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Improved allometric models to estimate the aboveground biomass of tropical trees

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Abstract

Terrestrial carbon stock mapping is important for the successful implementation of climate change mitigation policies. Its accuracy depends on the availability of reliable allometric models to infer oven-dry aboveground biomass of trees from census data. The degree of uncertainty associated with previously published pantropical aboveground biomass allometries is large. We analyzed a global database of directly harvested trees at 58 sites, spanning a wide range of climatic conditions and vegetation types (4004 trees ≥ 5 cm trunk diameter). When trunk diameter, total tree height, and wood specific gravity were included in the aboveground biomass model as covariates, a single model was found to hold across tropical vegetation types, with no detectable effect of region or environmental factors. The mean percent bias and variance of this model was only slightly higher than that of locally fitted models. Wood specific gravity was an important predictor of aboveground biomass, especially when including a much broader range of vegetation types than previous studies. The generic tree diameter–height relationship depended linearly on a bioclimatic stress variable *E*, which compounds indices of temperature variability, precipitation variability, and drought intensity. For cases in which total tree height is unavailable for aboveground biomass estimation, a pantropical model incorporating wood density, trunk diameter, and the variable *E* outperformed previously published models without height. However, to minimize bias, the development of locally derived diameter–height relationships is advised whenever possible. Both new allometric models should contribute to improve the accuracy of biomass assessment protocols in tropical vegetation types, and to advancing our understanding of architectural and evolutionary constraints on woody plant development.

Keywords: carbon, forest inventory, global carbon cycling, plant allometry, tree height, tropics

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Introduction

Over the past two decades, tropical land-use change, especially deforestation and forest degradation, has accounted for 12–20% of global anthropogenic greenhouse gas (GHG) emissions (Harris *et al*., 2012; le Quéré *et al*., 2012). Economic incentives to favor carbon sequestration in forests have been devised, commonly referred to as REDD (Reducing Emissions from Deforestation and Forest Degradation; Miles & Kapos,

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2008; Agrawal *et al.*, 2011). Aside from the serious political challenge in establishing a global mechanism to fund climate change mitigation activities (Fearnside, 2012; Tirole, 2012; Tulyasuwan *et al.*, 2012), its implementation critically depends on reliable ground-based monitoring, reporting, and verification (MRV) protocols of carbon storage. In the future, carbon MRV protocols will be increasingly based on remote-sensing techniques, yet their calibration will still rely on the accuracy of ground-based carbon storage estimation (Asner *et al.*, 2010; Saatchi *et al.*, 2011; le Toan *et al.*, 2011; Baccini *et al.*, 2012; Clark & Kellner, 2012). In tree-dominated ecosystems, the stock of aboveground biomass (henceforth denoted AGB; in kg of oven-dry matter) held in vegetation is usually inferred from ground census data. Tree biometric measurements are converted into biomass values using an empirical allometric model (Brown, 1997). However, the quality of these allometric models represents one of the most important limitations in assessing AGB stocks (Chave *et al.*, 2004; Skole *et al.*, 2011; Clark & Kellner, 2012; Baccini & Asner, 2013). The goal of this contribution is to describe a new generation of pantropical tree allometric models and to evaluate the uncertainty associated to them.

The development and testing of biomass allometric models depend on the availability of direct destructive harvest data, which are enormously time-consuming and expensive to acquire. Previously published studies have made progress toward addressing this problem. Brown (1997) proposed a scheme where different allometric models should be used depending on vegetation type and on the availability of total tree height information. As a compromise between environmental variation and data availability at the time, Brown (1997) proposed a classification of tropical forests into three forest types, dry, moist, and wet, following the Holdridge life zone system (Holdridge, 1967; Brown & Lugo, 1982). This seminal study was restricted to a few destructive harvest datasets. Chave *et al.* (2005) included many more datasets and a consistent statistical scheme of model selection. The Chave *et al.* (2005) models represented a major step forward in tropical forest carbon accounting, and they are currently being proposed for inclusion in the IPCC Emission Factor Database also used by REDD protocols.

However, one major issue with the Chave *et al.* (2005) allometries relates to the importance of direct tree height measurements in AGB stock estimation. If total tree height is available, allometric models usually yield less biased estimates. However, tree height has often been ignored in carbon-accounting programs because measuring tree height accurately is difficult in closed-canopy forests (Hunter *et al.*, 2013; Larjavaara & Muller-Landau, 2013). Whether or not to include tree height as a predictor of AGB has generated serious controversies in the global change community (Baccini *et al.*, 2012; Harris *et al.*, 2012; Baccini & Asner, 2013). Better calibration and analysis of tropical tree allometric equations are needed to avoid mismatches of otherwise convergent studies, whether from plot inventory or plot-inventory-calibrated remote sensing. Second, the Chave *et al.* (2005) models may lead to biased AGB stock estimates in some undersampled vegetation types. Over the past few years, numerous new tree harvest datasets have been produced, notably in Africa (Djomo *et al.*, 2010; Henry *et al.*, 2010; Ebuy *et al.*, 2011; Ryan *et al.*, 2011; Fayolle *et al.*, 2013; Mugasha *et al.*, 2013a), in dry forests and open woodlands (Nogueira *et al.*, 2008a; Vieilledent *et al.*, 2012; Colgan *et al.*, 2013), and in previously undersampled regions in South America (Martinez-Yrizar *et al.*, 1992; Alvarez *et al.*, 2012; Lima *et al.*, 2012; Goodman *et al.*, 2014).

Here, we analyze a globally distributed database of direct-harvest tree experiments in tropical forests, subtropical forests, and woodland savannas. Our dataset includes 53 undisturbed vegetation and five secondary forest sites spanning a wide range of vegetation types, for a total of 4004 trees with trunk diameter ranging from 5 to 212 cm. We address the following questions: (i) What is the best pantropical AGB model incorporating wood specific gravity, trunk diameter, and total height? (ii) How does our pantropical AGB model compare in performance with locally fitted AGB models? (iii) If only diameter and wood specific gravity (and not total tree height) are available, does the inclusion of environmental variables improve AGB estimation?

Materials and methods

Site locations and climates

The destructive harvest dataset assembled for the present study was distributed across the tropics and across vegetation types (Fig. 1). Local climatic information was extracted from global gridded climatologies, which interpolate data from available meteorological stations (New *et al.*, 2002; Hijmans *et al.*, 2005). Temperature and rainfall variables were acquired from the WorldClim database (Hijmans *et al.*, 2005), which reports gridded mean climate values from the 1950–2000 period. We downloaded the dataset at 2.5 arc min resolution, or about 5 km spatial resolution along the equator (http://www.worldclim.org/current). This product includes elevation as available from a digital elevation model produced by NASA's Shuttle Radar Topography Mission at ca. 90 m spatial resolution (Farr *et al.*, 2007). Because water stress is important in predicting the shape of local allometric equations, we also extracted monthly values of reference evapotranspiration (ET), as computed by the FAO Penman–Monteith equation (Allen *et al.*, 1998) at a 10 arc min resolution from a mean

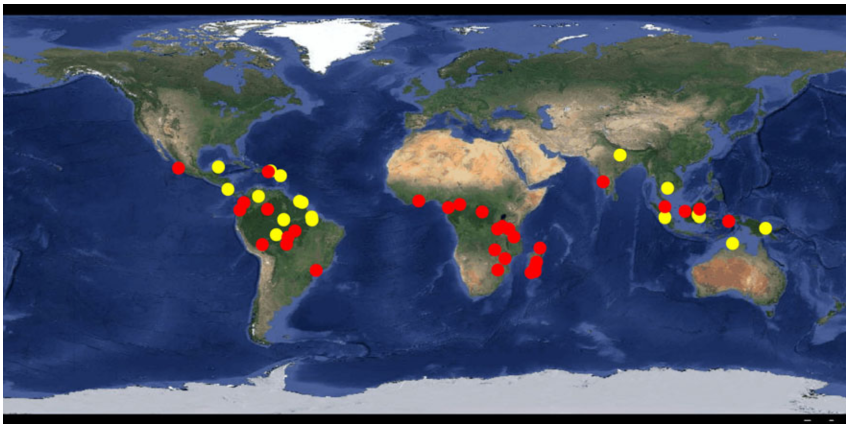

Fig. 1 Geographical locations of the study sites. Yellow circles indicate 20 studies included in Chave *et al.* (2005); red circles indicate 38 sites added to the present study.

monthly climatology developed by the Climate Research Unit (New *et al.*, 2002) over the 1960–1990 period (downloaded from http://www.fao.org/geonetwork/srv/en/ on 21 November 2012).

Preliminary analyses led us to focus on three bioclimatic variables: temperature seasonality, the maximum climatological water deficit, and precipitation seasonality. Temperature seasonality (TS), is the standard deviation (SD) of the monthly mean temperature over a year, expressed in degrees Celsius multiplied by 100. Temperature seasonality increases polewards from the equator, and also increases with altitude. The maximum climatological water deficit (CWD) is computed by summing the difference between monthly rainfall P_i and monthly evapotranspiration ET_i only when this difference is negative (water deficit): $\mathrm{CWD} = \sum_{i=1}^{12} \mathrm{Min}(0, P_i - ET_i)$. This definition differs slightly from that of Aragão *et al.* (2007) and Malhi *et al.* (2009) because in this study, we assume that CWD is caused by a single drought season. Also, we used the Climate Research Unit dataset value for ET instead of assuming a constant ET of 100 mm month^{-1}, because ET shows strong patterns of geographical variation even in the tropics (Jung *et al.*, 2010; Wang & Dickinson, 2012). A global gridded layer of CWD at 2.5 arc sec resolution is available at http://chave.ups-tlse.fr/pantropical_allometry.htm. Finally, precipitation seasonality (PS) is the coefficient of variation in monthly rainfall values, or the SD expressed in percent of the mean value.

To explore whether the sites included in the database were representative of the environmental conditions of tropical woody vegetation, we compared them with sites selected at random. We defined as tropical woody vegetation sites between the two tropics with at least 50% of canopy cover in the FAO forest-cover map (included in the Food Insecurity, Poverty and Environment Global GIS Database, Huddleston *et al.*, 2006). We randomly selected ca. 80 000 locations that fit the above criteria. For these locations, we extracted climate variables to define a realized range of climate values across tropical woody vegetation. We then graphically compared the distribution of environmental conditions at the study sites with the distribution observed over all selected sites. The result of this analysis is reported in Figure S1.

Harvest dataset compilation

We compiled tree harvest studies that had been carried out in old-growth or secondary woody vegetation, excluding plantations and agroforestry systems. The rationale for this choice is that the natural variability in plant allometry tends to be minimized in plantations. We considered only studies in which fieldwork was conducted by experienced ecologists or foresters.

To be included in the compilation, the following measurements had to be available for each tree: trunk diameter D (cm), total tree height H (m), wood specific gravity ρ (g cm^{-3}), and total oven-dry AGB (kg). We excluded trees with $D < 5$ cm because such trees hold a small fraction of AGB in forests and woodlands (Chidumayo, 2002; fig. 3), and would otherwise dominate the signal in regression models. The common practice for measuring D is to measure trunk diameter at 130 cm aboveground (diameter at breast height). Buttressed or irregular-shaped trees are measured above buttresses or trunk deformities. It was impossible to confirm that this convention had been followed, especially for the older datasets (e.g. Hozumi *et al.*, 1969), but the trunk diameter size structure was carefully checked and the retained datasets were those without obvious diameter measurement error. Measuring total height accurately may also be an issue in closed-canopy forests (Hunter *et al.*, 2013; Larjavaara & Muller-Landau, 2013). The compiled studies usually did not report how tree height was measured. However, it is likely that more effort was put into measuring tree height correctly in destructive harvest experiments than in nondestructive forest surveys.

Each tree was felled at ground level, and different sections were weighed fresh or their fresh volume measured. The fresh wood weight was then converted into oven-dry weight by directly measuring the moisture content in the different parts of the plant. In the largest trees, it was usually not practical to weigh the entire individual, so wood volume was often inferred from geometrical considerations (see e.g. Henry *et al.*, 2010; Fayolle *et al.*, 2013), and wood volume was converted into oven-dry weight by multiplying the volume by the wood specific gravity (Chave *et al.*, 2009; Williamson & Wiemann, 2010).

In many studies, the mass of the main stem (merchantable bole before the first branching), branches, and leaves were measured separately. In seasonally dry forests, it was often difficult to measure leaf biomass because of deciduousness, but leaf biomass usually contributes less than 5% of total AGB (Delitti *et al.*, 2006). Thus, we analyze only total oven-dry above ground biomass (the sum of the above ground biomass compartments).

Our dataset includes 58 study sites, from published and unpublished sources, for a total of 4004 individually harvested trees (see Data S2). The previous compilation, reported in Chave *et al.* (2005), included 20 study sites and 1481 individually harvested trees for which trunk diameter, total tree height, AGB, and wood specific gravity were all available. A few studies were removed from the Chave *et al.* (2005) compilation because the criteria for inclusion chosen here were more stringent (see Data S3). Sites included in this database comprise the first destructive harvest experiments reported from the Afro-tropical realm ($n = 1429$, including Madagascar), data from Latin America ($n = 1794$), and from Southeast Asia and Australia ($n = 781$). This also includes many new sites from woodlands and dry tropical forest types, both in Africa and Latin America. This compilation was carried out between 2008 and 2013. In a recent article, Feldpausch *et al.* (2012) published a reanalysis of the Chave *et al.* (2005) dataset, to which they added six datasets (349 trees). Of these additional datasets, we retained five in the present compilation. Because we also removed and corrected some data from Chave *et al.* (2005), the dataset analyzed here is more conservative than that of Feldpausch *et al.* (2012), but is also more than twice as large.

Wood specific gravity (here defined as the oven-dry wood mass divided by its green volume, and denoted ρ) is an important predictor of stand-level AGB (Baker *et al.*, 2004). In the field, green volume was measured from freshly cut wood samples. The samples were subsequently weighed after having been left in a drying oven until constant weight is reached. However, it should be acknowledged that even direct ρ measurement is prone to error (for a comprehensive review, see Williamson & Wiemann, 2010), and not all individuals had ρ directly measured in the field. The alternative is to assume that the ρ of a tree is equal to its species-mean value. The majority of the trees in our dataset were identified to species (81%). Taxonomic information was carefully checked for consistency (Boyle *et al.*, 2013). In case of inconsistencies, the most likely name was selected. In a few cases, trees were identified using a vernacular name, and we attempted to assign them to the most precise relevant taxonomic level, often to genus, based on expert knowledge. For those trees lacking direct ρ measurement but identified taxonomically, we extracted the species-mean from the comprehensive global wood density database (Chave *et al.*, 2009; Zanne *et al.*, 2009). In that database, wood specific gravity values are typically means across several individuals of the same species, and measurements were conducted in highly qualified wood science laboratories. In total, ρ was directly measured for 59% of the trees, and species-mean ρ was assumed for an additional 26% of the trees. For the remaining 15% of the trees, we assumed genus-mean (13%) or family mean (2%) wood specific gravity values as computed from the global database.

To test a possible bias in the selection of ρ from global compilations, we compared the values obtained directly from field values and from the global database for a total of 1194 trees. Because the errors are expected to be of the same magnitude in both variables, we used a reduced major axis regression and found that database values explained 67% of the variance in the field values, and the slope of the regression was of 0.993, very close to the expected slope of 1. Thus, we conclude that assigning species-mean wood specific gravity values to the trees of our database may introduce random errors but did not bias the analyses.

The tree harvest database used in the present study is available at http://chave.ups-tlse.fr/pantropical_allometry.htm.

Statistical analyses

Estimating AGB when tree height is available. Allometric model construction is based on regressing a dependent variable (i.e. AGB), against one or several independent variables. The possible independent variables included here were trunk diameter D (cm), wood specific gravity ρ (g cm^{-3}), total tree height H (m), or a combination thereof. We fitted the following log-log model relating AGB to the compound variable $\rho \times D^2 \times H$.

$$\ln(\mathrm{AGB}) = \alpha + \beta \ln(\rho \times D^2 \times H) + \varepsilon \qquad (1)$$

where α and β are model coefficients (derived from least-squares regression), ε is an error term, which we assume to be normally distributed with zero mean and SD σ [i.e. the random variables are identically independently distributed with a distribution $N(0, \sigma^2)$]. If a model such as Model 1 has p parameters, σ is defined by

$$\sigma = \sqrt{\frac{1}{N-p}\sum_{i=1}^{N} \varepsilon_i^2}$$

where N is the sample size. In the statistical literature, σ is also called residual standard error or RSE. Technically, the above formula is the residual maximum likelihood estimate for σ, and it may be shown to be unbiased (Harville, 1977). If $\beta = 1$, an isometric relationship exists between AGB and $\rho D^2 H$. In a likelihood-based framework, testing the hypothesis that $\beta = 1$ may be implemented by comparing the Akaike Information Criterion (AIC) of Model 1 with the nested model $\ln(\mathrm{AGB}) = \alpha + \ln(\rho \times D^2 \times H) + \varepsilon$. The AIC is a measure of the goodness-of-fit that penalizes parameter-rich models, as required by the principle of parsimony (Burnham & Anderson, 2002).

Model 1 may be used to infer the value of AGB for an individually measured tree. The estimated value $\mathrm{AGB}_{\mathrm{est}}$ can be written as:

$$\begin{aligned}\mathrm{AGB}_{\mathrm{est}} &= \overline{\exp[\alpha + \beta \ln(\rho D^2 H) + \varepsilon]} \\ &= \overline{\exp[\varepsilon]} \times \exp[\alpha + \beta \ln(\rho D^2 H)]\end{aligned}$$

where $\overline{\exp[\varepsilon]} = \int \exp(\varepsilon) N(\varepsilon) d\varepsilon$ and $N(\varepsilon)$ is the distribution of errors [assumed to be a normal distribution, $N(0, \sigma^2)$]. As first shown by Baskerville (1972), a simple algebraic manipulation yields $\overline{\exp[\varepsilon]} = \exp(\sigma^2/2)$. From this it follows that Model 1 may be used to give an unbiased estimate of AGB using the following equation:

$$\mathrm{AGB_{est}} = \exp[\sigma^2/2 + \alpha + \beta \ln(\rho D^2 H)] \tag{2}$$

Improvements to this formula are possible, especially accounting for the fact that the estimator of σ itself has uncertainty (Shen & Zhu, 2008). Recently, Clifford *et al.* (2013) have reviewed this issue and provided routines to implement corrections. We also tested this approach using our dataset. However, as our sample size is large, we found that applying the correction of Shen & Zhu (2008) to our data yielded AGB estimates within 0.5% of the values obtained with the Baskerville correction [Eqn (2)]. We therefore decided to retain the simpler [Eqn (2)] for the present study.

While the importance of trunk diameter in inferring AGB has been acknowledged since the development of tropical forestry (Dawkins, 1961; Ogawa *et al.*, 1965), the importance of ρ as a predictor of AGB has been debated only recently. Wood specific gravity varies greatly within individuals (Patiño *et al.*, 2009) and existing pantropical wood specific gravity compilations are incomplete (Clark & Kellner, 2012). Therefore, it has been argued that ρ may not be a useful variable in AGB estimation (Lima *et al.*, 2012). To test this hypothesis, we conducted a comparison of Model 1 with a similar model, but from which wood specific gravity was excluded, namely $\ln(\mathrm{AGB}) = \alpha + \beta \ln(D^2 \times H) + \varepsilon$. We asked whether this alternative model yields a goodness-of-fit comparable to that of Model 1, as evaluated by AIC.

For each of the 58 sites, we calculated measures of average systematic error (bias) and of total tree-level coefficient of variation (CV). As in Chave *et al.* (2005), the bias at individual sites was evaluated by comparing the empirical mean AGB at site j $B_{\mathrm{obs}}(j)$ to the estimated value $B_{\mathrm{est}}(j)$. The model bias was defined as follows:

$$\mathrm{Bias}(j) = [B_{\mathrm{est}}(j) - B_{\mathrm{obs}}(j)]/B_{\mathrm{obs}}(j)$$

To measure total error, including random error, we also computed the tree-level coefficient of variation in AGB for site j defined as

$$\mathrm{RSE}(j) = \sqrt{\frac{1}{N_j - p}\sum_{i \in [j]} [\mathrm{AGB_{est}}(i,j) - \mathrm{AGB_{obs}}(i,j)]^2}$$

$$\mathrm{MAGB}(j) = \frac{1}{N_j}\sum_{i \in [j]} \mathrm{AGB_{obs}}(i,j),$$

$$\mathrm{CV}(j) = \frac{\mathrm{RSE}(j)}{\mathrm{MAGB}(j)}$$

as in Colgan *et al.* (2013). $\mathrm{AGB_{obs}}(i, j)$ is the observed AGB of tree i belonging to site j, and $\mathrm{AGB_{est}}(i, j)$ is the estimated AGB value for the same tree. The first equation defines the residual standard error (RSE), the second defines the mean AGB at site j MAGB(j). Then, CV(j) is simply defined as the ratio of these two terms. CV(j) measures the typical relative error at site j that should be expected in the estimate of a single tree. A large value of CV(j) would be acceptable so long as the bias is low, because in general the model is applied to many trees within a site and thus random errors will tend to cancel.

The tree-level coefficient of variation (CV) and the bias were used to compare the performance of the model summarized in Model 1 with that of alternative models. We performed the analysis in three stages. First, at each study site we fitted Model 1 using all study sites except that of the focal site. We then computed the CV and the bias of the focal site with this model, ensuring that the calibration and validation datasets are independent. Second, we tested the hypothesis that local models perform significantly better than pantropical models. To this end, we constructed a local allometry excluding all study sites but the focal one, again using Model 1. We then computed the CV(j) and Bias(j) of the focal site based on the local model. We expect that the local models will have lower bias and variance (hence smaller CVs). However for local models (but not for the pantropical model), the same dataset is used to calibrate the model and to compute errors (validation stage). Thirdly, we repeated the same procedure as in stage 1, but using the predictor variable $D^2 \times H$ instead of $\rho \times D^2 \times H$ to test the hypothesis that wood density is an important predictor of AGB. We again compared the performance of the two models based on the CV and bias at each study site.

Estimating AGB when tree height is unavailable. When tree height is unavailable to estimate AGB, the inference is thought to be less accurate, and allometric equations are more likely to vary across vegetation types, as diameter–height allometry depends on environmental conditions. Pantropical or regional allometric equations to predict AGB based on only D and ρ have been developed previously (Brown, 1997; Ketterings *et al.*, 2001; Chave *et al.*, 2005; Feldpausch *et al.*, 2012), but here we provide a simpler framework. We seek a general model relating total tree height to trunk diameter and bioclimatic variables. We selected the relevant bioclimatic variables using a forward model selection approach where all possible combinations of bioclimatic variables were compared. If such a model does exist, then it should be possible to infer height from trunk diameter at each site. Here, we propose the following functional form:

$$\ln(H) = a + a' \times E + b \times \ln(D) + c \times \ln(D)^2 + \varepsilon' \tag{3}$$

The quadratic dependence of ln(H) on ln(D) was implicitly assumed in previous studies (Chambers *et al.*, 2001; Chave *et al.*, 2005), but to our knowledge it has never been tested directly as a diameter–height equation. In Eqn (3), E denotes an environmental variable, and model error is described by the SD of the residuals denoted σ' to avoid confusion with the σ of Model 1. More general models may be constructed similarly, assuming that all of the model parameters depend on E, but we here privileged the simplicity and consistency of the present approach. To select the environmental variable E, we performed a forward selection by sequentially including the bioclimatic variables that led to the greatest decline in model RSE.

Once total tree height has been estimated from Eqn (3), Eqn (1) can be used to estimate AGB even for trees without field measurements of H. Further, the mathematical form of the resulting AGB model is equivalent to that proposed in Chambers *et al.* (2001) and used by Chave *et al.* (2005). More precisely, using Eqn (3) to express ln(*H*) as a function of ln(*D*) and using this estimate in Eqn (1), yields a new pantropical allometric model

$$\mathrm{AGB_{est}} = \exp\left[\frac{\sigma^2}{2} + \beta^2\frac{\sigma'^2}{2} + \alpha + \beta\ln(\rho D^2) + \beta\{\ln(\mathrm{H})\}_{\mathrm{est}}\right]$$

where $\{ln(H)\}_{\mathrm{est}} = a + a' \times E + b \times ln(D) + c \times ln(D)^2$ is obtained directly from Eqn (3), and depends explicitly on the local bioclimatic variable *E*. We also compared the performance of Eqn (3) with the height equations proposed by Feldpausch *et al.* (2012).

Because of the quadratic form of Eqn (3), it would be theoretically possible that for large values of *D, H* would decrease when *D* increases. We therefore tested whether this regime was likely to be reached empirically. The function reaches a maximum at $D = \exp\ [-\mathrm{b}/(2c)]$, and we verified that this maximum is never reached in practical applications.

All statistical analyses were performed with the R statistical software (R Development Core Team, version 3.0.3).

Results

When we regressed tree AGB (kg) against the product $\rho \times D^2 \times H$, we found the best-fit pantropical model to be:

$$\mathrm{AGB_{est}} = 0.0673 \times (\rho D^2 H)^{0.976}$$
$$(\sigma = 0.357, \mathrm{AIC} = 3130, \mathrm{df} = 4002) \quad (4)$$

where *D* is in cm, *H* is in m, and ρ is in g cm^{-3}. This model performed well across forest types and bioclimatic conditions (Figures S2 and S3). The alternative model where the exponent was constrained to one:

$$\mathrm{AGB_{est}} = 0.0559 \times (\rho D^2 H)$$
$$(\sigma = 0.361, \mathrm{AIC} = 3211, \mathrm{df} = 4003) \quad (5)$$

gave a slightly poorer performance (greater σ and AIC). Model 4 tends to underestimate AGB by 20% for individual trees with observed AGB exceeding 30 Mg (n = 14; Fig. 2). The trend disappeared for trees in the range 10–30 Mg (2.7% overestimation, n = 94). Because of the spread of values for $\rho D^2 H$, we did not find suitable models to accommodate this bias.

In comparison to Model 4, the best-fit model excluding wood specific gravity as a predictor had an AIC = 3983 and σ = 0.418, which are significantly poorer than Model 4. Thus, we conclude that wood specific gravity is an important predictor of AGB, especially when a broad range of vegetation types is considered.

Compared with local models, average total tree-level prediction error was only modestly higher in the pantropical model (Fig. 3a), but the spread of systematic error across sites was more than three times higher (Fig. 3b). The mean of CV(*j*) across sites was 56.5% using the pantropical allometric Model 4 vs. 47.4% using the local allometric models. The mean bias was +5.31% across all sites for Model 4, vs. +0.38% for the locally developed models. The pantropical model tended to substantially overestimate the measured total, site-level AGB at seven sites (bias > 30%) and underestimate it (bias< −30%) at one site (Fig. 3b). This bias was not explained by vegetation type or by bioclimatic conditions (Figures S2 and S3). The site-mean form factor (AGB divided by $\rho \times D^2 \times H$) displayed a trend with forest type and bioclimatic factors, but this trend was significant only with CWD (climatic water deficit, R^2 = 0.17, P = 0.02, Figure S4).

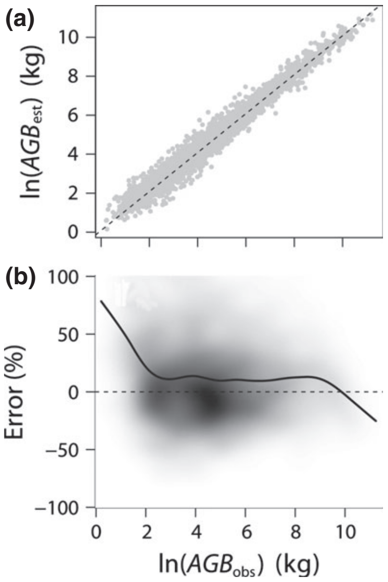

Fig. 2 Goodness-of-fit for Model 4. (a) AGB as estimated from the model vs. observed AGB (n = 4004, gray points), compared with the 1 : 1 line (dashed line). (b) Relative error (estimated minus observed AGB, divided by observed AGB, in%); the thick black line represents a spline regression of the data points, illustrating a slight negative bias at large AGB values (values >30 Mg). The background represents data-point density.

To compare more directly the influence of vegetation type and site on Model 4, we also conducted a nested analysis of variance on the relative residuals $100 \times \frac{\mathrm{AGB_{est}} - \mathrm{AGB_{obs}}}{\mathrm{AGB_{obs}}}$. The vegetation type factor explained 0.6% of the relative residual variance, the site factor explained 21.4%, and the within site variation explained 78%. Thus, most of the residual variation in the dataset was among trees within sites. Model 4 was plotted for each site in Data S2.

For cases in which total tree height is unavailable, we developed a diameter–height allometric equation of the form of Eqn (3). Using forward selection (see Methods), we found that among-site variation in diameter–height

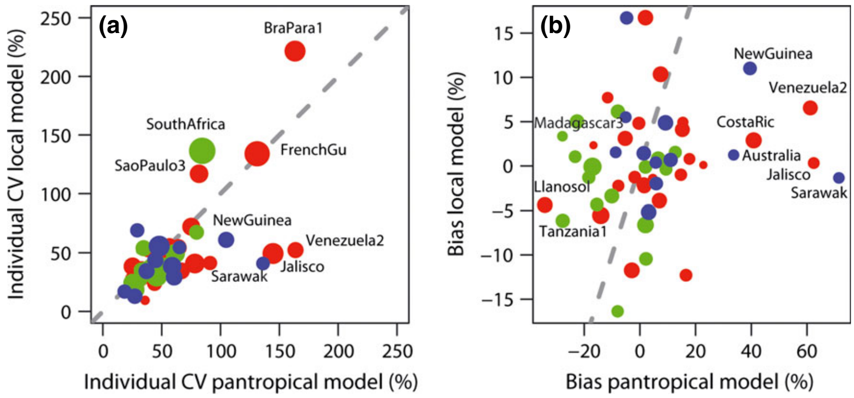

Fig. 3 Comparison of model performance between the pantropical allometric AGB Model 4 and local allometric models. (a) Individual coefficient of variation at each site for both types of allometries. Point size is proportional to sample size, red dots indicate Latin American sites, green African sites, and blue Southeast Asian and Australian sites. Outlying sites are labeled (sites such that CV >100% in any one direction). (b) Individual bias at each site for both types of allometries. Point color as in Panel (a), point size proportional to total AGB at the site. In color in the online version. Outlying sites – sites such that the absolute value of the bias exceeds 30% – have been labeled.

allometries was best explained by TS (temperature seasonality), CWD (climatic water deficit), and PS (precipitation seasonality), with only small further declines in model RSE with the sequential inclusion of additional bioclimatic variables (Figure S5). We thus propose the following pantropical diameter–height allometric model

$$\ln(H) = 0.893 - E + 0.760\ln(D) - 0.0340[\ln(D)]^2 \quad (6a)$$

(AIC = 47, RSE = 0.243, df = 3998), where E is defined as

$$E = (0.178 \times \mathrm{TS} - 0.938 \times \mathrm{CWD} - 6.61 \times \mathrm{PS}) \times 10^{-3} \quad (6b)$$

Equation (6b) has an intuitive interpretation. E is a measure of environmental stress. Indeed, E increases with temperature seasonality, which relates to the amount of time a plant is exposed to stressful temperature, and CWD (a negative quantity) increases in magnitude with increasing annualized water stress. The dependence of E on PS (precipitation seasonality) is less obvious but appears to be mostly driven by monsoon-dominated rainfall regime (Nemani *et al*., 2003). The dependence of diameter–height allometry on E is illustrated in Fig. 4. A global gridded layer of E at 2.5 arc sec resolution is available at http://chave.ups-tlse.fr/pantropical_allometry.htm. Equation (6a) predicts that the log-transform of tree height for a given diameter declines with both water and temperature stress. We also verified that the functional form of Eqn (3) is biologically consistent: for all E, the quadratic function in $\ln(D)$ reaches a maximum that far exceeds biologically realistic values for D. Combining Eqns (4) and (6a) directly, AGB can be inferred in the absence of height measurements (RSE = 0.431, df = 3999). Here, we prefer to fit the data directly, yielding the following model:

$$\begin{aligned}\mathrm{AGB}_{\mathrm{est}} = \exp[&-1.803 - 0.976E + 0.976\ln(\rho) \\ &+ 2.673\ln(D) - 0.0299[\ln(D)]^2]\end{aligned} \quad (7)$$

which yields a slightly lower RSE (AIC = 4293, σ = 0.413, df = 3999). The mean CV across sites and the bias were 71.5% and 9.71%, respectively. We therefore propose Model 7 for estimating AGB in the absence of height measurements. The performance of Model 7 was clearly worse than Model 4, as observed from a comparison of the AIC, and as would be expected (Model 7 vs. Model 4; CV: 71.5% vs. 56.5%; bias: 9.71% vs. 5.31%; Fig. 5a, b). We also verified that if the regional diameter–height models of Feldpausch *et al.* (2012) had been

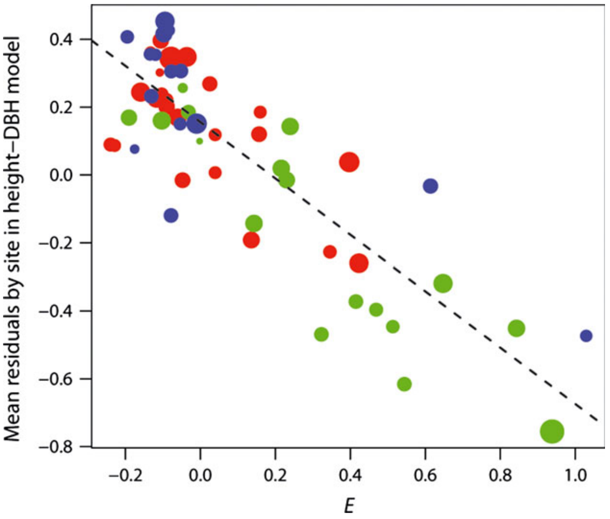

Fig. 4 Dependence of the diameter–height model on the environmental variable [E; Eqn (6b)]. Point color and size are as in Fig. 3.

used instead of Model 6a, the bias would have been much larger (mean bias: +22.41%; Figure S6).

Finally, we compared the performance of the models proposed in this study with that developed in Chave *et al.* (2005). Model 4 predicted results very similar to those obtained with Model I.3 of Chave *et al.* (2005). Across our sites, the mean CV(j) of Model I.3 was 56.2%, and the mean bias was −2.24%, and these values were similar to that obtained for Model 4. When tree height is unavailable, Chave *et al.* (2005) proposed model II.3. The mean CV(j) of Model II.2 was 80.5%, and the mean bias was +5.78%. Although it is simpler, our new Model 7 thus performed much better than the Chave *et al.* (2005) models.

Discussion

On estimating AGB when tree height is available

We here propose a single allometric equation to estimate tree AGB across vegetation types when wood specific gravity, trunk diameter, and total tree height are available (Model 4). Most of the variation was found within vegetation types, and the apparent variation among vegetation types appears to mostly reflect small sample sizes. This interpretation is supported by the fact that the form factor (ratio of AGB divided by $\rho D^2 H$) varies weakly across vegetation types (Figure S4). This convergence of tropical tree biomass allometries across biomes and continents is striking. The causes of variation in trunk tapering coefficient have been studied in depth (Dawkins, 1961; Niklas, 1994; Chave *et al.*, 2005), but the form factor depends also on the size and shape of the crown. One possible interpretation of our finding is that although trunk taper varies consistently across vegetation types, biomechanical design both of the hydraulic plant system and of the organism strongly constrains the overall architecture of self-supporting plants.

It is useful to contrast this result with the previous analysis of Chave *et al.* (2005). Here, we greatly increased the sampling effort in both dry and wet vegetation types. In the 2005 analysis, only three dry forest sites where tree height was measured were included to form the basis of the dry forest equation (Australia: 46 trees, Yucatan: 175 trees, IndiaCha: 23 trees). In comparison, the present study includes 22 dry vegetation sites, and 1891 trees. Likewise, Chave *et al.* (2005) included only three wet forest sites having height data (NewGuinea: 42 trees, PuertoRi: 30 trees, Cambodia: 72 trees), while the present analysis now includes 12 wet forest sites and 681 trees.

Although our dataset represents a significant improvement over previously published intercomparisons of tree harvest data, they are still limited in size, especially compared with those developed for temperate forests (Chojnacky *et al.*, 2014) or plantations (Paul *et al.*, 2013). One option for assembling whole-tree AGB measurements without harvesting the tree is to use terrestrial LiDAR to estimate the volume of individual branches and stems (Hildebrandt & Iost, 2012). With additional wood specific gravity measurements, it should be possible to estimate tree AGB to a good accuracy without felling the tree. This approach should accelerate the acquisition of tree biometric data.

Based on the data now available, it appears that separate regression parameters for the dry, moist, and wet vegetation types do not improve the statistical performance of the model. Our analysis thus suggests that it is more parsimonious to retain a single allometric model. Previously published estimates for moist forests using Chave *et al.* (2005)'s Model I.3 are very close to

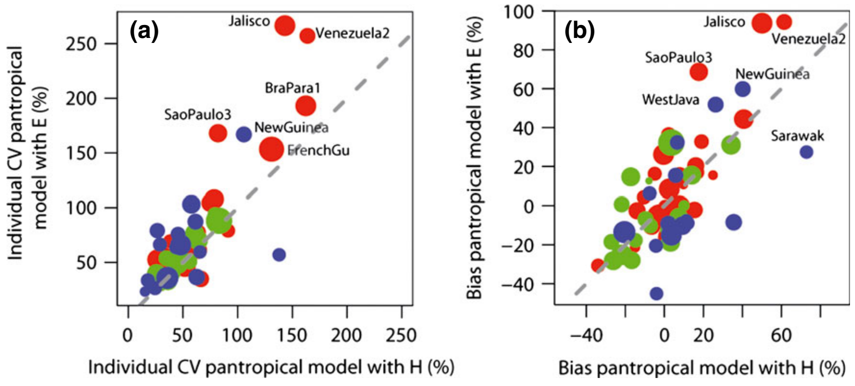

Fig. 5 Comparison between the pantropical allometric AGB Model 7 and pantropical allometric AGB Model 4. Panel (a) Individual coefficient of variation at each site for both types of allometries. Outlying sites are labeled (sites with an individual CV >150%). Panel (b) Comparison of the bias between Model 7 and Model 4. Point color and size are as in Fig. 3. Outlying sites are labeled (sites with an absolute bias >50%).

estimates obtained using Model 4, as may be evidenced in Table 1. This is important because most of the tropical forest carbon sequestration occurs in moist tropical forests and the corresponding Chave *et al.* (2005) allometry has been used frequently in the published literature (see e.g. Asner *et al.*, 2010 and the related discussion in Skole *et al.*, 2011). Thus, it is likely that the present equation will not drastically change AGB stock estimates for moist tropical forests. We also note that this new model holds for both old-growth and secondary vegetation types.

The previous classification of harvest experiments into forest types was based on the sparse bioclimatic information available at the time, and possible inconsistency in climatic measurements, which led to a misclassification of some of the sites. For instance, the Cambodia dataset is a forest close to the current locality of Thma Sa in the Kingdom of Cambodia. It was previously classified as ever-wet forest because annual rainfall exceeds 3300 mm yr^{-1}. However, it is a monsoonal climatic regime (ET exceeds rainfall during 6 months of the year and CWD is less than -400 mm yr^{-1}); thus, this site was now reclassified as dry forest for comparison with previous studies. This illustrates the importance of accurate estimates of bioclimatic variables, and of relying on quantitative climatic metrics, rather than on an *a priori* classification into vegetation types. Because global climatic compilations have greatly improved over the past decade (Hijmans *et al.*, 2005), it is now possible to obtain far better bioclimatic descriptors at ecological study sites than the ones derived from the Holdridge life zone system.

In a recent study, Goodman *et al.* (2014) emphasized that pantropical allometric models may underestimate the AGB of very large trees in areas where trees are shorter but have large crowns. We did detect a departure between observations and predictions for individual trees with an AGB greater than 30 Mg. For these very large trees, Model 4 underestimated AGB by an average of 20% (note that this bias vanishes for trees in the range 10–30 Mg). This is an issue given that these large trees may contribute a large fraction of the AGB stock in a tropical forest stand. However, we here suggest that sampling bias in the harvest dataset may also in part explain this pattern. Because harvesting very large trees is a laborious endeavor, we hypothesize that well-formed boles may have been preferentially selected over partly broken, or senescent large trees, especially when the study was conducted in relation to logging activity (as is the case for the Cameroon3 site, which includes eight of the 14 trees with AGB $\geq$ 30 Mg in our dataset). We therefore believe that the discrepancy of our model in these extreme values of AGB should not necessarily be interpreted as a failure of the model. In a recent essay, Clark & Kellner (2012) provided a constructive critique of current strategies for AGB model development, and they suggest that harvested trees are probably never selected at random, and that poorly conformed trees are seldom included in analyses. Models with few parameters are robust to biases generated by individual harvest datasets, and they are therefore an advantage in this situation.

It has often been argued that local allometric equations should be constructed in as many sites and for as many species as possible. In the same line of reasoning, many authors have contended that previous pantropical AGB allometries could not be used in Africa because no African site had been included in previous efforts for constructing pantropical AGB models (Chave *et al.*, 2005). However, our results show that once variation in diameter–height allometries are accounted for, pantropical AGB allometries are

Table 1 Estimation of the AGB (kg) when tree height is available, for trees of typical dimensions and for the four largest trees in the dataset. Four models are used: the three models called Model I.3 in table 2 of Chave *et al.* (2005), and Model 4 of the present study. The last four lines represent the parameters of trees in the dataset reported to have measured *AGB* over 50 Mg. Their measured *AGBs* are 51.7 Mg (*Cyclodiscus gabunensis* (Taub.) Harms), 60.5 Mg (*Entandrophragma cylindricum* (Sprague) Sprague), 70.2 Mg (*Tieghemella heckelii* (A.Chev), Pierre, ex Dubard), and 76.1 Mg (*Dipteryx micrantha* Harms), respectively

Trunk diameter (cm)	Height (m)	Wood specific gravity (g cm^{-3})	Model I.3 dry forests	Model I.3 moist forests	Model I.3 wet forests	This study model 4
10	9	0.7	41	32	33	36
30	25	0.6	680	687	592	723
70	40	0.6	4940	5986	4529	5980
100	45	0.5	8950	11 453	8335	11 265
136	48.5	0.78	25 302	35 615	24 215	34 092
178	52.4	0.57	33 364	48 169	32 162	45 776
180	61	0.62	42 274	62 371	41 005	58 906
158	44.1	0.83	32 310	46 510	31 120	44 237

consistent across sites. To quantify this claim, we compared error metrics between our pantropical equation and locally fitted equations. The pantropical approach was based on the estimation of two parameters (Model 4), while the local approach required the estimation of two parameters per site, i.e. 116 parameters in total. We found that the AGB of single trees was estimated to within 56.5% of the mean using the pantropical model and to within 47.4% of the mean with local allometric models (coefficient of variation; Fig. 3a). Thus, local allometric models do not perform much better than pantropical models in terms of model uncertainty: in both cases, the error in estimation of AGB for any single tree is on the order of 50% of the mean. Mean bias across sites was higher for the pantropical equation, averaging +5.31% vs. +0.38%. However, this is in part a simple consequence of the fact that, in the local case, fitting and evaluation are performed on exactly the same dataset. Indeed, if we measured bias as mean deviations in ln(AGB), then we would have zero bias for the local models by the very nature of the model fitting procedure, which minimizes the sum of squared errors in ln (AGB). Because we measure bias instead as the mean error in AGB, the local models have nonzero bias, but this bias is still inherently small.

Much of the increase in bias between the local and the pantropical allometries was contributed by six outlying sites (three moist forests and three wet forests; Fig. 3b). For these outlying sites, Model 4 tends to overestimate AGB. A number of interpretations could be put forward to explain this discrepancy. The dimensions of wet forest trees are difficult to measure because many trees are buttressed. Yet the majority of wet forest sites comply with the pantropical model (eight of 11). Also, methodological inconsistencies with the other studies included in the present compilation cannot be excluded. However, as several of these studies were conducted decades ago (NewGuinea, Venezuela2, Jalisco), it would be difficult to trace back such inconsistencies, if any. Thus, it is important to continue generating primary data with careful quality control/quality assurance procedures.

Tree-level uncertainty in AGB estimation from our model is about of 50% the mean, thus individual-tree AGB cannot be estimated precisely with any such model. However, assuming an average of 500 trees with $D \geq 10$ cm per ha, then the plot-based uncertainty in AGB can be computed as follows. If, as previously, we denote $\mathrm{AGB}_{\mathrm{est}}(i)$ the estimated value of AGB for tree i, and the SD for this tree $\sigma(i)$, then $\sigma(i) = \mathrm{CV} \times \mathrm{AGB}_{\mathrm{est}}(i)$, and CV = 50%. A simple calculation shows that plot-based uncertainty, $\mathrm{CV}_{\mathrm{plot}}$ is such that

$$\mathrm{CV}_{\mathrm{plot}} = \mathrm{CV} \times \frac{\sqrt{\Sigma_i [\mathrm{AGB}_{\mathrm{est}}(i)]^2}}{\Sigma_i \mathrm{AGB}_{\mathrm{est}}(i)} \tag{8}$$

where the sum runs over all the trees in the plot. Computing this for typical AGB distributions shows that plot-level uncertainty due to the allometric equation drops to ca. 10–15% for a ¼ ha plot and ca. 5–10% for a 1 ha plot. This plot-based uncertainty is larger than expected from a simple averaging because a few large trees contribute disproportionately to stand-level AGB (Chave *et al.*, 2004). However, even accounting for these terms, model-based uncertainty is typically less than 10% of the mean at the 1 ha scale, and the equation for $\mathrm{CV}_{\mathrm{plot}}$ allows to compute this uncertainty for any plot.

On inferring tree height from trunk diameter and bioclimatic variables

A large body of literature in forestry suggests that the diameter–height relations in trees depend on a range of physiological and environmental factors (Ryan & Yoder, 1997; Falster & Westoby, 2005; Ryan *et al.*, 2006; Niklas, 2007; Kempes *et al.*, 2011; Mugasha *et al.*, 2013a,b). These include climatic conditions (Wang *et al.*, 2006; Nogueira *et al.*, 2008b; Lines *et al.*, 2012) and altitude (Grubb, 1977; Aiba & Kitayama, 1999; Lines *et al.*, 2012; Marshall *et al.*, 2012), but also local edaphic factors (Aiba & Kitayama, 1999; Kempes *et al.*, 2011), evolutionary and architectural constraints (King, 1990; Niklas, 1994; Falster & Westoby, 2005; Goodman *et al.*, 2014), and competition for space (Henry & Aarssen, 1999). For instance, Lines *et al.* (2012) showed that in temperature- and/or water-stressed environments, tree height is typically much smaller than expected under a purely mechanical model, confirming the primary role of hydraulics in regulating the height of trees at a given trunk diameter (see also Kempes *et al.*, 2011).

Recently, Feldpausch *et al.* (2011) conducted a pantropical analysis of diameter–height tree allometries and concluded that regional variation in this allometry was an important source of variation in tree AGB. They then developed a set of region-specific diameter–height allometries to minimize bias due to the variation in canopy height across tropical forest regions (see also Banin *et al.*, 2012). They investigated whether some of the climatic variables in the WorldClim database may predict a significant fraction of the variation in the diameter–height relationship. For a given trunk diameter, they found a positive correlation between tree height and precipitation seasonality only. Their finding is counterintuitive because height should peak at intermediate precipitation seasonality values, and be lower in both dry and ever-wet forests (see e.g. Hall & Swaine, 1981; figure 5.1; Wang *et al*., 2006). This is probably because the Feldpausch *et al.* (2011) database did not include many dry vegetation sites.

Here, we readdressed the question of the bioclimatic dependency of the diameter–height relationship in tropical trees. Our dataset had only a limited overlap with that used in Feldpausch *et al.* (2011) and Banin *et al.* (2012), and we found different results. Our major finding is that the diameter–height relationship depends linearly on a compound bioclimatic variable E, which itself is a linear function of climatic water deficit, temperature seasonality, and precipitation seasonality. Indeed, we found that a large fraction of the residual variation in the diameter–height relationship is attributable to the variable E, and that a single model (Eqn 6) may be used to predict total tree height from trunk diameter and E across the tropics.

Our finding that the tree diameter–height relationship reflects the effect of drought tolerance and tolerance to temperature variability is consistent with a number of classic results in plant physiology. For instance, drought and temperature are known to modulate tree physiology and especially carbon assimilation (reviewed in Lloyd & Farquhar, 2008) but also ecosystem productivity (Nemani *et al*., 2003; Gatti *et al*., 2014). Also, our findings confirm those of Aiba & Kitayama (1999), Lines *et al.* (2012), and Kempes *et al.* (2011), but over a much larger geographical and environmental scale.

Carbon accounting and relevance to global change

The finding that AGB may be reliably inferred from wood specific gravity, trunk diameter, and the environmental variable E, has obvious consequences for Measurement, Reporting, and Verification (MRV) applications and carbon accounting activities. Indeed, many countries are currently implementing forest inventories where total tree height is not directly measured, because of logistical and financial consideration. Our Model 7 shows that information on wood specific gravity (as inferred from the taxonomic determination of the tree), trunk diameter, and the variable E (as inferred from the geolocation of the plot) is sufficient to provide a robust AGB estimate of this tree. We assessed the performance of Model 7 compared with our best Model 4 and found that it gave reliable results at most sites. We also quantified the performance in terms of the model's RSE, and this performance can be used in future error propagation studies (Eqn (8)). We conclude that the present strategy for AGB estimation is more robust than Model II.3 of Chave *et al.* (2005), and that it outperforms the strategy proposed by Feldpausch *et al.* (2012), as evidenced in Figure S6.

However, it cannot be overstated that this method provides estimates – not direct measurements – and model error should always be carefully examined and propagated through to the quantity of interest. Although Model 7 is an improvement over previously published generic biomass allometries, it is likely to provide unreliable results in some situations. For instance, some low-stature vegetation types in the tropics are driven not by the climate but by soil type (heath forests). Because these vegetation types may occur in limited areas, the diameter–height allometry may vary significantly at the landscape scale. Thus, we advise, whenever possible, developing a local diameter–height allometry, by measuring total height on a subsample of the trees stratified by trunk diameter and by forest type. In such projects, the accuracy of total tree height measurement is critical. We strongly advise using direct measurements of tree height. The most reliable method for large trees is to climb the tree and measure the distance from the top branch to the ground using a laser rangefinder with decimetric accuracy (such as the Laserace 1000, Trimble Navigation Limited, Sunnyvale, CA, USA, or the TruePulse Series, Laser Technology, Centennial, CO, USA). These instruments could also be used from the ground as classical hypsometers, or directly from the base of the tree, by aiming at the highest branch and taking repeated measurements. Whenever this approach is implemented, it should be preceded by a training session when operators can crosscheck their measurements.

Because the proposed models are applicable to already acquired datasets, we foresee that they will be broadly applicable to tree-dominated vegetation types in the tropics. For the UN Framework Convention on Climate Change to implement a Reduced Emissions from Deforestation and Degradation (REDD+) scheme, more accurate and precise country-based carbon inventories are needed (Pelletier *et al*., 2011). This method should also be complemented with belowground biomass estimation methods (Mokany *et al*., 2006; Niiyama, *et al*., 2010). Our allometric equations typically achieve 90% accuracy in AGB stock estimation at a 0.25 ha scale in a moist tropical forest, and the bias is on the order of 10%, on average. The recently published global cover maps for AGB stocks (Saatchi *et al*., 2011), and for changes in AGB stocks (Harris *et al*., 2012) could be then updated based on this new methodology. Specifically, we predict that the Harris *et al*. (2012) map may be modified in drier vegetation types, which harbor some of the highest carbon emission rates, such as the Brazilian arc of deforestation or the Indochinese peninsula. We hope that the present study will help advance the implementation of sound practices to devise a global mechanism to fund climate change mitigation activities.

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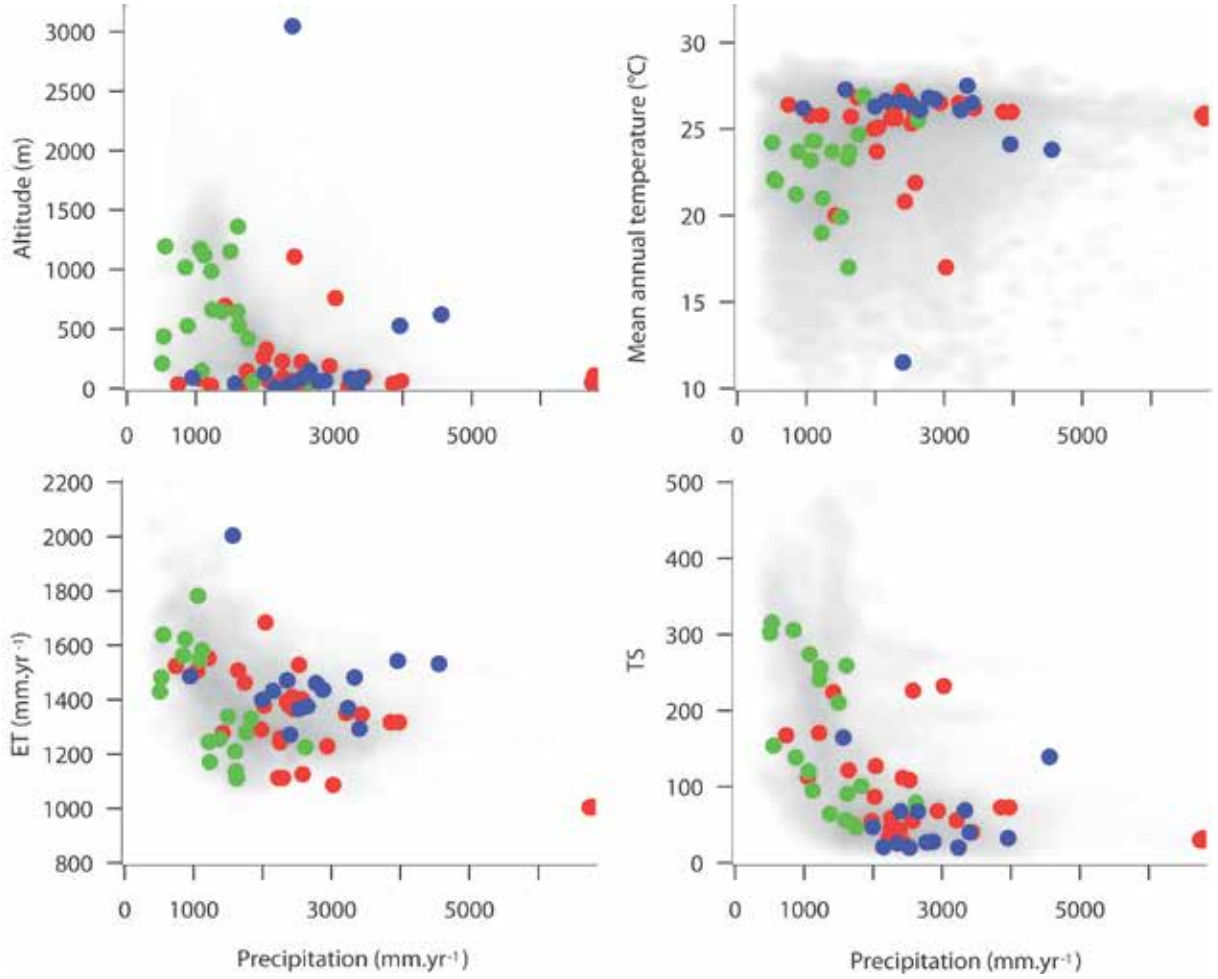
Supporting Information

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

Data S1. Figures.
Data S2. Description of the study sites.
Data S3. Details about the database construction.
Data S4. Illustration of the goodness of fit at each of the 58 study sites. The full dataset is plotted in the background (black). The foreground points and regression line represent the best-fit regression for local datasets.
Figure S1. Distribution of the 58 study sites in environmental space of altitude, mean annual temperature, mean annual evapotranspiration (ET, mm yr^{-1}), mean annual rainfall, and temperature seasonality (TS). The gray shades in the background represent the range of observed variation in currently forested areas in the tropical belt. Red dots indicate Latin American sites, green African sites, and blue Southeast Asian and Australian sites.
Figure S2. Among-site relationship of the individual coefficient of variation to bioclimatic variables (TS: temperature seasonality; CWD: climatic water deficit) across study sites, for Model 4. Each point represents the individual coefficient of variation CV(*j*) of a study site *j*, as inferred from Model 4. Point color and size are as in Fig. 3.
Figure S3. Among-site relationship of the site-level bias with bioclimatic variables (TS: temperature seasonality; CWD: climatic water deficit) for Model 4. Each point represents the Bias(*j*) for site *j* as inferred from Model 4. Point color and size are as in Fig. 3.
Figure S4. Among-site relationship of the form factor (ratio AGB $/\rho D^2 H$ with bioclimatic variables (TS: temperature seasonality; CWD: climatic water deficit). Each point represents the mean form factor of a study site (equivalent to the fitted parameter of Model 5). Correlation tests were performed on each dataset. In panel (a) $P = 0.09$ (Bartlett test); in panels (b) to (d), $P < 10^{-3}$, $P = 0.08$, $P < 10^{-3}$ (Spearman correlation). Point color and size are as in Fig. 3.
Figure S5. Forward selection for bioclimatic variables in Eqn (3). The first selected variable is TS (temperature seasonality), and including it results in a decline of the residual standard error (σ', noted RSE in the ordinate axis) from 0.430 to 0.292. The second selected variable is CWD (climatic water deficit), and including it results in a decline of the RSE from 0.292 to 0.272. The third selected variable is PS (precipitation seasonality), and including it results in a further decline of the RSE from 0.272 to 0.243. Additional environmental variables induced comparatively very little further decline in RSE (a gain of 0.022).
Figure S6. Comparison between the pantropical allometric AGB Model 7 and a model in which Feldpausch *et al.* (2012) regional diameter–height equations were used. (a) Individual coefficient of variation at each site for both types of allometries. (b) Bias at each site for both types of allometries. Point color and size are as in Fig. 3. The outlying sites are labeled.
Table S1. Study sites and their characteristics.
Table S2. Description of the variables included in the dataset ($n = 4004$).

SUPPLEMENTARY MATERIAL

SM1. Figures



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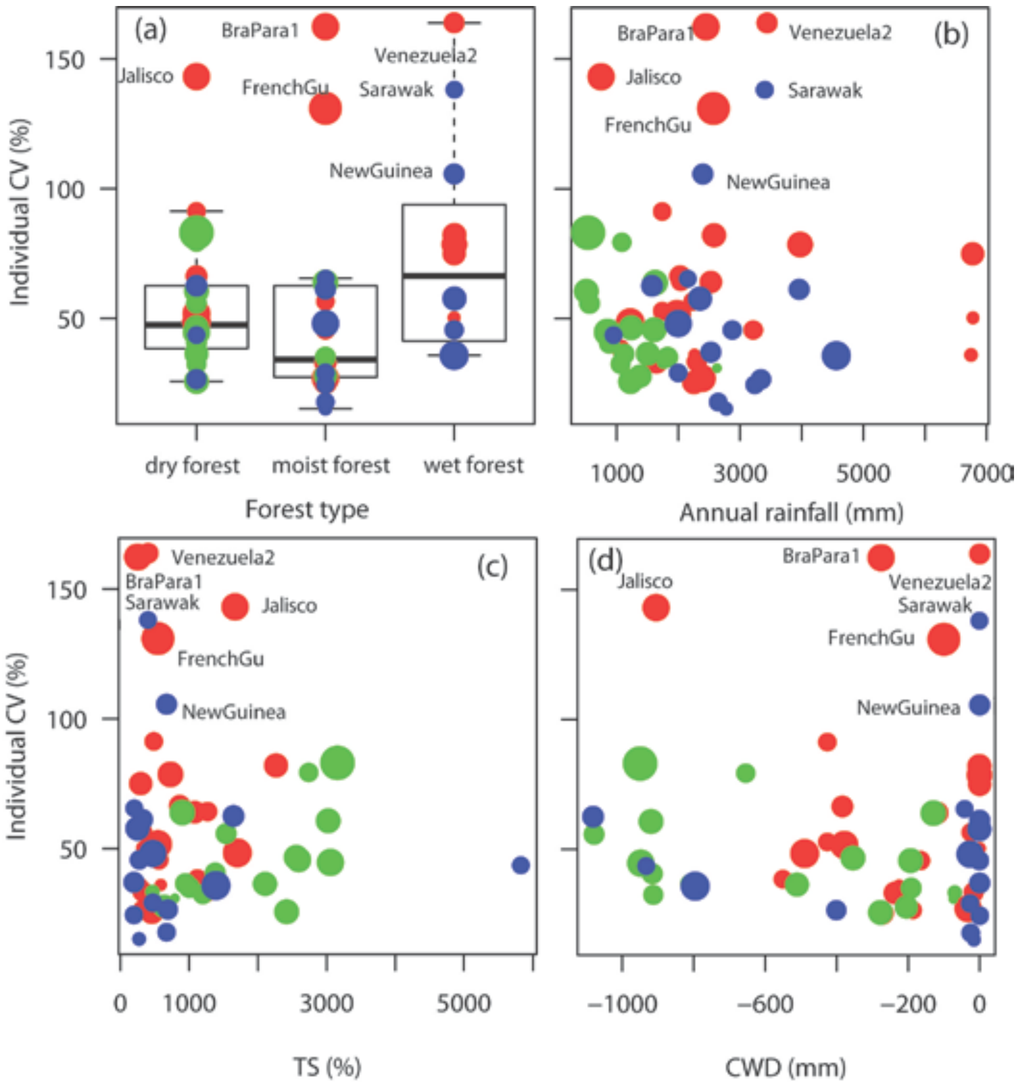

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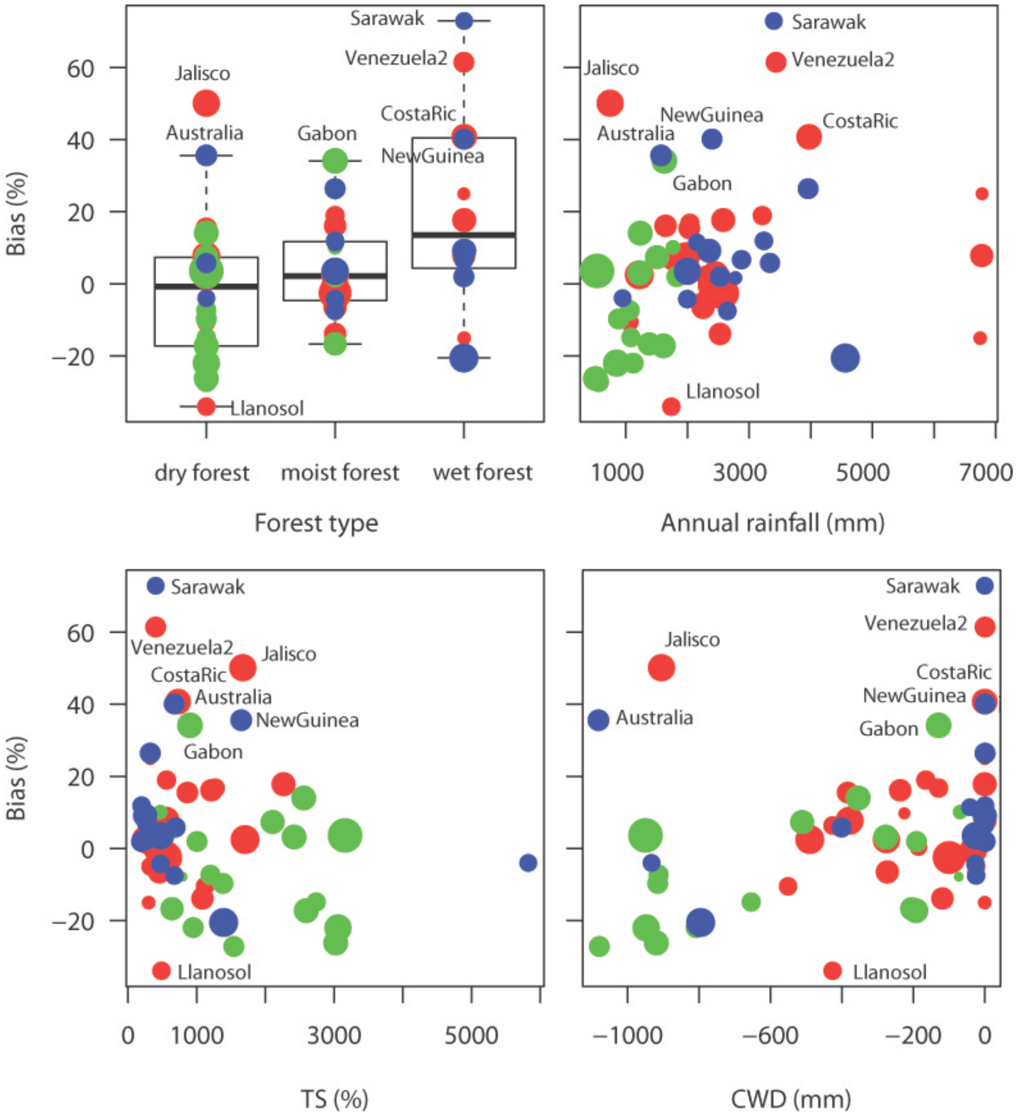
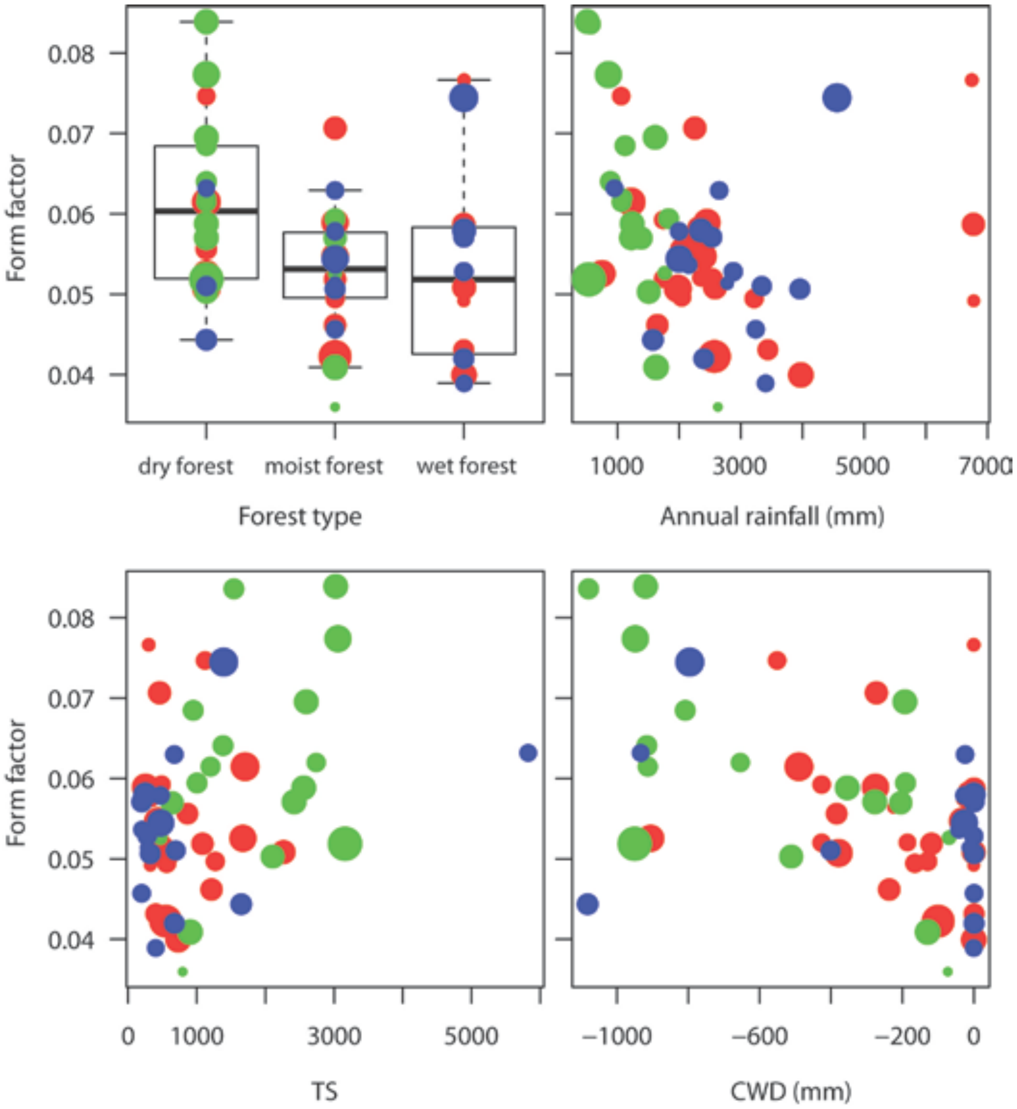


Figure S3. Among-site relationship of the site-level bias with bioclimatic variables (TS: temperature seasonality; CWD: climatic water deficit) for Model 4. Each point represents the Bias(*j*) for site *j* as inferred from Model 4. Point color and size are as in Fig. 3.



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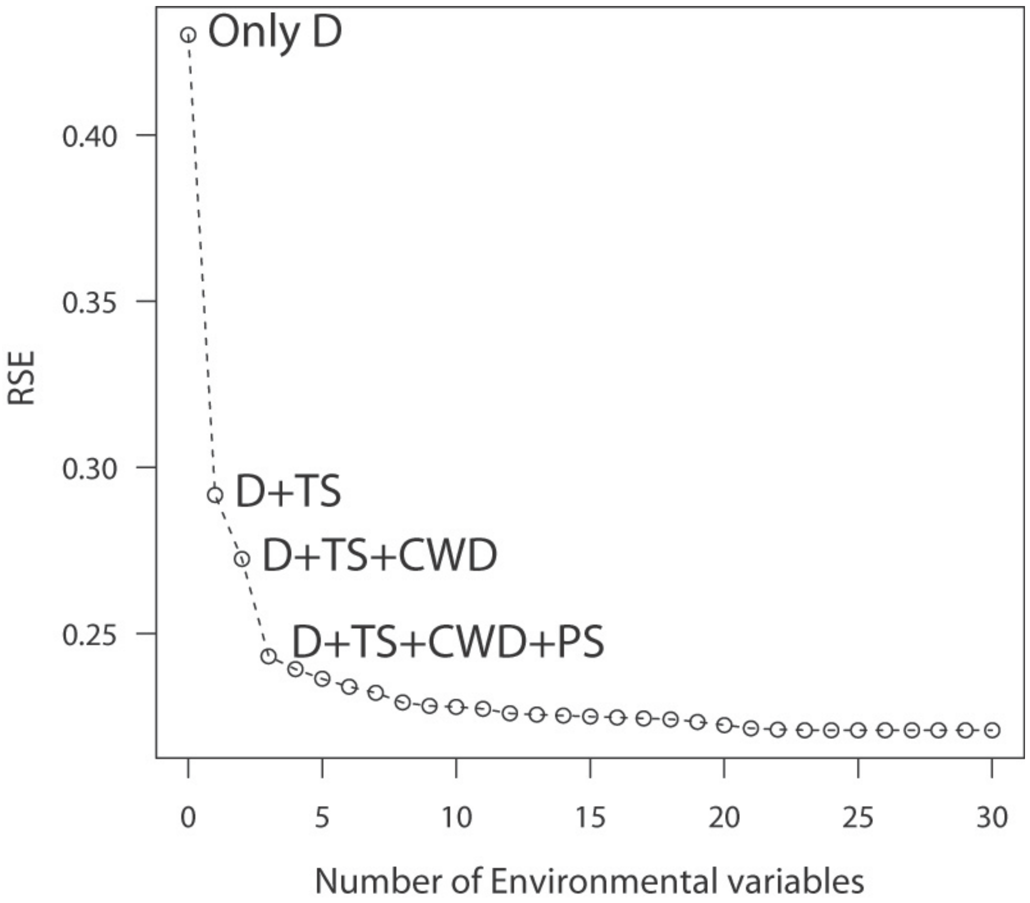

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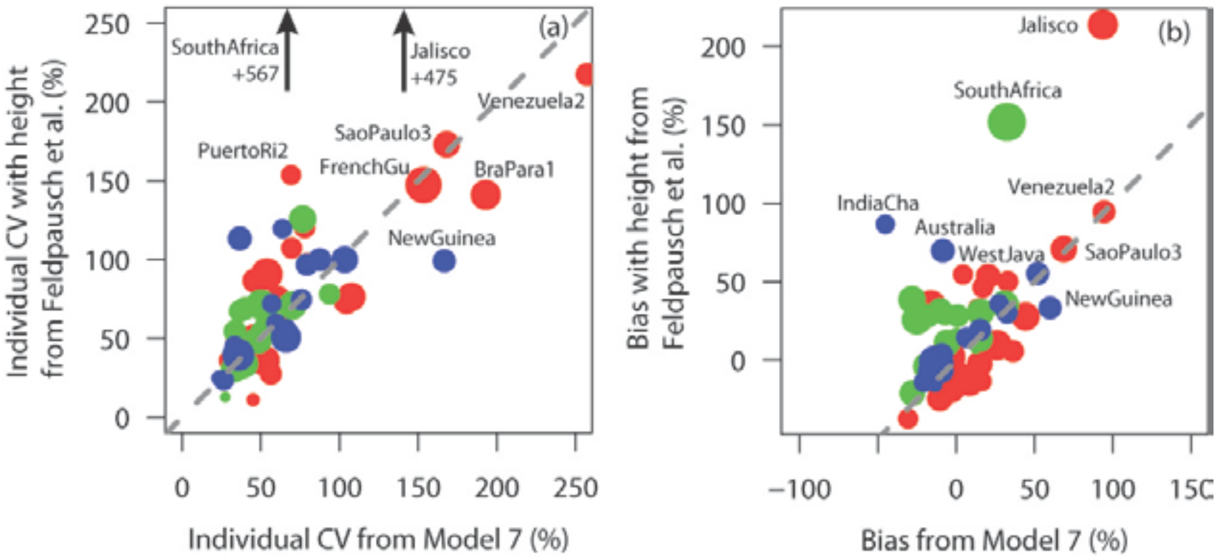

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SM2. Description of the study sites.

Table S1. Study sites and their characteristics.

Locality	No of trees	Available in 2005	Lat. (°N)	Long. (°E)	Locality	Forest type	Successional type	Mean annual temperature (°C)	Temp. Seasonality	Mean Annual Precip. (mm/yr)	Precip. Seasonality (%)	Altitude (m asl)	Evapotranspiration (mm/yr)	Dry months	CWD (mm/yr)	Ref
Australia	46	YES	-12.48	131.05	Darwin, Northern Territory, Australia	dry forest	old growth	273	1670	1547	104	39	2004	8	-1075	[1]
BraMan2	123	YES	-2.5	-60.17	Manaus, Amazonas, Brazil	moist forest	secondary	272	431	2358	33	64	1378	3	-39	[2]
BraPara1	127	YES	-2.5	-48.13	Tomé Açu, Para, Brazil	moist forest	old growth	268	259	2439	70	37	1366	6	-286	[3]
BraPara3	21	YES	-1.37	-48.28	Belem, Para, Brazil	moist forest	secondary	267	312	2377	54	22	1393	4	-172	[4]
BraRond	8	YES	-8.75	-63.38	Samuel Reservoir, Rondonia, Brazil	moist forest	old growth	260	589	2258	63	91	1259	4	-227	[5]
Cambodia	34	YES	10.93	103.4	Thma Sa (formerly Cheko), Cambodia	dry forest	old growth	275	690	3339	86	14	1481	6	-402	[6]
Cameroon	5	NO	2.67	10	Campo Ma'an, Cameroon	moist forest	old growth	255	781	2611	59	53	1226	3	-71	[7]

Cameroon 3	59	NO	3.94	14.81	Mindourou 2, South-west Cameroon	moist forest	old growth	236	625	1380	47	647	1256	6	-202	[8]
CentralAfric	12	NO	0.76	24.46	Yangambi, Democratic Republic of Congo	moist forest	old growth	248	480	1759	29	419	1281	2	-70	[9]
Colombia C1	60	NO	4.77	-77.18	Upland forest, departamento del Choco, Colombia	wet forest	old growth	257	287	6753	21	107	1007	0	0	[10]
Colombia G1	36	NO	1.64	-78.84	Swamp forest, departamento de Narino, Colombia	moist forest	old growth	256	330	2333	46	14	1113	2	-7	[10]
Colombia G2	10	NO	4.71	-77.18	Swamp forest, departamento del Choco, Colombia	wet forest	old growth	258	300	6737	21	50	1004	0	0	[10]
Colombia M1	24	NO	1.64	-78.89	Mangrove forest, departamento de Narino, Colombia	moist forest	old growth	256	331	2243	46	13	1113	2	-18	[10]
Colombia M2	9	NO	4.7	-77.26	Mangrove forest, departamento del Choco, Colombia	wet forest	old growth	259	323	6781	22	20	1004	0	0	[10]
CostaRic	97	NO	10.38	-83.98	Horquetas, Sarapiqui Costa Rica	wet forest	old growth	260	760	4042	28	62	1317	0	0	[11]

FrenchGu	360	YES	5.3	-53.5	Piste de Saint Elie, near Sinnamary, French Guiana	moist forest	old growth	259	542	2579	41	90	1402	2	-103	[12]
Gabon	101	NO	0.95	13.17	Makokou, Gabon	moist forest	old growth	231	889	1657	56	528	1110	5	-113	[13]
Ghana	39	NO	5.5	-2.67	Boi Tano Reserve, Ghana	moist forest	old growth	267	992	1842	58	61	1329	4	-188	[14]
IndiaCha	23	YES	25.05	83.21	Chakia, India	dry forest	secondary	262	5828	940	132	89	1487	9	-922	[15]
Jalisco	124	NO	19.5	-105.04	Chamela station, Jalisco state, Mexico	dry forest	old growth	261	1630	818	110	35	1524	10	-889	[16]
Kaliman1	23	YES	-0.4	116.45	Balikpapan, Kalimantan, Indonesia	moist forest	old growth	266	203	2146	29	10	1433	3	-43	[17]
Kaliman2	69	YES	-1.08	116.97	Sebulu, Kalimantan, Indonesia	wet forest	old growth	267	262	2377	20	38	1472	0	0	[18]
Kaliman4	40	NO	1.95	117.08	Berau Regency, Kalimantan, Indonesia	wet forest	old growth	264	204	2498	13	80	1366	0	0	[19]
Kaliman6	25	NO	-0.52	115.37	West Kutai, near Balikpapan, East Kalimantan, Indonesia	moist forest	old growth	261	197	3201	25	85	1369	0	0	[20]

Karnataka	189	NO	13.83	74.95	Kilandur Reserve Forest, Shimoga district, Karnataka State, India	wet forest	old growth	240	1392	4864	150	623	1533	7	-801	[21]
Llanosec	24	YES	7.43	-70.92	Llanos secondary, Venezuela	dry forest	secondary	268	483	1730	67	145	1463	4	-447	[22]
Llanosol	27	YES	7.43	-70.92	Llanos old-growth, Venezuela	dry forest	old growth	268	483	1730	67	145	1463	4	-447	[22]
Madagascar1	76	NO	-14.45	49.05	Bealanana, Analila, Madagascar	dry forest	old growth	190	2106	1497	91	1154	1338	8	-476	[23]
Madagascar2	90	NO	-20.45	47.6	Fandriana, Fiadanana, Madagascar	dry forest	old growth	178	2591	1714	74	1362	1138	6	-170	[23]
Madagascar3	87	NO	-24.96	45.23	Dry forest Manavy, Madagascar	dry forest	old growth	242	3027	505	84	210	1430	12	-921	[23]
Madagascar4	80	NO	-24.48	46.9	Moist forest, Beampingaratra, Madagascar	dry forest	old growth	207	2502	1239	65	986	1244	8	-279	[23]
Madagascar5	90	NO	-22.44	46.99	Ivohibe, Sakaroa, Madagascar	dry forest	old growth	210	2555	1258	85	662	1171	8	-353	[23]
Malaysia	139	YES	2.98	102.32	Pasoh, Malaysia	moist forest	old growth	263	478	1987	30	129	1399	3	-26	[24]
Malaysia2	24	NO	2.98	102.32	Pasoh, Malaysia	moist forest	old growth	263	478	1987	30	129	1399	3	-26	[25]

MFrenchG	29	YES	4.87	-52.32	Marais Leblond, Kourou, French Guiana	moist forest	old growth	265	558	3305	52	14	1351	3	-150	[26]
MGuadel	55	YES	16.27	-61.57	Grand Cul de Sac Marin, Guadeloupe	moist forest	old growth	257	1225	1613	41	13	1509	4	-321	[27]
Moluccas	25	NO	-3.05	129.43	Manusela National Park, Moluccas, Indonesia	moist forest	old growth	250	732	2701	29	147	1375	2	-1	[28]
Mozambique	28	NO	-18.97	34.17	Nhambita, Gorongosa district, Mozambique	dry forest	old growth	246	2701	1048	89	148	1548	8	-676	[29]
NewGuinea	42	YES	-6	145.18	Marafunga, New Guiena	wet forest	old growth	134	607	2216	38	3047	1271	0	-15	[30]
Peru	51	NO	-12.92	-69.27	South East Peru (Tambopata)	moist forest	old growth	253	1074	2546	52	222	1527	4	-115	[31]
PuertoRi	30	YES	18.32	-65.82	El Verde, Puerto Rico	moist forest	old growth	222	1258	2771	26	70	1685	3	-30	[32]
PuertoRi2	25	NO	17.98	-66.67	Ponce, Puerto Rico	dry forest	old growth	260	1130	997	56	82	1509	9	-486	[33]
SaoPaulo 3	75	NO	-23.99	-46.39	Restinga (sandy soil) forest, Sao Paulo, Brazil	wet forest	old growth	219	2264	2578	39	15	1125	0	0	[35]
Sarawak	21	NO	1.05	110.92	Sabal Forest reserve, Sarawak, Malaysia	wet forest	old growth	257	353	3344	23	96	1293	0	0	[36]
SouthAfrica	469	NO	-23.83	31.1	Pompey, Kruger Park, South Africa	dry forest	old growth	221	3169	529	78	436	1481	12	-948	[37]

SouthBrazil1	151	NO	-9.86	-58.41	Cotriguacu, Mato Grosso, Brazil	dry forest	old growth	249	547	1979	74	263	1290	5	-376	[38]
SouthBrazil2	49	NO	-12.85	-58.93	Juruena, Mato Grosso, Brazil	dry forest	old growth	237	868	2026	73	328	1378	5	-382	[38]
SouthBrazil3	64	NO	-7.14	-55.38	Novo Progresso, Para, Brazil	moist forest	old growth	257	453	2268	66	228	1244	4	-273	[38]
Sumatra	29	YES	-1.48	102.23	Sepunggur, Jambi, Sumatra, Indonesia	wet forest	secondary	267	275	2876	33	64	1436	0	0	[39]
Sumatra2	11	NO	-3.32	103.9	Bendar Udara Pendopo, Sumatra, Indonesia	moist forest	old growth	268	276	2782	38	60	1460	2	-16	[20]
Tanzania1	38	NO	-6.33	35.78	Manyara, Tanzania	dry forest	old growth	221	1538	561	112	1195	1639	12	-1094	[40]
Tanzania2	42	NO	-9.78	37.92	Lindi, Tanzania	dry forest	old growth	238	1386	872	104	526	1624	9	-920	[40]
Tanzania3	38	NO	-6.35	30.95	Katavi, Tanzania	dry forest	old growth	246	949	1117	91	1118	1582	6	-824	[40]
Tanzania4	34	NO	-5.3	32.97	Tabora, Tanzania	dry forest	old growth	232	1201	1062	91	1174	1782	7	-917	[40]
Venezuela2	40	NO	1.92	-67.03	San Carlos de Rio Negro, Venezuela	wet forest	old growth	262	415	3424	24	94	1344	0	0	[41]
WestJava	41	NO	-6.575	106.51	Bogor, West Java, Indonesia	moist forest	old growth	249	324	3966	20	526	1542	0	0	[20]
Yucatan	175	YES	20	-88	La Pantera, Yucatan, Mexico	dry forest	old growth	258	1678	1222	54	24	1554	8	-482	[42]
Zambia	141	NO	-15.25	29.83	Central Zambia	dry forest	old growth	221	3083	823	118	1017	1563	9	-968	[43]

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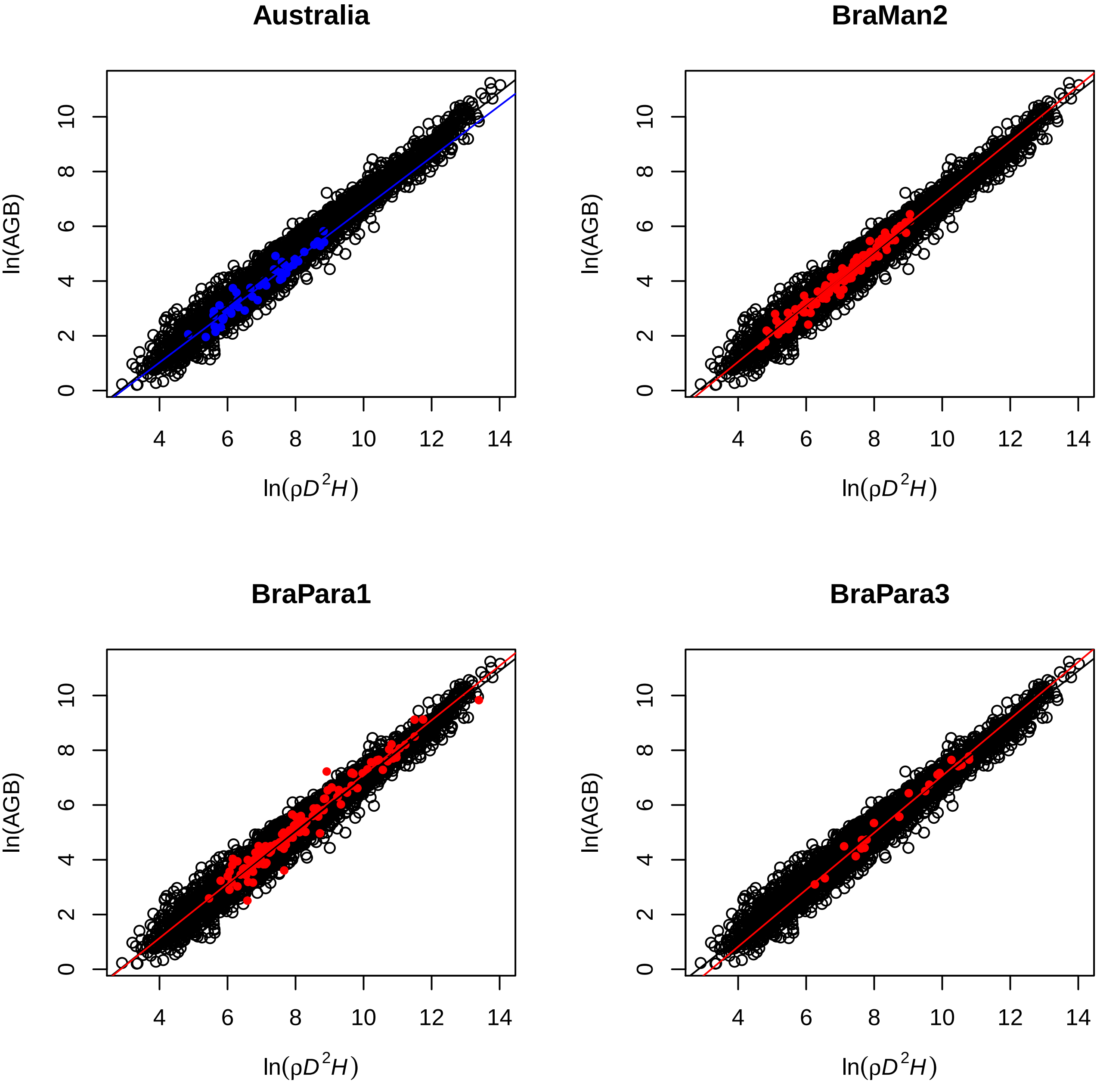
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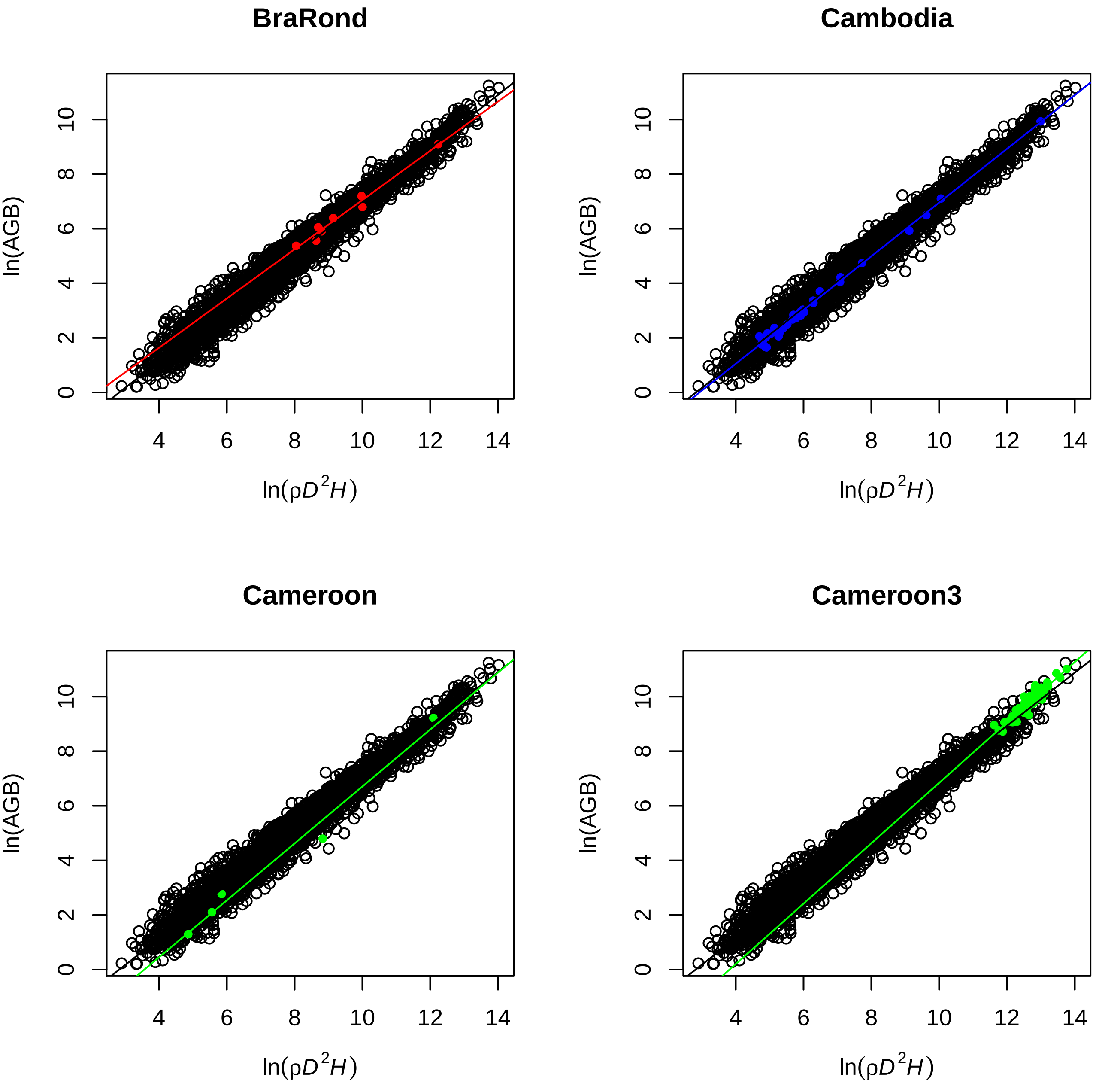
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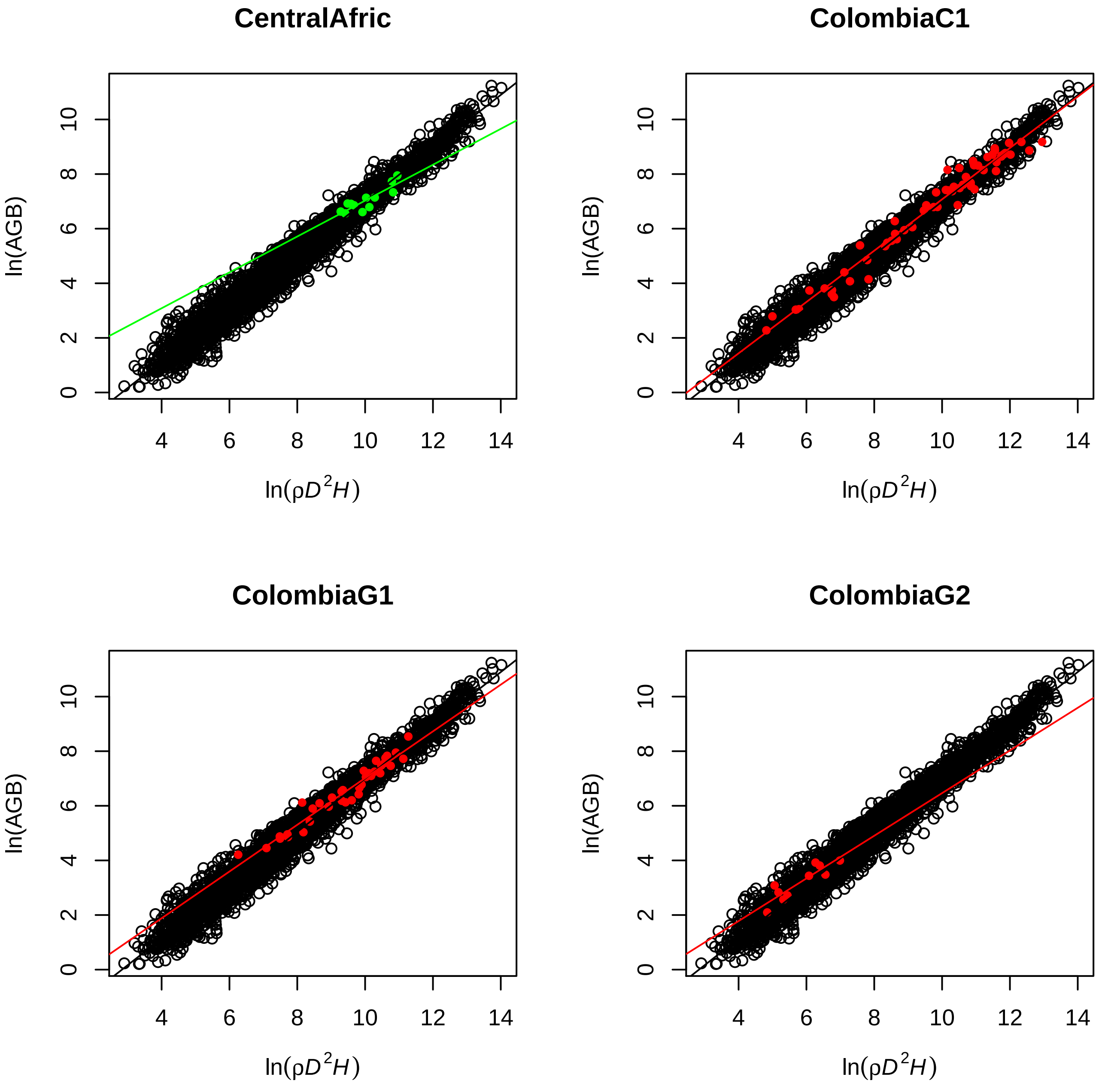

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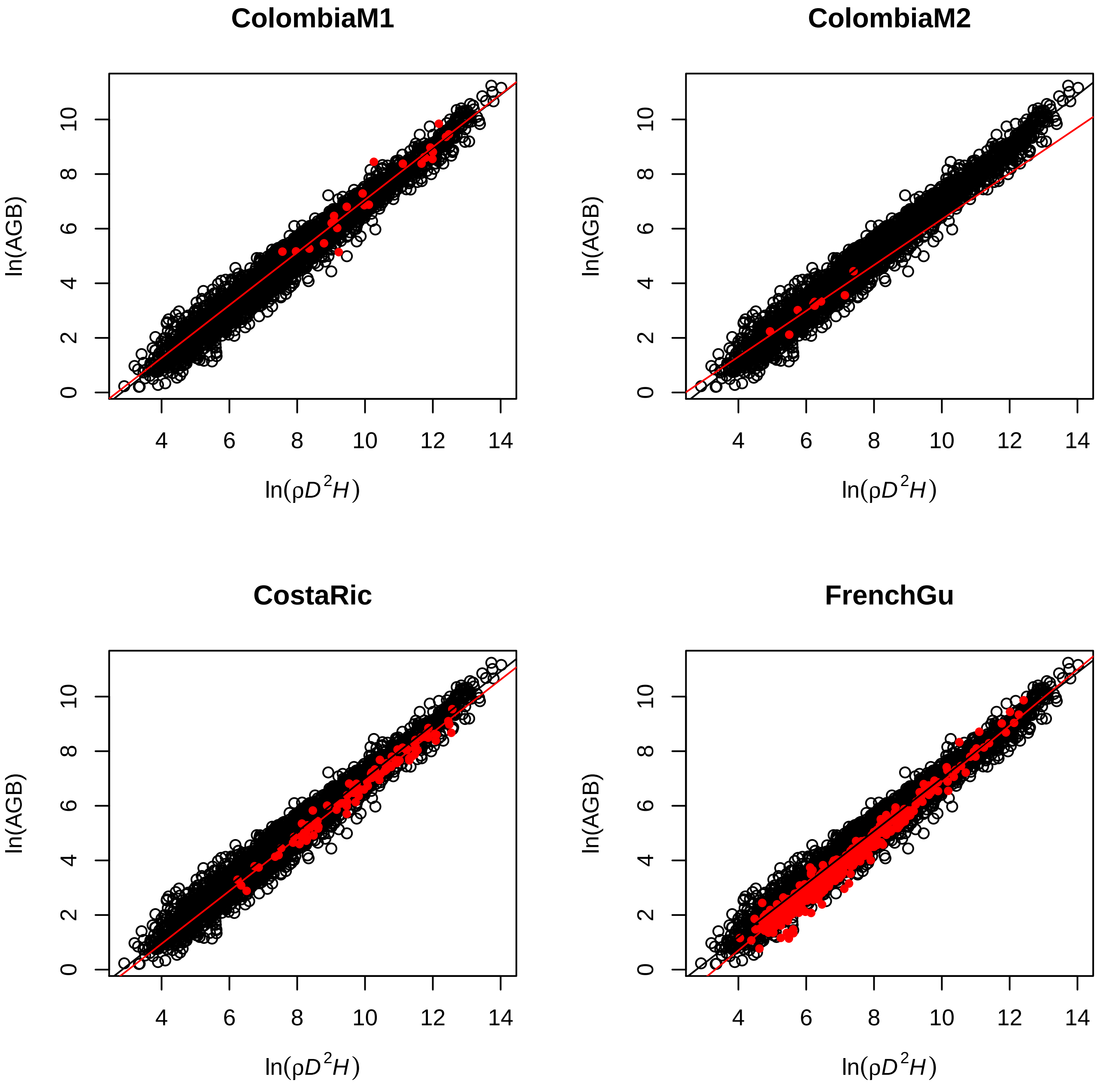
ColombiaG1

ColombiaG2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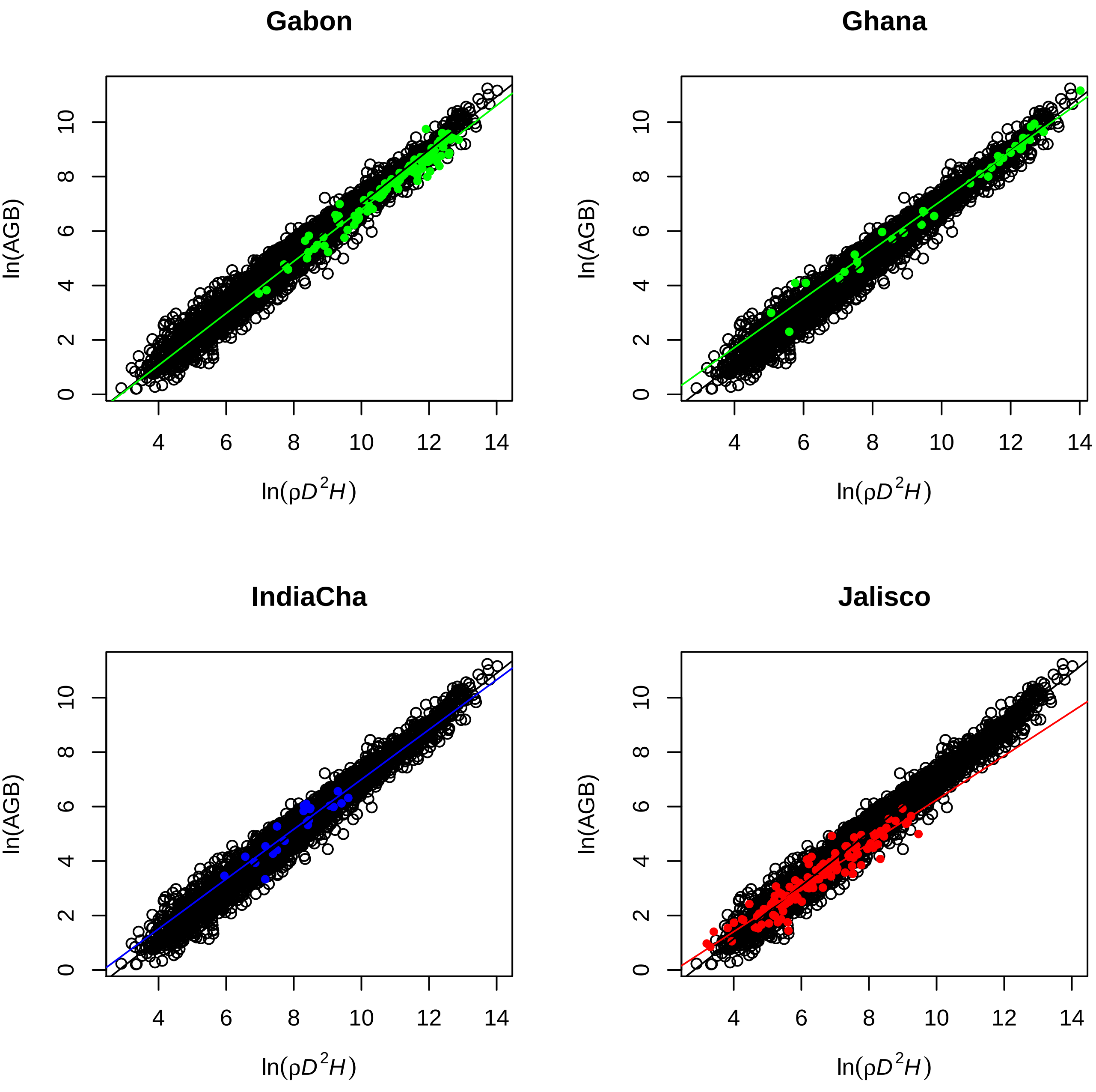
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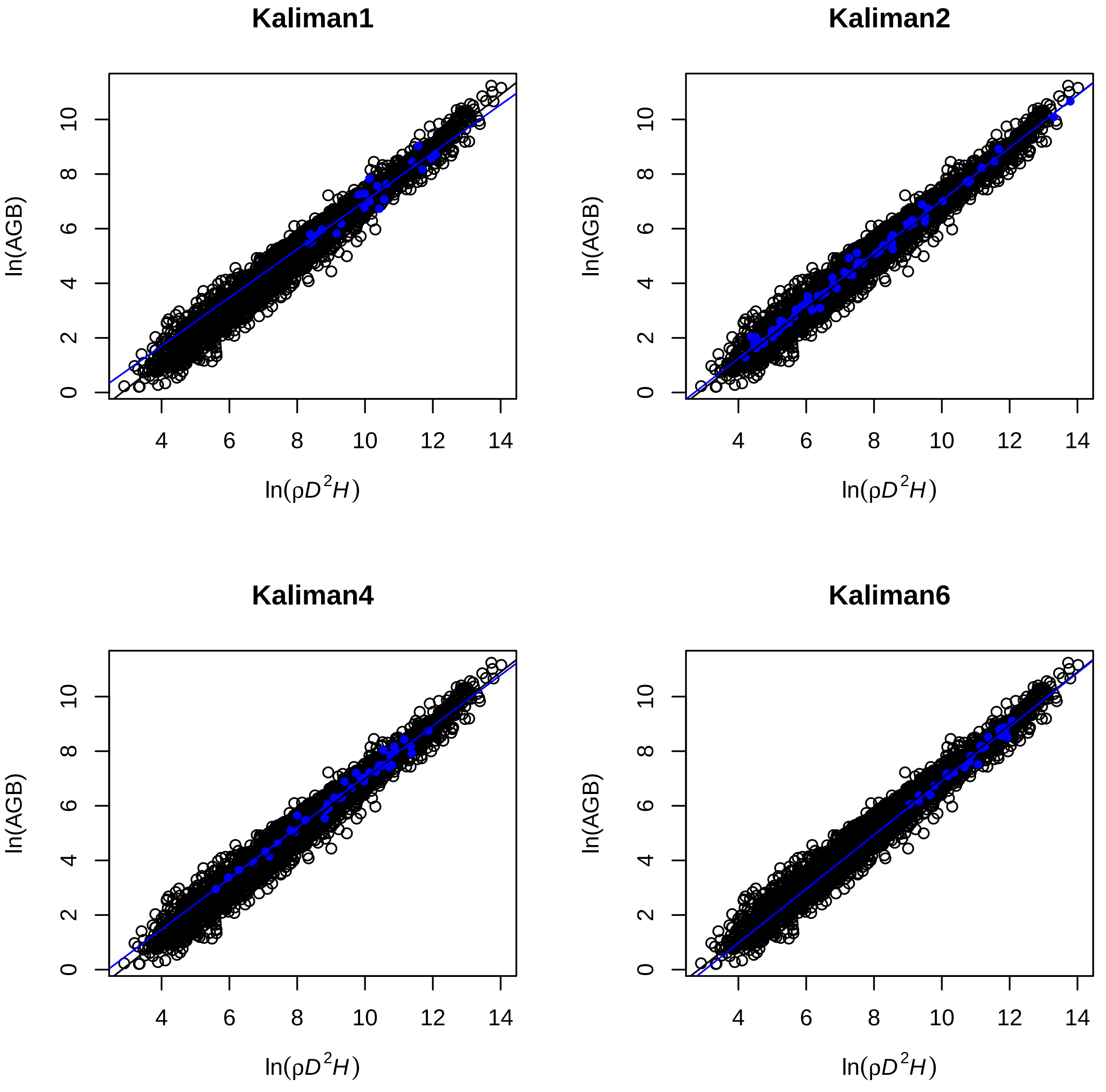
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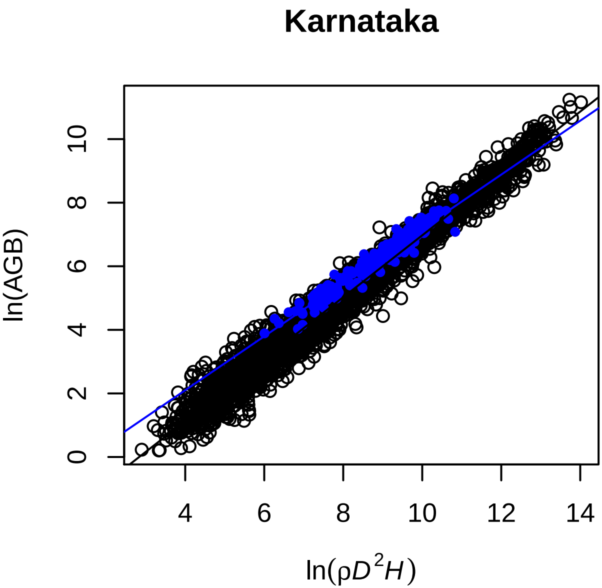
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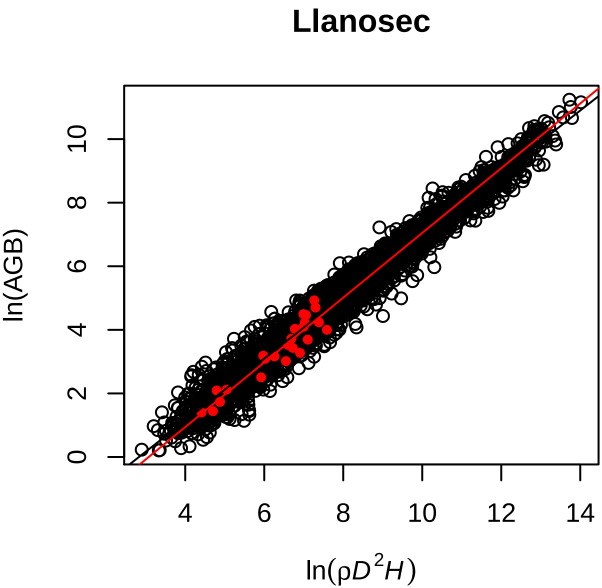
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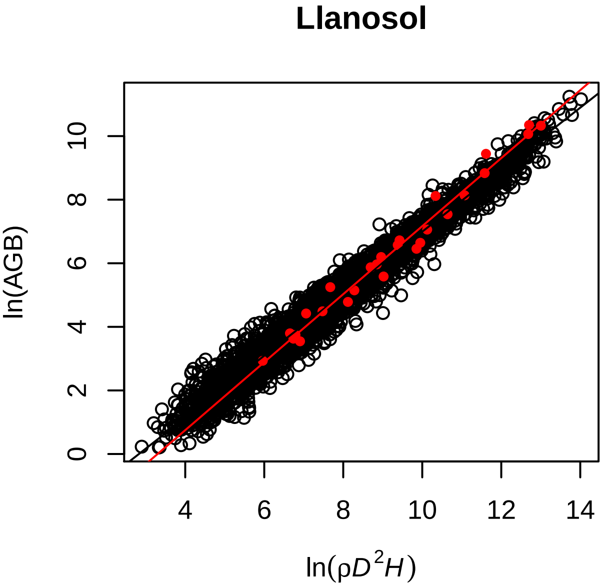
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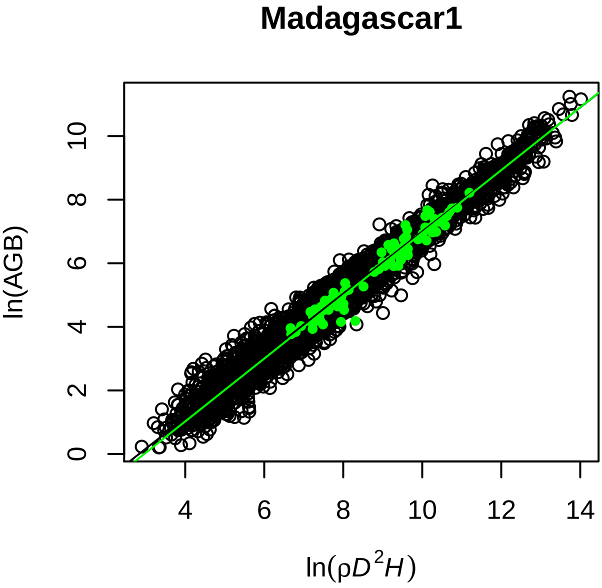
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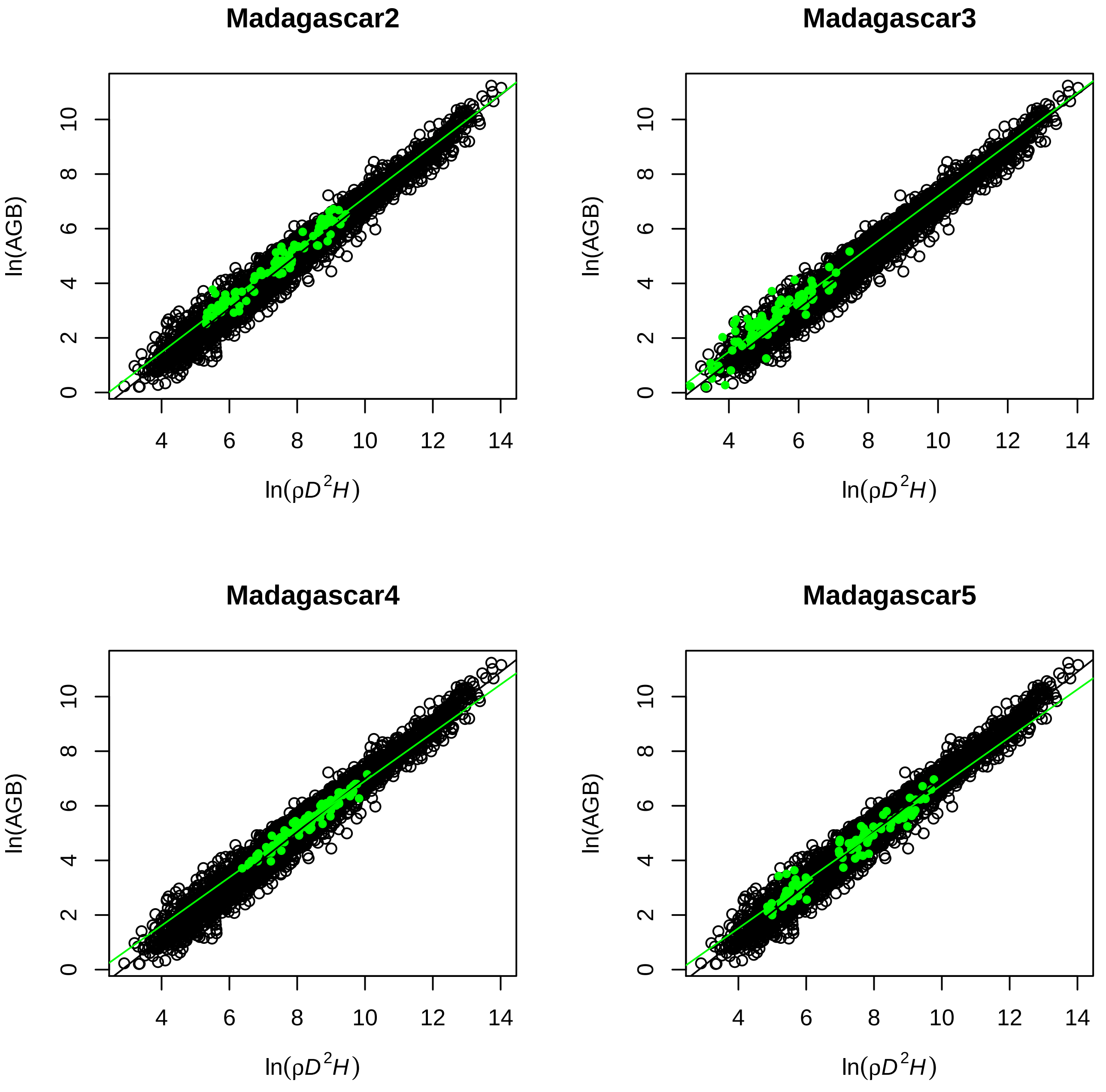
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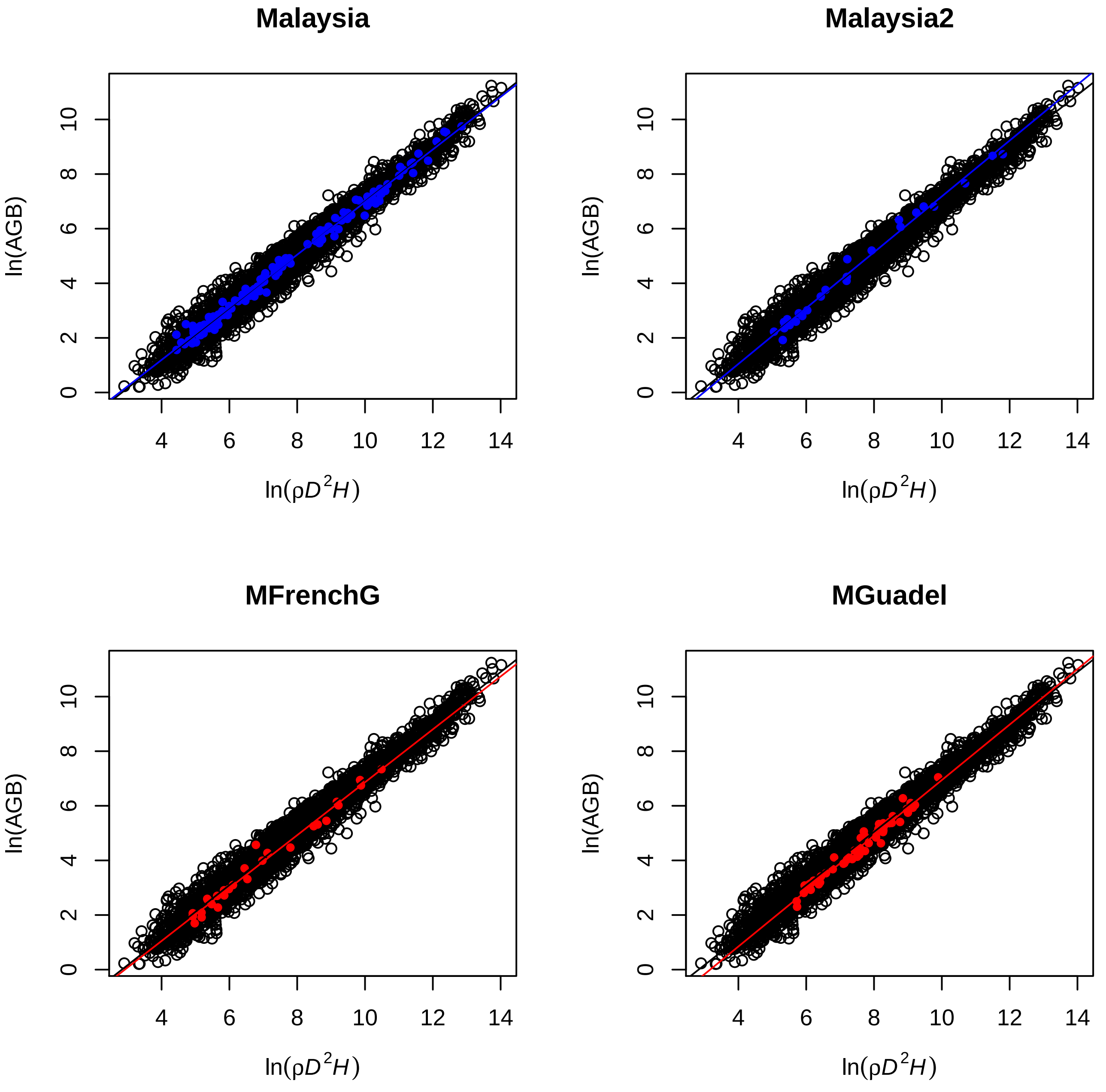
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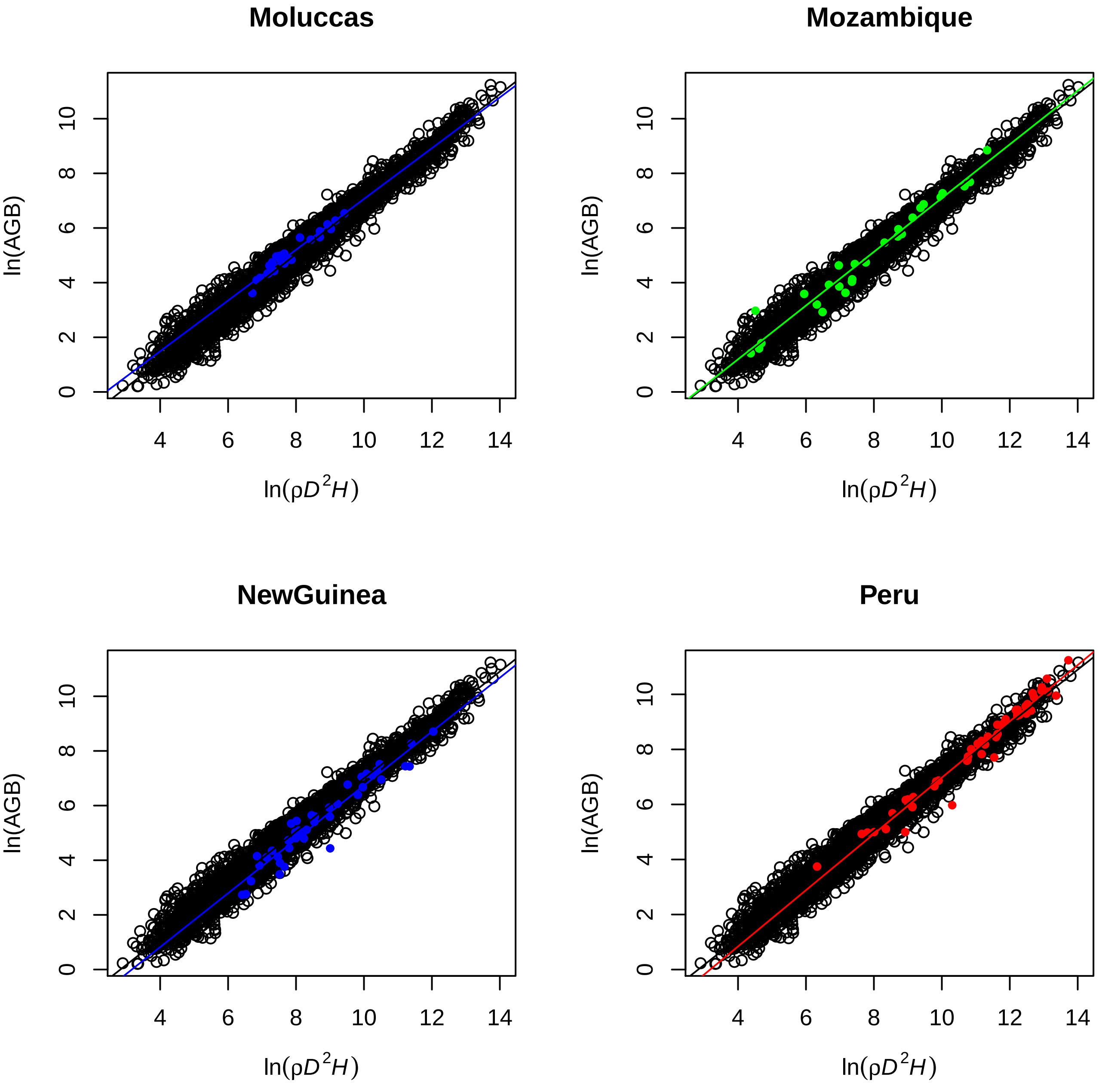
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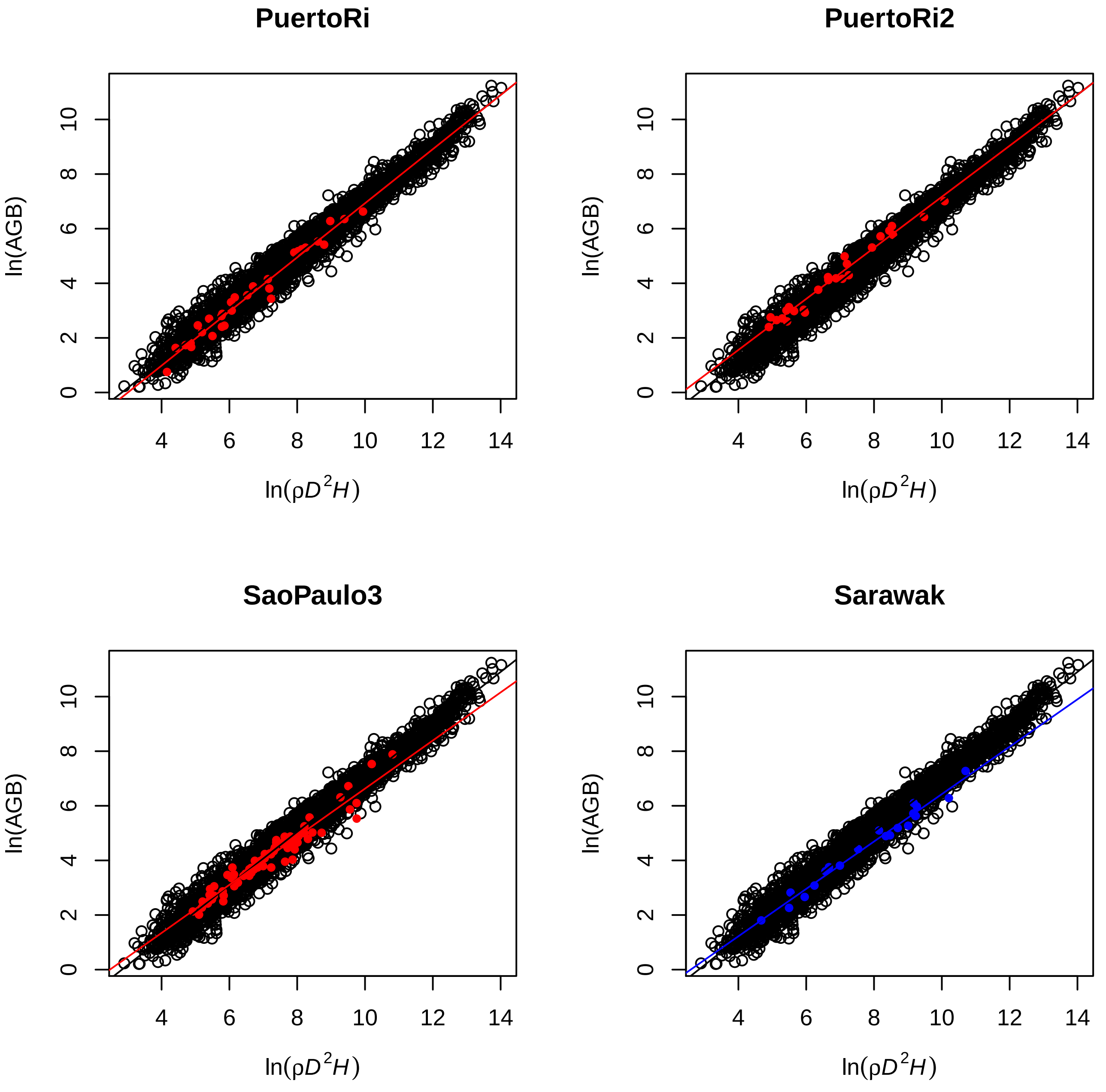
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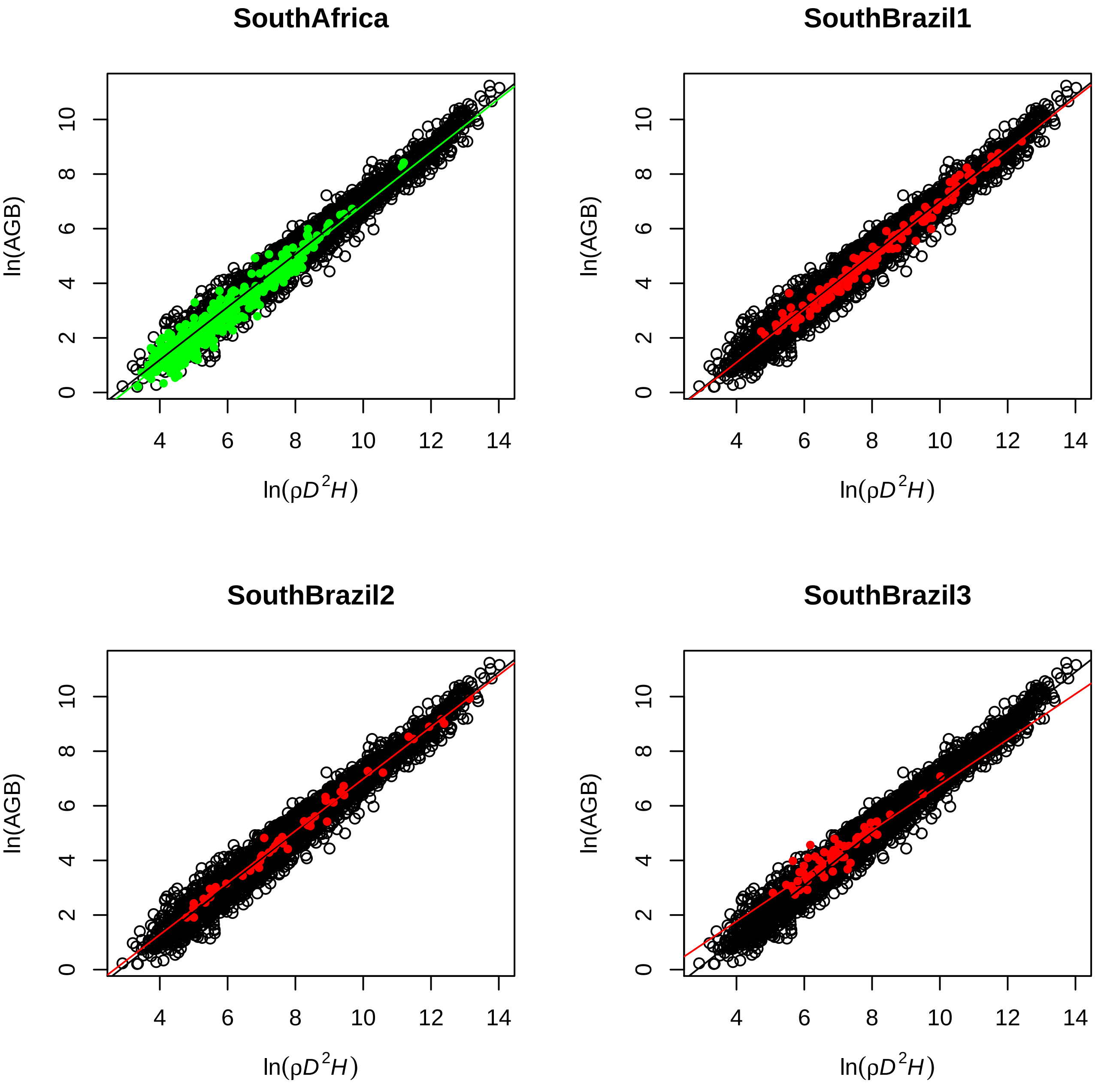
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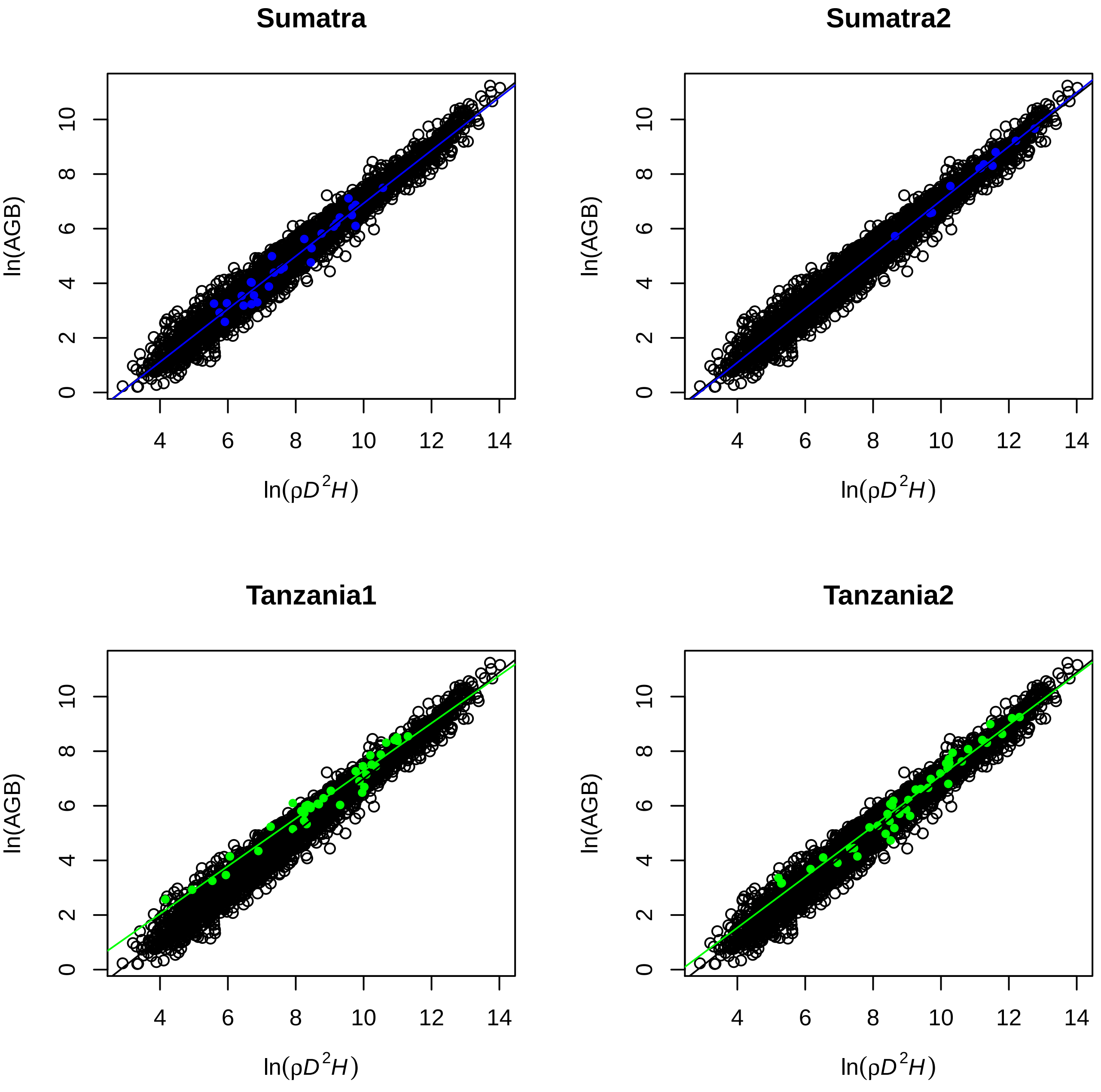

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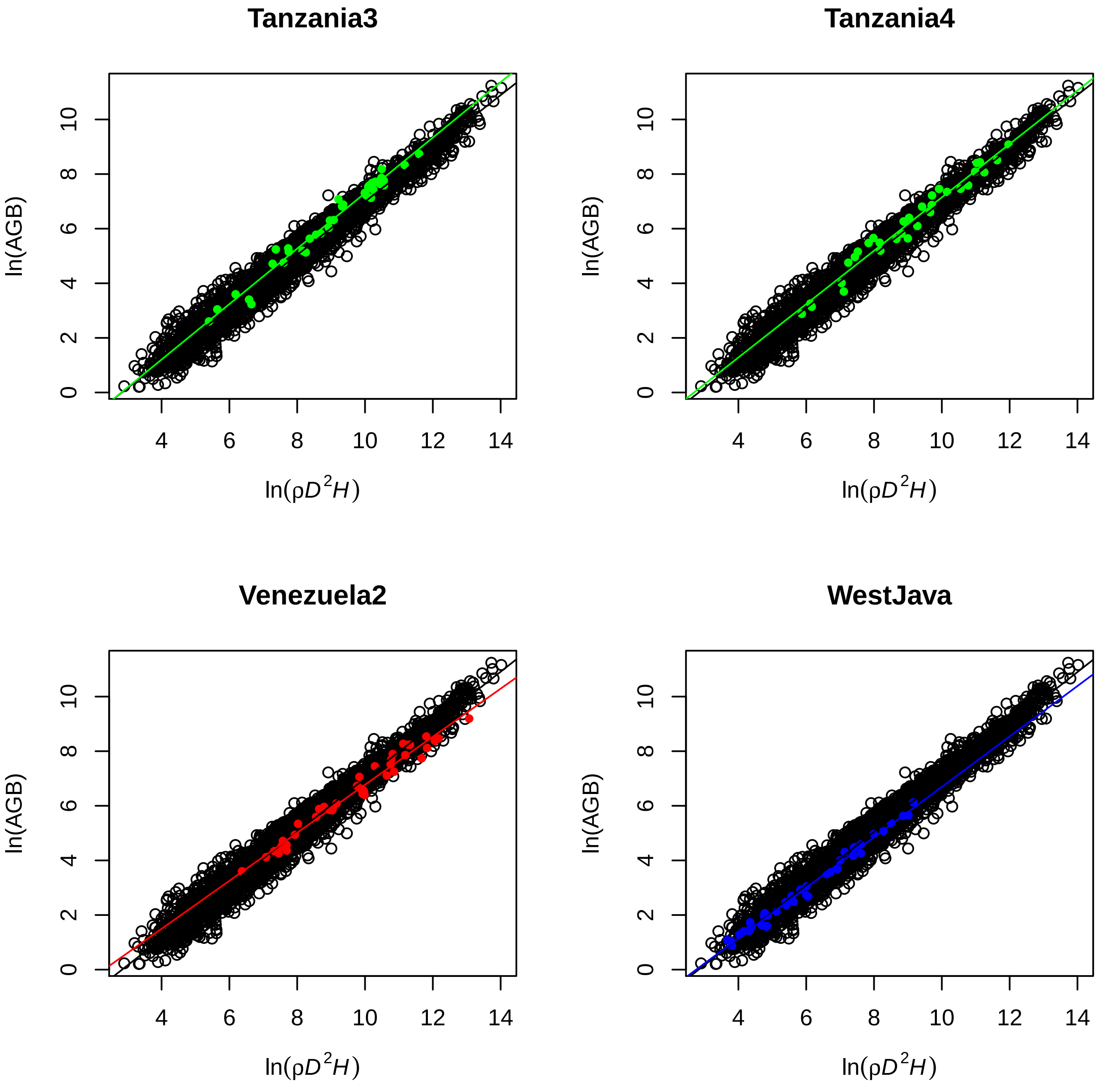
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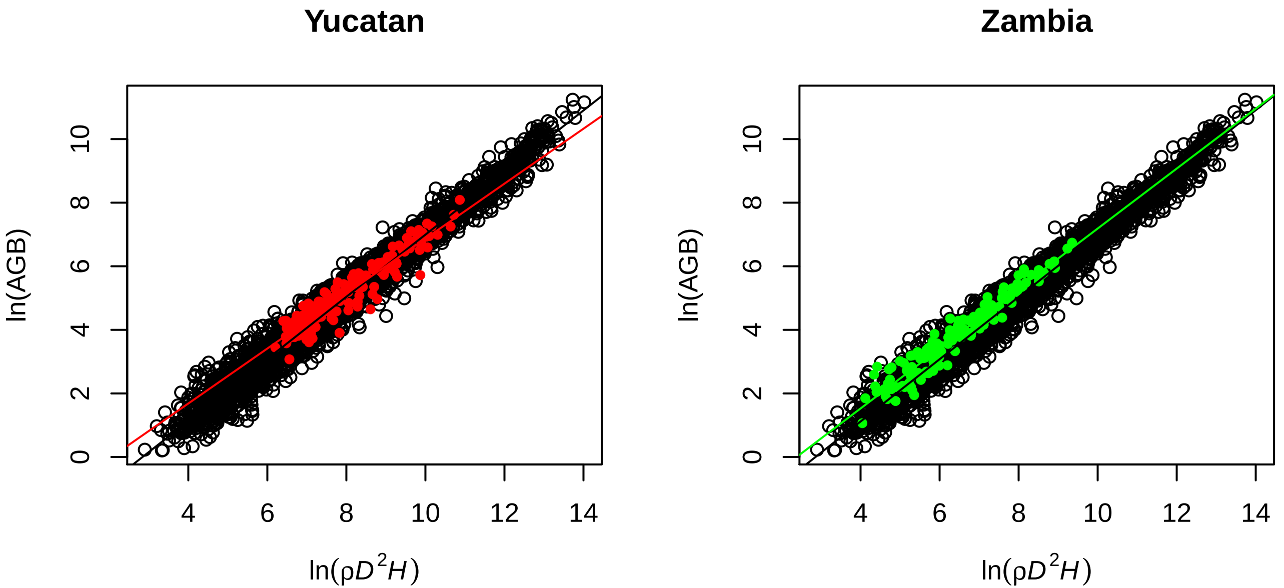
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