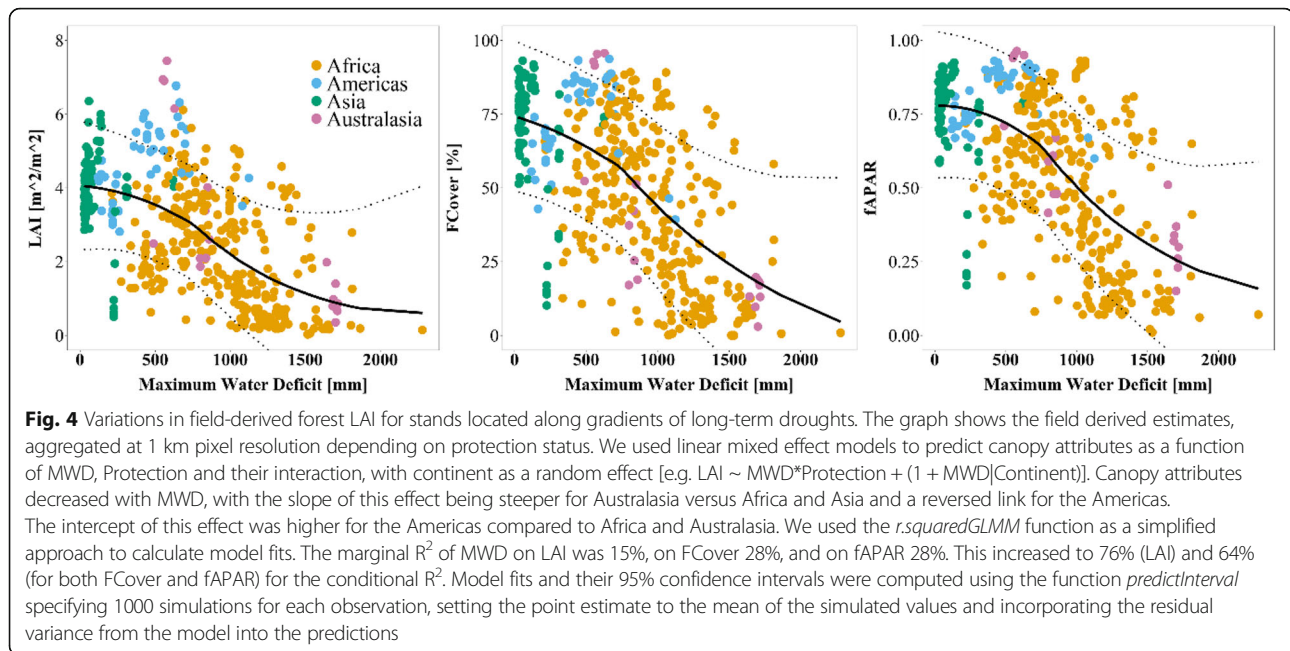
availability (Schuur 2003). However, our data from tropical forests suggests that a saturation response is more likely, in particular when looking at water availability as a driver of forest canopy structure (Additional file 1: Figure S2). We emphasize that we have used a consistent method to derive our canopy structure estimates for each plot. This is an important difference to previous analyses (Iio et al. 2014), because optical instruments can produce large discrepancies between canopy structure estimates in particular for low-height canopies and canopies with senescent vegetation and high spatial heterogeneity (Garrigues et al. 2008).

Our study is limited by the availability of data from across a range of forest types and environmental gradients for each geographic region. Our database, for example, currently lacks information from dry woody biomes in the Americas and in Asia. Also, the wet and humid tropics (e.g. Asian and American humid rainforests) are likely to be constrained by solar radiation (Nemani et al. 2003; Graham et al. 2003), which we did not measure directly in this study. And we did not look at the impacts of rising levels of CO₂, reported to increase forest productivity (so-called CO₂ fertilization effect) (Lloyd and Farquhar 2008) and forest water-use efficiency (Keenan et al. 2013). However, measurements from an old-growth lowland rainforest show that negative impacts of climatic stress (and in particular greater dry season water stress) on forest productivity greatly exceeded any small positive CO₂ fertilisation effects (Clark et al. 2013). We continue to expand our database to include a wider range of forest types from each geographic region, including tropical forests adapted to very dry and to very wet conditions.

Forest canopies and disturbance

Climate-forest canopy structure relationships that hold at large spatial scales are modulated by anthropogenic disturbance drivers affecting forest canopies at local scales (Pfeifer et al. 2012, 2014). Previous analyses for natural woody biomes in East Africa indicate that canopy LAI is higher within protected areas and increases with terrain steepness, a surrogate for passive forest protection as inaccessibility hampers human encroachment and degradation (Pfeifer et al. 2014). Forests provide important ecosystem services to local communities, including the provisioning of poles and firewood (Cuni-Sanchez et al. 2016). Rising human population pressure can hence have strong negative impacts on forest structure and functions. Our data confirm the additional positive impacts of forest protection and terrain topography on forest canopy leaf area and closure.

However, we still lack a detailed understanding of the extent to which disturbance can modulate climate - canopy structure relationships. Analyses from the humid forests of Borneo suggest that while selective logging can significantly impact forest canopies and productivity (Pfeifer et al. 2015), forest canopies are able to recover close to pre-disturbance level within one or two decades even if biomass does not (Pfeifer et al. 2016). Similarly, leaf area and associated forest functions can approach pre-disturbance levels in selectively logged Amazon forests within a decade (Asner et al. 2004). Whilst this is encouraging, other studies suggest that forests and their canopies may show non-linear responses to degradation and may enter positive climate-disturbance feedbacks leading to new stable forest regimes with more open canopies and



new sets of species once critical thresholds have been surpassed (Enquist and Enquist 2011; Trumbore et al. 2015). In a next step, advances made in individually-based, spatially explicit approaches can be utilised to test the processes we suggest are underlying the macro-scale patterns observed in this study (Beck et al. 2012).

The significantly lower estimates for canopy structure attributes measured in African forests may at least in part be attributed to many of the African plots being located near villages or roads. Distance to roads and towns can be used as an indicator of anthropogenic pressures contributing to forest degradation and loss (Laurance et al. 2009; Pfeifer et al. 2012). This is different to many of the American plots, which were located in remote mountain regions, and might be more likely to be protected de facto (Joppa et al. 2008; Pfeifer et al. 2012). Yet, even when African forests were protected by law and thus likely to be less affected by disturbance, they still had significantly less dense canopies with lower leaf area than protected forests in the Americas and in Asia.

To disentangle the compound impacts of climate and disturbance on tropical forest canopies at large spatial scales and identify possible pathways creating observed pattern we will need to increase our sampling efforts to cover gradients of disturbance within the context of the regional climate, and in particular increase the number of locations sampled in South America and South-East Asia. We suggest that acquiring such field data on long-term responses of forest canopies is necessary to allow us to predict the likely future of tropical forest functioning under climate change. This could be achieved through an expansion of objectives in longitudinal field studies on

forest dynamics, currently focussed on above-ground live tree carbon stocks and carbon fluxes (Lewis et al. 2009; Pan et al. 2011), to include assessments of spatial and temporal variations in canopy structure attributes. The Global LAI Project has approached the different key actors in these global longitudinal studies in the tropics, including RAINFOR and CTFS-ForestGEO, and we actively calling for researchers in this field to join our growing research network. Joining efforts and implementing canopy structure focussed field based measurements can additionally help to improve accuracy of satellite-based mapping of forest canopy structure (Pfeifer et al. 2014) and canopy functioning (Samanta et al. 2010, 2012). Field-derived assessment of forest canopy attributes over time would allow us to quantify rates and end states of canopy recovery pending disturbance extent and intensity. Importantly, they can also aid in assessing forest degradation impacts, particularly if we were able to revisit locations to test for possible positive and negative impacts, through drivers that will differ within and between regions.

Conclusions

Our analyses show that forest canopy structure and thus forest functioning may be largely a result of forest adaptation to the maximum water deficits they can experience within a given region. Forests in regions with higher water stress show reduced canopy leaf area and coverage. This is important in the context of expected climate changes in the tropics, which are likely to differ between regions, especially in terms of the duration and intensity of drought events, and in the context of regional differences in the sensitivity of forest stands to droughts (Hilbert et al.

2001). An increase in the frequency and intensity of droughts, predicted for tropical regions from climate models, will likely push forests beyond the safety margins of their hydraulic strategies ultimately requiring forests to adapt to new climatic regimes through changes in structure and most likely species with different hydraulic strategies. While protection from disturbance is likely to mitigate climate change impacts on forest canopy attributes relevant for forest productivity, our understanding of disturbance-climate-canopy relationships is limited by a lack of canopy structure data along gradients of disturbance within the context of the regional climate. We call for researchers working in tropical forest ecosystems to add canopy structure measurements to their objectives using the sampling methods and design of the GLOBAL LAI project and to join our growing research network allowing us to overcome this limitation.

Additional files

Additional file 1: Table S1. Attributes of each dataset used in the analyses. Locations of each plot are provided as *.pdf file (Additional file 2). N - Number of plots used for the analyses (we excluded plots that measured at less than eight sampling points). Year - Year of field measurements. Researcher - AB, Andrew Burt; ACS, Aida Cuni-Sanchez; AG, Alemu Gonsamo; AL, Alicia Ledo; ARM, Andrew R Marshall; BW, Beatrice Wedeux; DD, Dereje Denu; DS, Deo Shirima; HS, Hamidu Seki; JGT, Jose Gonzalez de Tanago Menaca; KC, Kim Calders; LC, Luis Cayuela; LAS, Lau Alvaro Sarmiento; MJM, Manuel J Macia; MP, Marion Pfeifer; ND, Nicolas Deere; PO, Pieter Olivier; PKP, Petri Pellikka; PJP, Philip J Platts; RT, Rebecca Trevithick; RH, Robin Hayward; RM, Robert Marchant; TP, Timothy Paine; WW, Woodgate William. **Figure S1.** Example maps of human population pressure, calculated from human population density grids using a range of sigma values ($\sigma = 5, 15, 25, 50$). Colours are graduated on a log base 2 scale (light colours, low pressure; dark colours, high pressure). The maps provide scope for capturing human-driven pressures at a variety of spatial scales (Platts 2012). For example, if $\sigma = 5$ then the weight given to remote populations (relative to the local population) halves over a distance of ~4 km, nearing zero by ~15 km, whereas if $\sigma = 25$ then the weight halves over a distance of ~20 km, nearing zero by ~60 km. We imposed a maximum distance of 100 km, beyond which no pressure is exerted.

Figure S2. Relationships between Annual Moisture Index (AMI) and Mean Annual Precipitation (MAP) and canopy attributes LAI, fAPAR and FCOVER. We fitted linear, polynomial and nonlinear (nls model 1: $y \sim a + b * I(x^2)$; nls model 2: $y \sim a / (1 + \exp(-(b + c * x)))$) models. **Upper panel:** polynomial models fitted to LAI ~ MAP, FCOVER ~ MAP and fAPAR ~ MAP relationships. The polynomial (RSS 1.464) and sigmoidal growth models (RSS 1.464) produced slightly better fits to the LAI data compared to the fits produced by the linear (RSS 1.47) and exponential (RSS 1.467) models. The polynomial model produced the best fit to the FCOVER (RSS 24.76) and fAPAR (RSS 0.2371) data. **Lower panel:** nls model 2 fitted to LAI ~ MAP, FCOVER ~ MAP and fAPAR ~ MAP relationships. The logistic growth model produced the best fit to the LAI data (RSS 1.347), the FCOVER data (RSS 22.95) and the fAPAR data (RSS 0.2191). (DOC 590 kb)

Additional file 2: Locations of each plot. (PDF 730 kb)

Abbreviations

AMI: Annual moisture index; CovP: Coefficient of variation in precipitation; Ele_min: Minimum elevation; fAPAR: Fraction of absorbed photosynthetically active radiation; FCOVER: Fractional Vegetation Cover; LAI: Leaf area index; MAP: Mean annual precipitation; MinT: Minimum temperature of the coldest month; MWD: Maximum water deficit; NPP: Net primary productivity; Popden: Human population density; Poppress: Human population pressure

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Availability of data and materials

The dataset supporting the conclusions of this article will be made available in the DRYAD repository. We request that permission is sought from the dataset authors before the use of the data in independent analyses.

Authors' contributions

MP and PJP designed the study and framed the research questions. MP processed the data collected for derivation of target variables and inclusion of data into the database. MP, PJP and LC implemented the statistical analyses. All authors contributed data, commented on earlier versions of the manuscript and read and approved the final manuscript.

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Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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