

A simulation method to infer tree allometry and forest structure from airborne laser scanning and forest inventories

Fabian Jörg Fischer, Fabian Jörg Fischer, Nicolas Labrière, Grégoire Vincent, Bruno Hérault, Alfonso Alonso, Hervé Memiaghe, Pulchérie Bissiengou, David Kenfack, Sassan Saatchi, et al.

▶ To cite this version:

Fabian Jörg Fischer, Fabian Jörg Fischer, Nicolas Labrière, Grégoire Vincent, Bruno Hérault, et al.. A simulation method to infer tree allometry and forest structure from airborne laser scanning and forest inventories. Remote Sensing of Environment, 2020, 251, pp.112056. 10.1016/j.rse.2020.112056 . hal-03005989

HAL Id: hal-03005989 https://hal.science/hal-03005989

Submitted on 5 Dec 2020 $\,$

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1	A simulation method to infer tree allometry and
2	forest structure from airborne laser scanning
3	and forest inventories
4	Fabian Jörg Fischer ^{a, *} , Nicolas Labrière ^a , Grégoire Vincent ^b , Bruno Hérault ^{c,d} ,
5	Alfonso Alonso ^e , Hervé Memiaghe ^f , Pulchérie Bissiengou ^g , David Kenfack ^h , Sassan
6	Saatchi ⁱ , and Jérôme Chave ^a
7	^a Laboratoire Évolution et Diversité Biologique, UMR 5174 (CNRS/IRD/UPS), 118
8	Route de Narbonne, 31062 Toulouse Cedex 9, France
9	^b AMAP, Univ Montpellier, IRD, CIRAD, CNRS, INRAE, Montpellier, France
10	^c Cirad, Univ Montpellier, UR Forests & Societies, F-34000 Montpellier, France.
11	^d INPHB, Institut National Polytechnique Félix Houphouët-Boigny, Yamoussoukro,
12	Ivory Coast
13	^e Center for Conservation and Sustainability, Smithsonian Conservation Biology
14	Institute, 1100 Jefferson Drive SW, Suite 3123, Washington DC 20560-0705, USA
15	^f Institut de Recherche en Écologie Tropicale (IRET), Centre National de la Recherche
16	Scientifique et Technologique (CENAREST), B.P. 13354, Libreville, Gabon
17	^g Institut de Pharmacopée et de Médecine Traditionnelles (IPHAMETRA)/Herbier
18	National du Gabon, Centre National de la Recherche Scientifique et Technologique
19	(CENAREST), B.P. 1165, Libreville, Gabon
20	$^{\rm h}$ Center for Tropical Forest Science -Forest Global Earth Observatory, Smithsonian
21	Tropical Research Institute, West Loading Dock, 10th and Constitution Ave NW,
22	Washington DC 20560, USA

- ⁱ Jet Propulsion Laboratory, California Institute of Technology, 4800 Oak Grove Drive,
- 24 Pasadena, CA 91109, USA
- 25
- 26 * Correspondence: fabian.j.d.fischer@gmx.de
- 27 **Keywords:** vegetation structure; tropical forest; individual-based modeling; airborne
- 28 lidar; approximate bayesian computation; allometry; biomass; canopy space filling

30 Abstract

Tropical forests are characterized by large carbon stocks and high biodiversity, but they are increasingly threatened by human activities. Since structure strongly influences the functioning and resilience of forest communities and ecosystems, it is important to quantify it at fine spatial scales.

35 Here, we propose a new simulation-based approach, the "Canopy Constructor", with 36 which we quantified forest structure and biomass at two tropical forest sites, one in 37 French Guiana, the other in Gabon. In a first step, the Canopy Constructor combines field 38 inventories and airborne lidar scans to create virtual 3D representations of forest 39 canopies that best fit the data. From those, it infers the forests' structure, including 40 crown packing densities and allometric scaling relationships between tree dimensions. 41 In a second step, the results of the first step are extrapolated to create virtual tree 42 inventories over the whole lidar-scanned area.

43

Across the French Guiana and Gabon plots, we reconstructed empirical canopies with a 44 45 mean absolute error of 3.98m [95% credibility interval: 3.02, 4.98], or 14.4%, and a small upwards bias of 0.66m [-0.41, 1.8], or 2.7%. Height-stem diameter allometries 46 47 were inferred with more precision than crown-stem diameter allometries, with 48 generally larger heights at the Amazonian than the African site, but similar crown-stem 49 diameter allometries. Plot-based aboveground biomass was inferred to be larger in 50 French Guiana with 400.8 t ha⁻¹ [366.2 – 437.9], compared to 302.2 t ha⁻¹ in Gabon 51 [267.8 – 336.8] and decreased to 299.8 t ha⁻¹ [275.9 – 333.9] and 251.8 t ha⁻¹ [206.7 – 52 291.7] at the landscape scale, respectively. Predictive accuracy of the extrapolation procedure had an RMSE of 53.7 t ha⁻¹ (14.9%) at the 1 ha scale and 87.6 t ha⁻¹ (24.2%) at 53

54	the 0.25 ha scale, with a bias of -17.1 t ha ⁻¹ (-4.7%). This accuracy was similar to
55	regression-based approaches, but the Canopy Constructor improved the representation
56	of natural heterogeneity considerably, with its range of biomass estimates larger by
57	54% than regression-based estimates.
58	
59	The Canopy Constructor is a comprehensive inference procedure that provides fine-
60	scale and individual-based reconstructions even in dense tropical forests. It may thus

61 prove vital in the assessment and monitoring of those forests, and has the potential for a

- 62 wider applicability, for example in the exploration of ecological and physiological
- 63 relationships in space or the initialisation and calibration of forest growth models.

64 **1. Introduction**

65 Tropical forests store more than half of terrestrial living biomass (Pan et al., 2011) and 66 shelter a disproportionate share of terrestrial biodiversity. Yet they are increasingly 67 threatened by human activities, from agricultural encroachment and fragmentation to 68 global climate change (Lewis et al., 2015). Tropical forests thus play a pivotal role in 69 carbon mitigation and conservation strategies such as natural regeneration and the 70 avoidance of deforestation (Chazdon et al., 2016; Grassi et al., 2017). To prioritize such 71 strategies and assess their efficacy, methods are needed that accurately quantify forest 72 structure, i.e. the vertical and horizontal arrangement of tree stems and crowns. 73 Forest structure shapes ecosystem functioning (Shugart et al., 2010), wood

quality (Van Leeuwen et al., 2011), microclimates and habitats (Davis et al., 2019), and
the resilience and resistance of ecosystems to disturbances (DeRose and Long, 2014;
Seidl et al., 2014; Tanskanen et al., 2005). Forest structure also varies across climates
(Pan et al., 2013) and across successional states and environmental conditions (Lutz et
al., 2013). Approaches to quantify forest structure should therefore be able to account
for local heterogeneities and be applicable over large areas (R. Fischer et al., 2019).

Field-based inventories provide detailed descriptions of diameter distributions across time and space and form the bedrock of research in forest ecology. However, the mapping, measuring and identification of trees is typically limited to a few hectares. Furthermore, it is usually difficult to obtain reliable measurements of tree height and other crown dimensions from the ground (Sullivan et al., 2018). As a result, it has long been a challenge to correctly describe the three-dimensional stratification of forests (Oldeman, 1974).

87 Much has changed, however, with the advent of laser scanning and its ability to 88 obtain data in three dimensions (Atkins et al., 2018; Disney, 2019). At regional scales, 89 airborne laser scanning (ALS), i.e. aircraft-mounted laser scanning devices, are now 90 commonly used to survey forest stratification over thousands of hectares. The data can 91 be used to infer canopy height and leaf density at sub-meter resolution (Riaño et al., 92 2004; Rosette et al., 2008; Vincent et al., 2017), with diverse purposes, from estimating 93 carbon stocks (Asner and Mascaro, 2014) to mapping animal habitats (Goetz et al., 94 2010). In some situations, even individual tree dimensions – especially tree height, 95 crown area and depth - can be deduced by segmenting dense ALS point clouds into 96 individual plants and their components (Aubry-Kientz et al., 2019; Ferraz et al., 2016; Hyyppä and Inkinen, 1999; Morsdorf et al., 2004). In particular for emergent and more 97 loosely spaced trees, full crowns are often visible in ALS datasets and can be monitored 98 99 from above (Levick and Asner, 2013; Meyer et al., 2018; Stovall et al., 2019). While this 100 technique has been well-researched in temperate and boreal forests, its implementation 101 is more difficult in the multistoried forests typically found in the tropics. In the latter 102 case, many trees are overtopped and difficult to delineate, so a large part of the 103 information on individual tree size is inaccessible. Furthermore, even when tree crowns 104 have been isolated, the matching of crowns to ground-measured diameters is made 105 difficult by asymmetries in tree growth and uncertainties in geo-positioning. 106 Here we propose an alternative, simulation-based strategy to infer forest 107 structure. It relies on a combination of ALS data and field inventories to first reconstruct 108 forests in 3D on local field plots, and then uses local summary statistics to create virtual 109 tree inventories over the whole ALS-extent. We call our method the "Canopy 110 Constructor". It is inspired by the fusion of forest simulators with lidar data (Fassnacht 111 et al., 2018; F. J. Fischer et al., 2019; Hurtt et al., 2004; Knapp et al., 2018; Shugart et al.,

2015), space-filling algorithms (Bohn and Huth, 2017; Farrior et al., 2016; Taubert et al.,
2015) and the use of synthetic forests to link lidar and ground inventories (Palace et al.,
2015; Spriggs et al., 2015). The Canopy Constructor brings these approaches together to
provide a comprehensive picture of forest canopies in space, with applications in
biomass mapping, the study of remote sensing techniques and the initialization or
calibration of forest growth models (F. J. Fischer et al., 2019).

118 To implement it, we used the assumptions of the spatially explicit and individual-119 based forest growth model TROLL (Maréchaux and Chave 2017) and notions from 120 allometric scaling theories, i.e. that tree dimensions can be predicted through allometric 121 relationships (Niklas 2007) and that space-filling concepts translate between the properties of individual trees and those of the whole stand (Niklas et al., 2003; West et 122 123 al., 2009). Unlike general theories of allometric scaling, however, the Canopy 124 Constructor seeks to infer realized scaling relationships from local plot data, and then 125 uses these to predict tree positions and dimensions in space.

126 Here, we describe the Canopy Constructor algorithm, and apply it at two tropical 127 rain forest sites, one in French Guiana (Chave et al., 2008a), one in Gabon (Memiaghe et 128 al., 2016), to infer the allometric relationships between trunk diameter and crown 129 dimensions, and to create virtual tree inventories across several thousands of hectares, 130 from which fine-scale above-ground biomass maps can be deduced. Specifically, we 131 asked the following questions: (i) How well can we reproduce 3D scenes of tropical 132 forests from relatively simple principles, (ii) Are tree inventories and ALS data sufficient 133 to infer allometric scaling relationships between tree dimensions, and how do these 134 relationships differ between sites? (iii) What is the biomass density at both sites and how is it distributed across the landscape? (iv) How accurate is the Canopy Constructor 135 136 approach in extrapolation and does it have an advantage over conventional biomass

- 137 mapping methods? We evaluated the Canopy Constructor's predictions through
- 138 independent data and cross-validation, compared the accuracy against regression-based
- approaches, and, for practical purposes, provide an assessment of its accuracy with a
- 140 reduced set of simulations.

141 **2. Materials and Methods**

142 **2.1 Study sites**

To answer our research questions, we selected two tropical sites, one in French Guiana, and one in Gabon. The two sites were chosen based on their location in the Earth's two largest tropical forest biomes, with high biomass and biodiversity, which makes it a challenge to correctly estimate their structure. Furthermore, their biomass has been recently quantified, so we had empirical data sets and estimates at hand to compare our approach with (Labriere et al., 2018). Throughout, we refer to them as study sites, while tree inventories are referred to as plots.

150 The French Guiana site is the Nouragues Ecological Research Station (4.06°N, 151 52.68°W). The site is characterised by a lowland tropical rainforest (except for a granitic 152 outcrop at 430m asl), ca. 2900 mm yr⁻¹ rainfall, a 3-month dry season in September-153 November, and a shorter one in March. Its forest forms part of the Guiana Shield, at the 154 northeastern tip of Amazonia, a region with high tree wood densities and biomass, and a 155 large fraction of legume species (ter Steege et al., 2006). Tree inventories have been 156 carried out since 1992, including a 10-ha plot called "Grand Plateau" and a 12-ha plot 157 called "Petit Plateau" (Chave et al., 2008b). Trees with diameters \geq 10 cm at 1.30m 158 above the ground (diameter at breast height, dbh) or above deformities and buttresses 159 are mapped, tagged and identified at species level when possible. The two plots differ in 160 their disturbance regime and canopy structure (cf. Figure S1 for their canopy height 161 models), but a typical hectare includes between 500 and 600 trees \ge 10cm dbh and \ge 162 150 tree species. Dominant species are Eschweilera coriacea, Quararibea duckei, Lecythis 163 persistens, Vouacapoua americana, Eperua falcata and the palm Astrocaryum sciophilum (Poncy et al., 2001). Several ALS surveys have been conducted since 2008 (Réjou-164 165 Méchain et al., 2015), with a Riegl lidar (LMS-Q560) mounted on a fixed-wing aircraft.

We here used the 2012 tree inventory and ALS dataset which covers 2,400 ha at a pulse
density of ~12 per m² (based on density of last returns) and an overall point density of
~18 per m² (all returns; Réjou-Méchain *et al.*, 2015).

169 The second site, Rabi, is located in southwestern Gabon's Gamba Complex, 170 (1.92°S, 9.88°E). The site is characterized by annual rainfall of ca. 1970 mm yr⁻¹ 171 (Anderson-Teixeira et al., 2015a), and is covered with a lowland old-growth tropical rain 172 forest, with local human disturbances by oil operations and selective logging. A 25 ha 173 plot has been censused twice, including all trees \geq 1 cm dbh, in 2010-2012 and 2016-174 2017 (Memiaghe et al., 2016), following the ForestGEO protocol (Condit, 1998). The plot has an estimated 84 species ha⁻¹ and 447 trees \geq 10 cm dbh ha⁻¹ (Memiaghe et al., 2016). 175 176 The legume family contributes a large fraction of species, trees and biomass, with four 177 species, Tetraberlinia moreliana, Tetraberlinia bifoliolata, Gilbertiodendron ogoouense, 178 and *Amanoa strobilaceae*, accounting for ca. 45% of canopy tree species (Engone Obiang 179 et al., 2019). An airborne lidar campaign over 900 ha was carried in 2015, using a 180 helicopter-based RIEGL VQ-480i, with pulse densities of \sim 2.5 per m², and the plot is part 181 of the AfriSAR campaign (Fatoyinbo et al., 2017).

182

183 **2.2 The Canopy Constructor algorithm**

The Canopy Constructor algorithm consists of two steps. In a first step, the 3D-forest structure is reconstructed over a local plot ("calibration plot"), relying on a tree inventory, a co-registered ALS-scan and stand-average allometric relationships that relate trunk diameter, tree height and crown radius. After an initial, random reconstruction, tree properties are swapped until a high degree of similarity between the empirical, ALS-derived canopy and the simulated canopy is achieved, but without altering the underlying allometric structure. If allometric parameters are not known

empirically, they are inferred through Bayesian inversion where the routine is run with
a wide range of parameters (see e.g., Hartig *et al.*, 2011). At the end this step, several
best-fit 3D scenes are obtained, representing the most likely structural configurations
and allometric scaling relationships on the calibration plot.

In a second step, the routine is extended to create a tree-by-tree reconstruction
over the whole extent of the airborne lidar scan. Trees are drawn from the local stem
diameter probability distribution and crowns are packed into the canopy until densities
match those of the calibration plot. In the following, we describe both steps in detail.



199

Trees designed by Freepik

Figure 1: The two-step procedure of the Canopy Constructor algorithm. Step 1 uses tree inventory
data, and a canopy height model (CHM). To infer the position and size of each tree, the algorithm creates
an initial reconstruction drawing randomly dimensions from allometric relationships between tree
dimensions. In ill-fitting regions (red), deviations from the allometric means are swapped between trees
until a good spatial fit is obtained (green). Step 2 extrapolates the results of step 1 and creates virtual
inventories across thousands of hectares, following the same fitting algorithm as in step 1, but with fitted
trees drawn from a distribution (see main text for details).

207 The code was developed in C++ and is available online

208 (https://github.com/fischer-fjd/CanopyConstructor). Statistical analysis and

209 visualization were carried out in R (R Development Core Team, 2019) with the packages

210 *data.table, raster, ggplot2, and viridis* (Dowle and Srinivasan, 2018; Garnier, 2018;

Hijmans, 2016; Wickham, 2011) and their dependencies.

212

213 2.2.1 Forest structure inference and model calibration

214 The Canopy Constructor inputs tree diameters and locations from a forest inventory,

215 predicts tree heights and crown diameters from allometric scaling and fills up an initial

216 3D-canopy for the fitting procedure (resolution of 1m³), as in the TROLL model

217 (Maréchaux and Chave, 2017). To summarize canopy structure, we chose the canopy

218 height model (CHM), defined as the top-of-canopy height above ground for a given grid

cell (here at 1m² resolution). For the tree-by-tree reconstruction, the minimal trunk

diameter size was set to 1 cm. Each surveyed tree was assigned to a grid with 1m² cell

size. If several trees co-occured on the same cell, their positions were slightly jittered to

fill up adjacent cells. For multistemmed trees, a single effective stem dbh was retained,

equal to $dbh_{eff} = \sqrt{\sum_{i} dbh_{i}^{2}}$. For simplicity, we refer to dbh_{eff} as dbh. For tree

inventories with a higher cutoff than 1 cm (e.g. *dbh_{cutoff}* = 10cm or 30cm), power-law and
exponential dbh-size distributions were assumed to fill up and randomly place trees < *dbh_{cutoff}* (Taubert *et al.*, 2015, Farrior et al., 2018).

227

228 Allometric relationships

229 To predict canopy structure from the field-measured stems, the Canopy Constructor

assumes the following allometric models:

$$h = \frac{hmax \times dbh}{(a_h + dbh)} \times \exp(\varepsilon_h)$$
(1)

231 and

$$cr = \exp(a_{cr} + \varepsilon_{cr}) \times dbh^{b_{cr}}$$
(2)

232 In Equation (1), *h* is total tree height, *dbh* diameter at breast height, while *hmax* and a_h 233 are Michaelis Menten coefficients interpreted as the asymptotic height that trees reach 234 at large trunk diameter values and the approximately linear slope of the increase of 235 height with diameter at small trunk diameters, respectively. In Equation (2), cr is the 236 tree's crown radius, and a_{cr} and b_{cr} are the intercept and slope of a log-log regression, i.e. 237 a power law model. Equation (1) was chosen instead of a power model to better capture 238 the saturating relationships typically found in tropical rain forests (Cano et al., 2019). 239 The ε_h and ε_{cr} are the respective error terms – i.e. the natural variation in allometry –, 240 given by:

$$\varepsilon_h \sim N(0, \sigma_h)$$
 (3)

241 and

$$\varepsilon_{cr} \sim N(0, \sigma_{cr}) \tag{4}$$

The error terms generate a multiplicative error structure that accounts for the heteroscedasticity in crown and height allometries (Molto et al., 2014). We assumed that allometric variation did not depend on species identity, that ε_h and ε_{cr} were independent, and that crown depth could be simply calculated as a proportion of *h*, as in the TROLL model (Maréchaux and Chave, 2017). To model crown shape more realistically, we defined the ratio γ between the

radius at the top of the crown and its base, with a linear slope linking both layers. γ varies between 0 and 1: if $\gamma = 0$, the tree crown is a cone, while if $\gamma = 1$, it is a cylinder (as in Maréchaux & Chave, 2017). For the purposes of this study, we set γ to 0.8. This resulted in an improvement in the convergence of the crown fitting algorithm compared
to simpler cylindrical shapes, better modelled the less clear-cut edges found empirically
and accounted for the fact that real tree crowns are smaller than their cylindrical
envelopes.

Based on the crown shape parameter as well as a particular realization of the six allometric parameters (*hmax*, a_h , a_{cr} , b_{cr} , ε_h , ε_{cr}), we created an initial 3D forest mockup, with deviations from allometric means randomly assigned to trees.

258

259 Optimization algorithm

The Canopy Constructor then optimizes the spatial overlap of the simulated and the ALS-derived CHMs by readjusting trees and their crowns in space. To this effect, we looped repeatedly through all trees on the grid, in random order, and applied one of three operations described below. The loop was stopped when improvements in canopy structure were marginal (< 1% acceptance rates), usually achieved after 100-200 iterations. A similar algorithm was implemented in Taubert *et al.* (2015).

266 For the majority of field-measured trees, we picked pairs of trees and swapped 267 their respective values of ε_h (deviation in height) and ε_{cr} (deviation in crown radius). 268 We then recalculated the new dimensions of both trees and kept the change if it resulted 269 in an increase in the overall goodness of fit between the simulated and ALS-derived 270 CHM. To keep the overall variance structure, trees were binned into logarithmic dbh 271 classes and only swapped when they were in the same dbh class. This procedure rapidly 272 redistributed deviations from the allometric means across the population of trees so as 273 to improve spatial fits, but preserved the initial allometric structure.

We defined two exceptions. First, large tree crowns are crucial to obtain a good
canopy reconstruction, but only have limited opportunities to swap dimensions due to

their low numbers. Therefore, if there were less than 10 trees within a dbh bin across
the plot, we drew new tree sizes from equations (1) and (2). If the new draw resulted in
a better fit to empirical data, it was retained. To prevent bias in the allometric structure,
the expected crown radii and heights had to be preserved. We used a simple method,
allowing positive deviations from the mean only if the previous bin average deviated
negatively from the expected value, and vice versa.

Second, for trees with dbh < dbh_{cutoff}, initial positions were chosen at random, so we did not change the trees' dimensions, but instead relocated the entire tree, within a radius dependent on its height (but at least 10 m). If the new location increased the goodness of fit, the change was accepted. Few small trees were visible in the CHM, so this procedure rarely modified the canopy, except in canopy gaps.

287 Plot boundaries bisect crown areas and may thus introduce errors in estimation 288 procedures (Mascaro et al., 2011). To prevent biased estimates, we calculated the crown area outside the plot CA_i^{out} and the total crown area CA_i for each tree *i*, summed both 289 across all n trees per plot and computed the ratio $R = \frac{\sum_{i=1}^{n} CA_{i}^{out}}{\sum_{i=1}^{n} CA_{i}}$. During the optimization 290 291 procedure, we forced R to remain approximately constant. If during the fitting process, R 292 exceeded its initial value, then the trial was accepted only if it lowered *R*, and vice versa. 293 We further observed that the Canopy Constructor could assign large crowns to 294 lower canopy layers that barely affected the CHM and fit small crowns on the tallest 295 trees to mimick natural heterogeneity, a phenomenon similar to oversegmentation in 296 tree delineation approaches. To prevent this, we circled through all trees within a 297 distance $dist = CR_{tree} + CR_{treemax}$, for every newly fitted crown with CR_{tree} , and rejected 298 crown fittings that resulted in tree configurations where a large tree with a small crown 299 pierced a small tree with a large crown.

300

301 Goodness-of-fit metrics

Each time a tree crown was updated, we tested whether this change increased the fit
with empirical values. To assess the goodness of the fit between virtual and empirical
CHMs, we used the mean of the absolute errors:

$$MAE = \frac{1}{s_{total}} \sum_{s=1}^{s_{total}} \left| chm_{emp}(s) - chm_{sim}(s) \right|$$
(5)

where each *s* represents a $1m^2$ grid cell of forest, chm_{emp} the empirical canopy height of that grid cell, chm_{sim} the simulated canopy height, derived from the highest non-empty voxel, and s_{total} the total number of grid cells within the plot. MAE measures the matching of local canopy height patterns and was used instead of a mean squared error, because it is more robust with regard to outliers (Hill and Holland, 1977).

Since initial tests showed that the size of large trees would be underestimated by
shrinkage towards the mean from an optimization of *MAE* alone, we also used the
dissimilarity index of the canopy height distributions:

$$D = \frac{1}{2} \sum_{h=0}^{h=hmax} \left| d_{emp}(h) - d_{sim}(h) \right|$$
(6)

where h is a discrete height index (in m), and d_{emp} and d_{sim} are the densities of the 313 314 empirical and simulated height histograms across the surveyed area, i.e. total number of 315 canopy height occurrences, normalized by the number of $1m^2$ grid cells. The factor $\frac{1}{2}$ 316 normalizes the metric to 1 and allows us to interpret it as a measure of distribution 317 overlap: the lower the dissimilarity, the higher the overlap. In the limit of D = 0, both 318 distributions are identical, in the limit of D = 1, there is no overlap at all. Formally, if OVL is the distribution overlap, then D = 1 - OVL, with $OVL = \sum_{h=0}^{hmax} \min \left(d_{emp}(h), d_{sim}(h) \right)$ 319 320 (Inman and Bradley, 1989; Swain and Ballard, 1991).

We fitted the tree crowns using both metrics independently first, until a low acceptance rate was achieved for each (< 1% for trees > 10cm dbh, typically reached within 50 iterations for the *MAE*, and within 5 iterations for the dissimilarity). We then used the difference between initial and final fits to normalize both metrics and combined the normalized values to an overall error as follows:

$$\delta = \sqrt{MAE_{norm}^2 + D_{norm}^2} \tag{7}$$

In a final number of iterations, we minimized δ . The combined metric ensured that crowns did not only fit spatially at local scales, encapsulated by a low *MAE*, but also preserved the overall canopy height model distribution, as measured by *D*.

329

330 Inferring Allometric Parameters by Approximate Bayesian Computation

331 The optimization algorithm finds the best canopy reconstruction, given a set of 332 allometric parameters. However, allometric parameters are rarely known, so we used an 333 Approximate Bayesian Computation rejection scheme (Csilléry et al., 2010; Hartig et al., 334 2014; F. J. Fischer *et al.*, 2019) to infer them. The prior probability distribution of the six 335 allometric parameters, (*hmax*, a_h , a_{cr} , b_{cr}) and (σ_h , σ_{cr}) was approximated by 10,000 336 random draws. We applied the Canopy Constructor to the allometric parameter 337 combinations, and retained only the best 1% of canopy reconstructions (Csilléry et al., 338 2010). The retained parameter values were used to generate a posterior probability 339 distribution over credible allometric parameterizations given the data.

We chose flat parameter priors by drawing from uniform distributions within globally observed ranges of tree allometries (Jucker et al., 2017). Parameters were drawn on logscales, except for the crown allometry intercept *a_{cr}*, drawn from a uniform distribution on the back-transformed scale. A Latin hypercube scheme was employed to minimize the computational burden, and correlation between allometric coefficients was accounted for using an algorithm of the R package 'pse' (Chalom et al., 2013),
rewritten in C++ for speed. Covariance coefficients were taken from the Jucker *et al.* data
set (2017). Since crown depth did not influence canopy height – and thus did not
directly affect the fitting procedure –, it was fixed to 20% of tree height throughout the
procedure.

350 To assess goodness of fit, we again used the mean absolute error (*MAE*) and 351 dissimilarity *D*. But instead of normalizing by the within-simulation range, we 352 normalized by the range across all simulations and combined the metrics to $\delta_{ABC} =$

$$353 \quad \sqrt{MAE_{normABC}^2 + D_{normABC}^2}.$$

354

355 2.2.2 Model extrapolation

In step 2, the Canopy Constructor uses the local fit from step 1, extrapolates the trunk
diameter probability distribution and allometric scaling relationships across the whole
ALS-covered area and constructs virtual tree inventories from space-filling principles.
We implemented the same fitting procedure as before, but since the location and size of
stem diameters have to be inferred, now all trees are drawn from a distribution and
then relocated to create better spatial fits.

362

363 Space-filling principles

As a measure of space-filling, we used the crown packing density $\varphi = \frac{1}{V_{max}} \sum_{i} V_{i}$, where V_{max} is the maximally available volume within a section of the canopy, and V_i the volume contribution of each tree to that section (Jucker et al., 2015; Taubert et al., 2015). The crown packing density is the ratio of unit crown volume to unit canopy volume (m³ per m³). It can be calculated for single voxels, subsets of voxels or for the entire canopy.

We defined the crown packing density at height *h*, with $0 \le h \le h_{max}$, and with 369 370 h_{max} top-of-canopy height, so that crown packing density was dependent on the 371 canopy's height. We then defined the following quantity: $\boldsymbol{\varphi}(h, h_{max})$, the packing density 372 matrix, where columns represent top-of-canopy height h_{max} and rows represent within-373 canopy height layers h (cf. Figure S2, left panel). We set the size of height bins to 1 m, 374 and their numbers ran from 0 m to maximum canopy height. On a per-voxel basis, each 375 tree's volume contribution to a voxel could thus be either 0 or 1 m³, but due to the 376 idealized crown shapes assumed in the Canopy Constructor, crown overlaps were more 377 frequent than in real forest stands, resulting in local packing densities $> 1 \text{ m}^3$.

378

379 Inferring virtual inventories

380 To infer virtual tree inventories across the whole ALS-covered area, we divided the lidar 381 scene into grid cells, roughly equivalent in size to the local field inventories. We then 382 used the CHM of each grid cell, combined it with the packing density matrix $\boldsymbol{\varphi}$ obtained 383 from the 3D reconstructions of the local calibration plot and predicted crown volume 384 per height layer. This was achieved by calculating the ALS-derived canopy height 385 distribution for each grid cell, denoted \bar{c}_{ALS} , and formalized as a vector of top-of-canopy 386 height frequencies. Multiplying the ALS-derived canopy height vector with the packing 387 density matrix yielded the vector $\bar{v}_{ALS} = \boldsymbol{\varphi} \bar{c}_{ALS}$ (Figure S2). The quantity \bar{v}_{ALS} is an 388 estimate of total crown volume per height layer within the extrapolation cell. For grid 389 cells that reached canopy heights larger than the calibration plot from which the packing 390 density matrix was derived, $\boldsymbol{\varphi}$ was calculated by averaging over the five non-empty 391 layers just beneath the missing layer.

392 Once the maximum space filling was determined, trees were drawn until a virtual 393 forest with a crown volume distribution $\bar{v}_{virtual}$ similar to \bar{v}_{ALS} was obtained. We drew

394 diameters from the calibration plot's probability distribution and used the previously 395 inferred allometric relationships to predict tree height and crown radius. After 396 randomly placing a tree on the grid, we updated $\bar{v}_{virtual}$ and determined by how much the new tree improved the fit with \bar{v}_{ALS} . To do so, we calculated the change in $\bar{v}_{diff}(h) =$ 397 398 $\bar{v}_{ALS}(h) - \bar{v}_{virtual}(h)$ for every height layer h. If the crown volume in h had not yet reached the reference value ($\bar{v}_{diff}(h) > 0$), every added unit of crown volume improved 399 400 the fit and was counted positively. As soon as the crown volume in the layer reached or 401 exceeded the ALS-predicted volume ($\bar{v}_{diff}(h) \leq 0$), every added crown volume unit 402 penalized the fit and was thus discounted. We then summed units of crown volume over 403 all layers *h*, and we accepted the tree if the overall balance was positive. Otherwise, the 404 tree was rejected. Each drawing cycle comprised *n* draws, where *n* is the number of 405 potential tree locations (i.e. the m² area) under consideration. When the rejection rate 406 reached 100% after a full cycle, we stopped the procedure.

After the initial distribution of trees in space was obtained, it was gradually
improved upon. This was done by displacing trees in relation to their height until an
optimal spatial fit was achieved, as described for step 1. Again, we found that 100-200
iterations were sufficient to reach low rejection rates (< 1%). To propagate uncertainty,
the procedure was carried out for each of the 100 posterior reconstruction of the ABC
approach from step 1, with all grid cells collated to produce final maps.

413

414 **2.2.3 Application at the study sites**

At Nouragues, we used the geographically separated Petit Plateau (12 ha) and Grand
Plateau (10 ha). Applying the inference step on each of them individually allowed for a
comparison with previous studies and an assessment of within-site heterogeneity. We
also split the 25-ha plot at Rabi into two subplots (10-ha and 15-ha, respectively). We

419 used plot sizes of \geq 10ha because they minimized edge effects and kept a balance 420 between the computational burden of the procedure and the sample sizes needed to 421 swap random terms between crowns. On each subplot, we inferred forest structure (tree 422 dimensions, allometric parameters and crown packing densities). We then used the 423 larger plots at both sites (i.e. the 12 ha Petit Plateau and the 15 ha Rabi plot) to 424 extrapolate the virtual inventories across the whole landscape, subdivided into 400m x 425 400m grid cells (16 ha). Grid cells at the edges were discarded, and we created virtual 426 forest inventories over 2,016 ha at Nouragues and 832 ha at Rabi.

427 To create the CHMs, lidar data were classified via TerraScan and then post-428 processed with LAStools to obtain pit-free CHMs (Isenburg, 2018; Khosravipour et al., 429 2014). While the ALS data differed in point densities at the two sites (with considerably 430 lower densities at Rabi), the Canopy Constructor method was robust to such differences 431 because it was based on the CHM alone. Aboveground biomass (AGB) was estimated for each tree (kg), using the formula $AGB = 0.0673 \times (\rho \times dbh^2 \times h)^{0.976}$ (Chave et al., 2014), 432 where p represents species-level wood density, obtained from a global database (Chave 433 434 et al., 2009; Zanne et al., 2009). For biomass mapping, tree biomass estimates were 435 aggreggated at 1 ha and 0.25 ha resolutions (t ha⁻¹), a common grid size in biomass 436 mapping (Labrière et al., 2018; Réjou-Méchain et al., 2015). For consistency with 437 previous work, we computed AGB only for trees with dbh \geq 10cm. Diameter 438 measurement errors usually have small effects on plot-scale estimates (Réjou-Méchain 439 et al., 2017), and since neither p nor error in the AGB equation directly affected the 440 Canopy Constructor algorithm, we did not propagate error in these quantities. 441

442

444

445 **2.3 Evaluation**

446 We assessed the accuracy of the Canopy Constructor's reconstructions (step 1) by 447 comparing the inferred allometric relationships between trunk diameters and tree 448 dimensions to allometric relationships derived from field measurements of tree height 449 and diameter. We computed the mean absolute and mean relative deviation (in %) 450 between height predictions. For biomass, we compared our predictions to previous 451 estimates of plot biomass for both sites and landscape-scale maps obtained with a 452 pooled regression model, all reported in Labriere et. al. (2018). 453 To more formally assess the extrapolation to landscape scale (step 2), we first

454 evaluated the consistency of the extrapolation model with the reference estimate, derived from the field inventory and Canopy Constructor-calibrated allometries (step 1). 455 456 We did so by applying the extrapolation step to each plot itself and assessed the fit of the 457 extrapolation model. We quantified the accuracy and precision of biomass estimation 458 via four commonly reported metrics, namely R² (squared Pearson's r), RMSE (root mean 459 squared error, t ha-1), MAE (mean absolute error, t ha-1) and MBE (mean bias of the 460 error, t ha⁻¹). All metrics, except R², were also computed relative to the reference AGB. 461 We then evaluated the sensitivity to plot characteristics through a cross-validation 462 procedure where we used the summary statistics from one plot per study site 463 (calibration plot) to extrapolate to the other plot at the study site (extrapolation plot), 464 and vice versa. As before, we quantified accuracy with respect to reference AGB 465 estimates through R², RMSE, MAE and MBE. Finally, we also compared the reference and 466 predicted diameter distributions, both for the model fit and in cross-validation. 467 To evaluate the Canopy Constructor's utility for biomass estimates compared to

468 more conventional methods, we compared its accuracy to the accuracy of log-log

469 regression models of AGB vs. median canopy height (Labriere et al., 2018; Réjou-470 Méchain et al., 2015). We fitted log-log regression models against median canopy height, 471 again for each of the four plots at both 1 ha and 0.25 ha resolution and assessed both 472 model fit at the calibration plot and predictions between cross-validation plots. To 473 mirror the Canopy Constructor setup, we did not use any field-inferred height 474 allometries for the AGB estimates, but inferred height from a bioclimatic predictor 475 (Chave et al., 2014; Réjou-Méchain et al., 2017). Accuracy was reported with the same 476 metrics as above (R², RMSE, MAE, MBE).

Throughout this study, we carried out a comprehensive Bayesian inference with
10,000 prior and 100 posterior simulations. This gave a good approximation of the
Canopy Constructor's posterior distributions, but, more importantly, also allowed us to
assess the method's sensitivity to simulation numbers. To this effect, we resampled 100
sets of 1,000 simulations from the 10,000 prior simulations, and 100 sets of 10
simulations from the 100 posterior simulations, and repeated both steps of the Canopy
Constructor to assess accuracy and precision in a computationally more efficient setting.

484 **3. Results**

485 **3.1 Reconstructions of tropical forest canopies in 3D**

486 Across all plots, the Canopy Constructor yielded good fits for the canopies with a final 487 error in mean canopy height of 0.66m [95% credibility interval: -0.41, 1.8] or 2.7% of 488 mean canopy height, and a mean absolute error of 3.98m [3.02, 4.98] or ~14.4% of 489 mean canopy height. Figure 2 visualizes the approach at the Petit Plateau plot for a 490 posterior simulation after 200 iterations of fitting. The initial draw (panel a) already 491 mirrored average properties of the empirical canopy, but not the spatial location of its 492 features (panel b). Swapping the deviations in allometries greatly improved the spatial 493 structure (panel c).



494

Figure 2: Example of canopy reconstruction at the Petit Plateau plot, Nouragues. Shown are the
initial canopy height model (CHM) where tree dimensions are randomly drawn from site-specific
allometries (a), the ALS-derived CHM (b), and the final reconstruction of the Canopy Constructor (c).

499 **3.2 Allometric scaling relationships**

Tree inventories and ALS data were sufficient to infer allometric relationships between tree dimensions at both sites. Across all plots, we found substantial covariation between allometric parameters (Table S1, and Figure S3, left panels), but height allometries had lower uncertainties than crown radius allometries (Figure 3, Figure S3, Table 1). High within-site similarity was found for height allometries at both Nouragues and Rabi (Figure 3). Crown allometries, on the other hand, showed a divergence at Nouragues, with larger crown radii predicted at Petit Plateau than at Grand Plateau. The sites were
clearly distinct in their height allometries, with generally taller trees at Nourages than at
Rabi, but not in their crown allometries.





521	At both sites, parameter estimates were close to those previously obtained from
522	field measurements of tree height (cf. Figure 3, top row). At Nouragues, the Canopy
523	Constructor's height estimates were slightly lower than empirical ones at small
524	diameters and exceeded them at large diameters, but mirrored their qualitative
525	patterns, i.e. the larger heights predicted at Petit Plateau compared to Grand Plateau.
526	The difference to empirical height predictions never exceeded 1m (or 2%) at Petit
527	Plateau, versus 3.2 m (or 7.8%) at Grand Plateau. At Rabi, the pattern was inversed, with
528	lower predictions of tree height at large diameters than from empirical data, but
529	differences never exceeded 11% (Supplementary Figure S4).
530	Table 1: Inferred parameters. Mean of posterior distributions for allometric parameters at the two sites.
531	Plots are Grand Plateau (GP) and Petit Plateau (PP) at Nouragues, and the 10 ha and 15 ha rectangular

 $532 \qquad \text{strips at Rabi} \text{ (Rabi10 and Rabi15, respectively). } a_h \text{ and } h_{max} \text{ are given in } m, \text{ all other variables are unitless.}$

	a_h	h_{max}	σ_h	a_{CR}	b _{CR}	σ_{CR}
GP	0.41	56.88	0.39	2.19	0.55	0.24
PP	0.39	58.38	0.23	2.29	0.56	0.22
Rabi10	0.32	47.52	0.37	2.2	0.53	0.25
Rabi15	0.28	43.67	0.35	2.23	0.55	0.27

533

534

535 **3.3 Biomass mapping at landscape scale**

536 Aboveground biomass was estimated to be 400.8 t ha⁻¹ at the Nouragues plots [366.2 –

537 437.9] and 302.2 t ha⁻¹ [267.8, 336.8] at Rabi. Within-site standard deviation at hectare

538 scale was 105.1 t ha⁻¹ [86.5, 120.7] at Nouragues and 71.0 t ha⁻¹ [60.5, 83.6] at Rabi. At

539 both sites, biomass density decreased at the landscape scale to an average of 299.8 t ha⁻¹

- 540 [275.9, 333.9] and 251.8 t ha⁻¹ [206.7, 291.7], respectively, but with considerable
- 541 heterogeneity (Figure 4, a and d). Map uncertainty was highest at vegetation edges and
- 542 low biomass areas, and generally higher at Rabi (median coefficient of variation of
- 543 ~0.24) than at Nouragues (~0.16, cf. also Figure 4, b and e). At both Nouragues and Rabi,

biomass reached similar extreme values, of over 1100 t ha⁻¹ at the 0.25-ha

545 scale.



546



548 Maps show the mean aboveground biomass values (t ha-1) predicted with the Canopy Constructor 549 approach across 2,016 ha at Nouragues (panel a) and 832 ha at Rabi (panel d), as well as the respective 550 coefficient of variation across 100 simulations (panels b and e, dimensionless). Also given are the overall 551 distributions of aboveground biomass (panels c and f, red distributions, in t ha-1) and previously obtained 552 estimates (panels c and f, yellow) from a pooled regression-model (Labrière et al. 2018). Clearly evident is 553 the shrinkage towards the mean in the regression-based approach, as opposed to much stronger variation 554 in the Canopy Constructor approach. Please note that the geographic extent of the maps has been rescaled 555 for visualization purposes.

Biomass estimates were close, but lower at both sites than previous estimates of
404.6 t ha-1 at the plot and 328.6 t ha⁻¹ at landscape scale at Nouragues, and 314.6 t ha⁻¹
282 t ha-1 at Rabi (Labriere et al., 2018). However, the spread in aboveground biomass
density was much larger than in previous biomass maps, with a larger fraction of both
low- and high-density grid cells (Figure 4, c and f).

561

578

562 3.4 Extrapolation accuracy

563 Across both sites, the extrapolation model's biomass predictions were consistent with 564 the locally inferred reference values (Figure 5, a and c), with an R² of 0.84 at the 1 ha 565 scale, and 0.67 at the 0.25 ha scale. The RMSEs were 53.2 t ha⁻¹ (14.7%) and 87.3 t ha⁻¹ 566 (24.1%). The calibration plots were also representative of the local environment, as the 567 quality of the inference did not decrease in cross-validation, with identical R² values and 568 similar RMSE as before, i.e. 53.7 t ha¹ at the one-hectare scale, and 87.6 at the 0.25 ha 569 scale, or 14.9% and 24.2%, respectively (Figure 5, b and d). The good predictive 570 accuracy was mirrored by diameter distributions that matched well empirical ones, both 571 when fit at the calibration site and in cross-validation (Figures S5 and S6, Table S2). 572 Regression-based approaches generally produced better model fits at the 573 calibration sites than the Canopy Constructor, but there was no clear advantage in cross-574 validation, with $R^2 = 0.72$ at the 1 ha scale and 0.55 at the 0.25 ha scale, and an RMSE of 575 51.6 t ha⁻¹ (14.6%) and 81.4 t ha⁻¹ (18.3%), respectively (Figure S7). Bias was slightly

576 higher in the Canopy Constructor, at -4.7%, compared to a +1.2% in regression, but the

577 Canopy Constructor predicted much larger heterogeneity than the regression-based

approach. In the calibration step, it had a 95% range in AGB of 489.7 t ha⁻¹, compared to

579 458.5 t ha⁻¹ at the 0.25 ha scale, and the difference was even larger in extrapolation,

580 with a predicted range of 568 t ha⁻¹ against 368.3 t ha⁻¹ from regression (54% increase).



581

582 Figure 5: Evaluation of aboveground biomass predictions in extrapolation (step 2). Shown are the 583 predictions of aboveground biomass (median of 100 posterior simulations, given in t ha⁻¹) at the 1 ha scale 584 (a, b) and 0.25 ha scale (c, d). The left column shows the results when the space-filling approach is applied 585 at the calibration plot from which allometries and packing densities were derived ("Model fit"), the right 586 column the results when the approach is transferred between plots ("Cross- validation"). The Nouragues 587 results are plotted in red/orange, and for Rabi in dark/light green. Goodness of fit values are provided in 588 the bottom-right corner of the panels. MBE does not change between 0.25 and 1 ha scales and is thus only 589 given in the top panels. For visualization purposes, we only plot error bars at the hectare scale, 590 representing the interquartile ranges of estimates from 100 posterior simulations.

591	All our estimates were stable and had low uncertainties when resampling smaller
592	sets of simulations. Within plots, height allometric parameters were similar to the full
593	simulation set (example inference in Figure S8). Average AGB was also similar to the full
594	simulation set, with 399.2 t ha ⁻¹ at Nouragues and 305.0 t ha ⁻¹ at Rabi, and small
595	standard deviations of 5.7 t ha-1 (1.4%) and 5.6 t ha-1 (1.8%). The average R^2 in
596	extrapolation was 0.65 at the 0.25 ha scale with an average RMSE of 90.7 t ha ⁻¹ , and
597	standard deviations of 0.02 and 2.8 ha ⁻¹ , respectively (or \sim 3% for both metrics).
598	

599 **4. Discussion**

600 We described and applied a new approach to quantifying forest structure, the Canopy 601 Constructor. The Canopy Constructor inputs local forest tree inventories and airborne 602 lidar scanning and outputs estimates of forest structure, allometric relationships among 603 tree dimensions and virtual landscape-scale tree inventories. These results provide 604 insights on tree allometric relationships and the distribution of carbon stocks. Below we 605 discuss how the method advances our knowledge on both issues, and we reflect on the 606 underlying assumptions and computational limitations. We applied our approach at two 607 tropical forest sites, one in the Guiana Shield of South America, the other in the Guineo-608 Congolian rainforest of Africa. We selected the two sites because they are geographically 609 and floristically distinct, but represent high-carbon stock forests, those for which classic 610 airborne lidar scanning (ALS) methods of biomass mapping are the most error prone. 611 We also discuss whether the Canopy Constructor method is applicable beyond closed-612 canopy tropical forests, e.g., in landscapes with land-use mosaics, and in temperate and 613 boreal forests.

614

615 Inferring allometric relations in forest trees

We used the first step of the Canopy Constructor in a Bayesian setting to infer the
allometric relationships between tree height and trunk diameter (dbh), and between
crown size and dbh. Such allometric relationships are essential for scaling up from
individual trees to forest canopies, and we found that they could be well-inferred from a
combination of field inventories and ALS data alone.

In particular, we found that height-diameter relationships differed more strongly
between than within sites, suggesting that biogeographic constraints at the macroscale
outweighed micro-environmental effects, such as disturbances, in shaping the two

624 forests' height scaling relationships. Crown radius allometries, on the other hand, had 625 higher uncertainties and were not clearly separated between sites. However, the French 626 Guiana plots displayed considerable within-site differences in their crown radius 627 allometry. While trees generally show both plasticity in height growth and the lateral 628 extension of the crown (Henry and Aarssen, 1999, Jucker et al., 2015; Pretzsch and 629 Dieler, 2012), height growth is also strongly influenced by physiological limitations 630 (Niklas, 2007). Horizontal crown growth, on the other hand, may depend strongly on 631 canopy openings, particularly so for mid-sized canopy trees, which might explain why 632 we recorded such a notable difference at the Nouragues site, where the two plots have 633 very different disturbance regimes.

634 One key assumption of our approach is that a single functional form holds across 635 a wide range of environmental conditions, forest cover types and functional groups. 636 Specifically, equations (1) and (2) assume a Michaelis Menten model for the dbh-height 637 relationship, and a power-law model for the dbh-crown size relationship, and we make 638 the strong assumption that variation in tree architecture can be summarized by variation in six pre-defined allometric parameters (h_{max} , a_h , σ_h , a_{cr} , b_{cr} , σ_{cr}). On the one 639 640 hand, there is considerable empirical evidence for global scaling relationhips between 641 plant dimensions (Jucker et al., 2017), and there are strong theoretical arguments for 642 their generality due to constraints on resource uptake and hydraulics (West et al., 1999; 643 Niklas, 1994; Niklas, 2007). On the other hand, physiological constraints depend on 644 climatic conditions and are shaped by the organisms' evolutionary history and 645 ecological niches (Niklas, 1994), so allometric relationships vary strongly across 646 environments, among species and co-vary with growth strategies and plant functional traits (Cano et al., 2019; Lines et al., 2012). Empirical data also show deviations from 647 648 idealized allometric relationships due to disturbances and size-dependent competition

among plants (Coomes et al., 2003). In light of this knowledge, there is currently not
enough evidence that equations (1) and (2) are valid across all of the world's forest
types. However, they are flexible enough to accommodate a wide range of tree forms
and have been previously found to yield good fits at our study sites and for other
tropical rain forests (Labriere et al., 2018; Feldpausch, et. al. 2012).

654 In tropical forests, in particular, the Michaelis-Menten functional form has been 655 shown to well-represent the saturating scaling relationships between diameter and tree 656 height (Molto et al., 2014, Cano et al., 2019) and is commonly used to improve biomass 657 estimates (Feldpausch et al., 2012, Réjou-Méchain et al., 2017). However, field data on 658 tree height are difficult to obtain, so the number of empirically derived dbh-height 659 allometric models remains limited in the tropics (Sullivan et al., 2018). The retrieval of 660 crown radius is equally, if not more challenging in dense canopies. The Canopy 661 Constructor approach circumvents such data acquisition problems by parameterizing 662 the scaling relationships directly from a combination of geo-located trunk diameters and 663 ALS-derived canopy height models. At both our study sites, in French Guiana and Gabon, 664 the approach considerably narrowed down the parameter ranges for the inference of 665 dbh-height tree allometries and dbh-crown radius allometries. Independent field data 666 for the dbh-height allometry further confirmed that our inference matched the 667 relationships derived from empirical measurements. The Canopy Constructor thus 668 provides an important approach to estimate tree crown dimensions and biomass 669 estimates where field measurements are scarce.

The allometric models described in equations (1) and (2) account for interindividual variation in allometry through the parameters σ_h , σ_{cr} . For each allometry, a single terms is thus used to model variation due to life histories (King, 1996), species differences (Poorter et al., 2006; Thomas, 1996), and environmental conditions (Lines et

674 al., 2012). If allometries were inferred for different species or different functional 675 groups, much lower variation around allometric means would be expected, with a 676 probable reduction in uncertainty and more accurate representation of the underlying 677 ecological relationships (Cano et al., 2019). However, there is also a tradeoff between 678 increasing the number of model parameters to reduce uncertainty, and overfitting the 679 model. Another risk is that few forest types currently have the level of information to 680 implement species-specific versions of equations (1) and (2). In tropical forests, for 681 example, there would likely not be enough field measurements to infer allometric 682 relationships for rare species, and data might have to be pooled except for the most abundant species. 683

684 Recently, a wealth of information about tree allometry has been made available 685 by the lidar scanning of entire trees from the ground (Dassot et al., 2011). Terrestrial 686 lidar scanning (TLS) has reached a stage of maturity where it can now be applied to 687 mixed-species forests, and even to all canopy trees from a stand (Calders et al., 2015; 688 Momo Takoudjou et al., 2017; Newnham et al., 2015; Stovall et al., 2018). Furthermore, 689 it allows the implementation of detailed canopy space-filling models (Pretzsch, 2014) 690 and creates high-resolution renditions of the 3D architecture of individual trees. This 691 novel source of information poses great challenges at the analysis stage (Åkerblom et al., 692 2017), but has become the best approach to test the generality of allometric exponents 693 (Lau et al., 2019). In the future, it would be possible to either directly integrate TLS 694 information into the Canopy Constructor at the parameter estimation stage (step 1), e.g. 695 as an additional constraint on how the 3D voxel volume is filled, or to test the validity of 696 the inferred scaling relationships.

697 This could be of particular value in heavily disturbed landscapes with few trees,698 where the simulation approach and its idealized crown shapes may fail to capture inter-

699 individual variation in tree architecture. However, it would likely have the strongest 700 benefits for small understory species that are mostly hidden from the Canopy 701 Constructor's fitting procedure. The latter do not only increase the range of allometries 702 that fit the local forest plot and thus contribute strongly to the uncertainty in allometric 703 inference, but they also increase the computational burden without considerably 704 improving the 3D-fits . Nevertheless, it is vital to include small trees in our approach, 705 since they reduce the bias in allometric estimates. Without them, the algorithm would 706 extend crowns from the understory into gaps to improve the fit of the canopy height 707 model and both underestimate tree heights and overestimate crown radii.

708 An alternative to the Canopy Constructor approach is to search for individual 709 crown features by tree crown segmentation of ALS point clouds (Aubry-Kientz et al., 2019; Dalponte and Coomes, 2016; Ferraz et al., 2016) and to mtach the crowns to stems 710 711 on the ground. In the future, a merging of both techniques could prove interesting: the 712 Canopy Constructor algorithm has advantages for forest canopies where individual trees 713 cannot be easily segmented, while individual tree crown segmentation methods are 714 effective for emergent trees and more open forest landscapes. One option would be to 715 first isolate easily identifiable trees, and then pass information on crown shape and size 716 on to the Canopy Constructor. This would narrow down priors on allometric parameters 717 and provide tie-points for the spatial fitting procedure.

Another important objective would be the improvement of the inference of crown radii, which showed higher uncertainty than inferred tree heights. So far, we did not impose any restrictions on crown overlap. This is at odds with observations (Goudie *et al.*, 2009) and may have increased the uncertainty, since crowns can be hidden within each other. A solution could be the simulation of phototropism and plasticity (Purves et al., 2008; Strigul et al., 2008), or the incorporation of leaf-level constraints, e.g. a

condition that assimilated carbon should be greater than respiration losses, as in the
TROLL model (Maréchaux and Chave, 2017). We hypothesize that this would restrict the
range of crown sizes, particularly in the understory where light limits tree growth.

728 Virtual forest inventories and carbon mapping

In the second step of the Canopy Constructor, the locally calibrated models are used to
generate large-scale virtual tree inventories across thousands of hectares covered by
ALS. We tested this approach at the two study sites and validated its performance
through cross-validation. One of the main applications for these virtual tree inventories
is the evaluation of carbon mitigation and conservation strategies.

734 Forest biomass is concentrated in a small number of large trees (Bastin et al., 735 2015; Lutz et al., 2018; Meyer et al., 2018), and mapping the spatial distribution of these 736 trees is key to achieving high-resolution biomass estimates. Using ALS-data to 737 extrapolate virtual inventories, the Canopy Constructor showed good predictive 738 accuracy, mirroring well empirical tree densities and their biomass heterogeneity 739 (Figure 4). The extrapolation uncertainty did not increase between the calibration and 740 cross-validation plots. We validated this at Nouragues, where the plots have different 741 disturbance regimes and different canopy height distributions (Figure S1). This suggests 742 that the Canopy Constructor is an efficient method to map aboveground biomass across 743 an entire landscape.

Specifically, the Canopy Constructor led to an improved biomass inference
compared to regression-based approaches. Regression-based approaches, also known as
area-based approaches (Coomes et al., 2017), infer mean stand biomass from ALSderived canopy features, such as mean or median canopy height (Asner and Mascaro,
2014; Næsset, 2002; Zolkos et al., 2013). However, all regression-based inferences tend

to shrink the extreme values to the mean when uncertainty in the predicted variable is
not propagated or when there is strong variation in the independent variable, a
phenomenon sometimes called "dilution" bias (Réjou-Méchain et al., 2014). Because the
Canopy Constructor factors in the influence of large trees and makes use of the whole
canopy height model, we expected that it would mitigate this issue.

754 Indeed, we found a similar predictive accuracy for both methods, but the Canopy 755 Constructor better represented the heterogeneity of the canopy. The 95% range of 756 biomass estimates at the 0.25 ha scale was higher across both Canopy Constructor steps, 757 with an overall increase of 54% compared to an equivalent regression procedure. 758 Particularly noticeable were low biomass estimates for low-canopy forests that led to an 759 overall decrease in landscape-wide estimates at both Nouragues and Rabi compared to 760 previous biomass maps (Figure 4). Since many field inventories in the tropics are 761 established within primary forest, regression-based estimates are often calibrated on 762 tall canopies, and while additional field data would be required to validate this claim, it 763 may be that our individual-based approach better captures forest structure outside the 764 regression model's calibration range. Similarly, it likely better accounts for the large 765 multiplicative errors in tall canopies. Such fine-scale structural representations are 766 particularly important in identifying high-priority areas for carbon mitigation and 767 conservation, and when monitoring the impact of human interventions such as selective 768 logging on ecosystem functioning and animal habitats.

Furthermore, we hypothesize that there is considerable room for improvement of future canopy reconstructions, since additional considerations on crown overlapping and carbon balance or species' ecological strategies would likely improve the spatial positioning of trees. The Canopy Constructor thus has the potential to be more widely applicable across biomes and environmental conditions than currently used individual-

or area-based models (Coomes et al., 2017) and could provide an efficient means to
assimilate forest inventories and ALS surveys into high-resolution aboveground biomass
maps for the validation of remote-sensing biomass missions (Duncanson et al., 2019; Le
Toan et al., 2011).

Nevertheless, the accuracy of biomass predictions with the Canopy Constructoralso depends on the quality and the representativeness of the calibration sites.

780 First, while we do not assume that stem diameter probability distributions are 781 identical across the whole area, we assume that they are similar enough to sample the 782 entire diameter range. Ideally, they should not considerably over- or underrepresent a 783 particular size-class. When the calibration plot covers a sufficiently large area (≥ 10 ha), 784 microenvironmental features are likely well-sampled, and the space-filling approach of 785 the Canopy Constructor will mostly compensate for deviations. However, in more 786 heterogeneous landscapes than the ones selected for this study, it is essential to ensure 787 that calibration plots are representative of all vegetation types.

788 Second, we assume that the vertical distribution of crown packing density within 789 the canopy, as described by the local packing density matrix, is representative of the 790 whole lidar-covered area. This crown packing matrix provides within-canopy densities 791 conditional on top-of-canopy height and thus reflects disturbance regimes visible in the 792 canopy height distribution. At the study sites, we found that a 10-ha forest inventory 793 was sufficient to provide robust estimates of biomass even if the plot was not 794 representative of the sampled area, as shown in the Nouragues forest. So, even if more 795 studies are needed to fully explore this issue, we conclude that the assumptions of the 796 Canopy Constructor do not lead to serious bias in biomass mapping as long as the 797 sampled area is large.

798 Third, we extrapolate locally fitted allometries between tree dimensions across 799 the entire landscape. This raises the question of whether an allometric model is valid 800 beyond the stand where it was generated. Recently Jucker et al. (2017) have explored 801 the generality of allometric relationships, with the aim to inform the link between field 802 inventories and remote sensing. Compilation of empirical evidence suggests that some 803 allometric relationships among tree dimensions are applicable outside of the locality 804 where they have been constructed, but this may, again, need to be qualified if there is 805 strong regional environmental variation or shifts in species composition (Beirne et al., 806 2019, Lines et al., 2012). Provided that enough data were available, separate allometric 807 relationships for functional or species groups, likely more conserved across the 808 landscape, could alleviate this problem in the future.

809 One of the main issues in extrapolation are understory trees, as they do not show 810 up in the canopy height model and thus exclusively depend on the diameter 811 distributions and crown packing densities of the calibration plots. The assumption of 812 similar understory tree densities may be violated, for example due to browser pressure 813 (Anderson-Teixeira et al., 2015b) or when the forest is more or less fragmented than at 814 the calibration sites (Laurance et al., 2006). While the effect on biomass will be 815 comparatively weak, understory densities can have important consequences for 816 ecological dynamics, such as regrowth and resilience.

Here, we only had two calibration plots per site and they where either immediately adjacent (Rabi) or geographically close to each other (Nouragues), so the effect of spatial auto-correlation across the landscape could not be fully assessed. Any changes in soil characteristics, topography and floristic composition that may generate bias in our biomass maps, would, however, also affect regression-based approaches and can only be solved by more accurate sampling (Babcock et al., 2015; Spriggs et al., 2019).

Since most forest sites around the world involve small plots (0.25 ha or 1 ha) that are
spread out in space to sample heterogeneous environments, a future evaluation of the
Canopy Constructor's assumptions across forest types should not pose a problem.

827 Applicability across forest types and processing considerations

828 Many sites worldwide offer a combination of high-quality local forest inventories and 829 ALS surveys (Duncanson et al., 2019), but far fewer provide quantitative information on 830 the vertical arrangement of individual trees and within-canopy forest structure, so the 831 Canopy Constructor was designed to be as widely applicable as possible. It only requires 832 a canopy height model that covers the sampling area and a sufficiently large number of 833 stem diameter measurements to accurately sample the diameter distribution. These 834 conditions are likely already met within a few hectares in closed-canopy forests, and our 835 results at two tropical forest stands provide evidence for this hypothesis.

836 The Canopy Constructor should, however, also be applicable to temperate and 837 boreal forests, or more open landscapes, such as woodlands, savannas or heavily 838 disturbed forests. Variable crown shapes can be accomodated through a crown shape 839 parameter, ranging from cylindric to conic forms, and non-measured trees below a stem 840 diameter cutoff can be supplemented by drawing from power-law or exponential 841 functions, as done in the present study. Due to its simulation approach and need for 842 representative calibration data, the Canopy Constructor reaches its limits in 843 insufficiently or unequally sampled landscapes with low tree densities and strong 844 floristic variation, but there, tree crown delineation would likely perform well and could 845 complement it.

846 When applied across a wide range of forests, variation in wood density beyond847 the species level and variation in biomass allometries beyond a global mean would need

to be considered (Réjou-Méchain et al., 2017). This would likely further increase the
local heterogeneity of simulated canopies, differentiate out between different
successional stages and thus achieve a more realistic picture. However, since neither
wood density nor biomass directly affect the Canopy Constructor procedure and since
wood density is distributed normally around species means (Chave et al., 2009, Kattge et
al., 2011), both uncertainties could be propagated in a relatively simple way.

854 The main limitation of the Canopy Constructor compared to more conventional, 855 regression-based approaches are its computational requirements. On one core of an 856 Intel Skylake 6104 processor at 2.3 GHz, computational burden of the Canopy 857 Constructor was ca. 3 minutes for a simulation of the typical field inventory in this study 858 (~10ha), with moderate memory needs (~300 MB). For the full set of 10,000 859 simulations tested here, this amounted to ~400 cpu core hours per plot for allometric 860 inference and ~700 cpu core hours for reconstructing tree-by-tree assemblies at the 861 landscape scale. Reduced sets of simulations yielded nearly identical results, with very 862 low standard deviations of the estimates (typically 1-2%, and always lower than 5%) 863 but on our hardware, the approach still required 50-100 cpu core hours for a typical 864 data configuration. The procedure is thus beyond desktop computers at the moment, but 865 since simulations within step 1 or step 2 are fully independent, the inference procedure 866 can be parallelized and is relatively easily executed on a modern cluster.

For future reconstructions, there are a number of ways to reduce the Canopy
Constructor's runtime. The computationally most expensive part of the procedure is the
creation of precise spatial fits, because it involves the constant swapping of tree crown
variation across the whole plot. While this is crucial for spatial predictions of biomass
and forest structure, unbiased estimates of allometric scaling relationships may already
be possible with the initial, non-optimized canopy reconstruction. In this case, runtime

873 reduces to a few seconds and becomes executable on a desktop computer or within an R 874 package. Furthermore, the two goodness-of-fit metrics currently employed may not 875 yield the best convergence time towards a spatially accurate canopy reconstruction, and 876 the use of a single, feature-based pattern recognition metric such as Earth Mover's 877 Distance (Rubner et al., 2000) may be preferable. Similarly, the rudimentary rejection-878 based Approximate Bayesian Computation could also be replaced by sequential 879 approaches that converge more rapidly and can be analyzed with state-of-the-art tools 880 (Csilléry et al., 2012; Nunes and Prangle, 2015).

881 However, what the Canopy Constructor lacks in computational rapidity, it makes 882 up for in comprehensiveness. Where regression-based predictions address one question 883 at a time, the Canopy Constructor's individual-based approach infers a wide range of 884 canopy features simultaneously, most of which we have not explored in this study (e.g., 885 vertical stratification, tree overtopping, and exposure to wind, variation in tree densities 886 and clustering). Furthermore, the simulation-based approach and its Bayesian 887 framework render the integration of further data sources, such as hyperspectral imaging 888 or photogrammetry, relatively straightforward. Such data could extend the approach 889 even further in space and time and increase its precision (Dalponte and Coomes, 2016; 890 Goodbody et al., 2019; Vaglio Laurin et al., 2014), or make use of species-specific 891 properties to predict variation in leaf functional traits and community composition. The 892 consideration of repeated ALS acquisitions could yield individual-based estimates of 893 mortality and growth. And, since it models every individual tree down to 1 cm dbh, the 894 Canopy Constructor could also be used to calibrate and initialize vegetation models, 895 particularly the individual-based forest TROLL model on which much of its code is based 896 (Maréchaux and Chave, 2017), thus contributing to a model-data synthesis at global 897 scales (Shugart et al., 2015). This could provide a link between existing 3D

reconstruction approaches at local scales (Calders et al., 2018) and their extrapolation inspace via ALS.

900

901 Conclusion

902 Tropical forests account for over half of the carbon stored in live tissue (Pan et al., 903 2011), and mapping these stocks at high resolution is essential to assess the impact of 904 ongoing forest deforestation and degradation (Asner et al., 2010). One major challenge 905 of carbon mapping in tropical regions is that national forest inventories are missing and 906 that natural tropical forests are difficult to monitor using traditional forestry techniques 907 (Schimel et al., 2015). Mapping carbon stocks accurately is of prime importance in global 908 carbon cycle research because tropical deforestation is an important cause of 909 anthropogenic carbon dioxide emissions, and a likely cause of major climatic shifts 910 (Boisier et al., 2015; Nobre et al., 2016). The uncertainty of future anthropogenic 911 pressures and climatic changes in African rain forests (Malhi et al., 2013) as well as the 912 recent acceleration of deforestation in the Amazon can only increase the urgency of 913 providing accurate and repeated methods for carbon stock monitoring (Amigo, 2020). 914 The Canopy Constructor transforms information available at biomass validation 915 sites (sensu Duncanson et al., 2019) into virtual tree inventories that best match 916 empirically measured forest structure. This creates a unifying framework that brings 917 together traditionally separate fields, such as the demographics of plant communities, 918 their underlying physiological constraints and ecosystem functioning, and its results can 919 be used as input for the upscaling to global scales (Dubayah et al., 2020), for dynamic 920 vegetation modelling (F. J. Fischer et al., 2019) or for radiative transfer studies to test

921 how remote sensing signals interact with vegetation, especially radar applications

922 (Tebaldini et al., 2019). Such methods, creating virtual systems that mirror the

- 923 complexity of real systems, considerably increase our ability to predict future vegetation924 dynamics under increased human pressure and climatic changes.
- 925

926 **Declaration of competing interest**

927 The authors declare that they have no known competing financial interests or personal
928 relationships that could have appeared to influence the work reported in this paper.
929

930

931 Acknowledgements

932 We thank Isabelle Maréchaux for her helpful comments on an initial draft of the

933 manuscript. This work has benefitted from "Investissement d'Avenir" grants managed

934 by Agence Nationale de la Recherche (CEBA, ref. ANR-10-LABX-25-01; ANAEE-France:

935 ANR-11-INBS-0001, TULIP: ANR-10-LABX-0041), from CNES, and from ESA (CCI-

Biomass). This work was granted access to the HPC resources of CALMIP

937 supercomputing centre in Toulouse under allocation p17012. In Gabon, CENAREST

938 granted permission and provided personnel to establish and study the Rabi plot. Shell

939 Gabon, the society Compagnie des Bois du Gabon provided financial and logistical

940 support. ForestGEO provided technical advice and funding for fieldwork and data

analysis. This is contribution #193 of the Gabon Biodiversity Program.

943 Literature

- 944 Åkerblom, M., Raumonen, P., Mäkipää, R., Kaasalainen, M., 2017. Automatic tree species
- 945 recognition with quantitative structure models. Remote Sens. Environ. 191, 1–12.
- 946 https://doi.org/10.1016/j.rse.2016.12.002
- 947 Amigo, I., 2020. When will the Amazon hit a tipping point? Nature.
- 948 https://doi.org/10.1038/d41586-020-00508-4
- 949 Anderson-Teixeira, K.J., Davies, S.J., Bennett, A.C., Gonzalez-Akre, E.B., Muller-Landau,
- 950 H.C., Joseph Wright, S., Abu Salim, K., Almeyda Zambrano, A.M., Alonso, A., Baltzer,
- 951 J.L., Basset, Y., Bourg, N.A., Broadbent, E.N., Brockelman, W.Y., Bunyavejchewin, S.,
- 952 Burslem, D.F.R.P., Butt, N., Cao, M., Cardenas, D., Chuyong, G.B., Clay, K., Cordell, S.,
- 953 Dattaraja, H.S., Deng, X., Detto, M., Du, X., Duque, A., Erikson, D.L., Ewango, C.E.N.,
- 954 Fischer, G.A., Fletcher, C., Foster, R.B., Giardina, C.P., Gilbert, G.S., Gunatilleke, N.,
- 955 Gunatilleke, S., Hao, Z., Hargrove, W.W., Hart, T.B., Hau, B.C.H., He, F., Hoffman, F.M.,
- 956 Howe, R.W., Hubbell, S.P., Inman-Narahari, F.M., Jansen, P.A., Jiang, M., Johnson, D.J.,
- 957 Kanzaki, M., Kassim, A.R., Kenfack, D., Kibet, S., Kinnaird, M.F., Korte, L., Kral, K.,
- 958 Kumar, J., Larson, A.J., Li, Y., Li, X., Liu, S., Lum, S.K.Y., Lutz, J.A., Ma, K., Maddalena,
- 959 D.M., Makana, J.R., Malhi, Y., Marthews, T., Mat Serudin, R., Mcmahon, S.M., McShea,
- 960 W.J., Memiaghe, H.R., Mi, X., Mizuno, T., Morecroft, M., Myers, J.A., Novotny, V., de
- 961 Oliveira, A.A., Ong, P.S., Orwig, D.A., Ostertag, R., den Ouden, J., Parker, G.G., Phillips,
- 962 R.P., Sack, L., Sainge, M.N., Sang, W., Sri-ngernyuang, K., Sukumar, R., Sun, I.F.,
- 963 Sungpalee, W., Suresh, H.S., Tan, S., Thomas, S.C., Thomas, D.W., Thompson, J.,
- 964 Turner, B.L., Uriarte, M., Valencia, R., Vallejo, M.I., Vicentini, A., Vrška, T., Wang,
- 965 Xihua, Wang, Xugao, Weiblen, G., Wolf, A., Xu, H., Yap, S., Zimmerman, J., 2015a.
- 966 CTFS-ForestGEO: A worldwide network monitoring forests in an era of global
- 967 change. Glob. Chang. Biol. 21, 528–549. https://doi.org/10.1111/gcb.12712

- 968 Anderson-Teixeira, K.J., Mcgarvey, J.C., Muller-Landau, H.C., Park, J.Y., Gonzalez-Akre,
- 969 E.B., Herrmann, V., Bennett, A.C., So, C. V., Bourg, N.A., Thompson, J.R., Mcmahon,
- 970 S.M., Mcshea, W.J., 2015b. Size-related scaling of tree form and function in a mixed-
- 971 age forest. Funct. Ecol. 29, 1587–1602. https://doi.org/10.1111/1365-2435.12470
- 972 Antin, C., Pélissier, R., Vincent, G., Couteron, P., 2013. Crown allometries are less
- 973 responsive than stem allometry to tree size and habitat variations in an Indian
- 974 monsoon forest. Trees Struct. Funct. 27, 1485–1495.
- 975 https://doi.org/10.1007/s00468-013-0896-7
- 976 Asner, G.P., Mascaro, J., 2014. Mapping tropical forest carbon: Calibrating plot estimates
- 977 to a simple LiDAR metric. Remote Sens. Environ. 140, 614–624.
- 978 https://doi.org/10.1016/j.rse.2013.09.023
- 979 Asner, G.P., Powell, G.V.N., Mascaro, J., Knapp, D.E., Clark, J.K., Jacobson, J., Kennedy-
- 980 Bowdoin, T., Balaji, A., Paez-Acosta, G., Victoria, E., Secada, L., Valqui, M., Hughes,
- 981 R.F., 2010. High-resolution forest carbon stocks and emissions in the Amazon. Proc.
- 982 Natl. Acad. Sci. U. S. A. 107, 16738–16742.
- 983 https://doi.org/10.1073/pnas.1004875107
- 984 Atkins, J.W., Bohrer, G., Fahey, R.T., Hardiman, B.S., Morin, T.H., Stovall, A.E.L.,
- 285 Zimmerman, N., Gough, C.M., 2018. Quantifying vegetation and canopy structural
- 986 complexity from terrestrial LiDAR data using the forestr r package. Methods Ecol.
- 987 Evol. 9, 2057–2066. https://doi.org/10.1111/2041-210X.13061
- 988 Aubry-Kientz, M., Dutrieux, R., Ferraz, A., Saatchi, S., Hamraz, H., Williams, J., Coomes, D.,
- 989 Piboule, A., Vincent, G., 2019. A comparative assessment of the performance of
- 990 individual tree crowns delineation algorithms from ALS data in tropical forests.
- 991 Remote Sens. 11. https://doi.org/10.3390/rs11091086
- Babcock, C., Finley, A.O., Bradford, J.B., Kolka, R., Birdsey, R., Ryan, M.G., 2015. LiDAR

- based prediction of forest biomass using hierarchical models with spatially varying
- 994 coefficients. Remote Sens. Environ. 169, 113–127.
- 995 https://doi.org/10.1016/j.rse.2015.07.028
- 996 Bastin, J.F., Barbier, N., Réjou-Méchain, M., Fayolle, A., Gourlet-Fleury, S., Maniatis, D., De
- 997 Haulleville, T., Baya, F., Beeckman, H., Beina, D., Couteron, P., Chuyong, G., Dauby, G.,
- 998 Doucet, J.L., Droissart, V., Dufrêne, M., Ewango, C., Gillet, J.F., Gonmadje, C.H., Hart, T.,
- 999 Kavali, T., Kenfack, D., Libalah, M., Malhi, Y., Makana, J.R., Pélissier, R., Ploton, P.,
- 1000 Serckx, A., Sonké, B., Stevart, T., Thomas, D.W., De Cannière, C., Bogaert, J., 2015.
- 1001 Seeing Central African forests through their largest trees. Sci. Rep. 5.
- 1002 https://doi.org/10.1038/srep13156
- 1003 Beirne, C., Miao, Z., Nuñez, C.L., Medjibe, V.P., Saatchi, S., White, L.J.T., Poulsen, J.R., 2019.
- 1004 Landscape-level validation of allometric relationships for carbon stock estimation
- 1005 reveals bias driven by soil type. Ecol. Appl. https://doi.org/10.1002/eap.1987
- 1006 Blanchard, E., Birnbaum, P., Ibanez, T., Boutreux, T., Antin, C., Ploton, P., Vincent, G.,
- 1007 Pouteau, R., Vandrot, H., Hequet, V., Barbier, N., Droissart, V., Sonké, B., Texier, N.,
- 1008 Kamdem, N.G., Zebaze, D., Libalah, M., Couteron, P., 2016. Contrasted allometries
- 1009 between stem diameter, crown area, and tree height in five tropical biogeographic
- 1010 areas. Trees Struct. Funct. 30, 1953–1968. https://doi.org/10.1007/s00468-016-
- 1011 1424-3
- 1012 Boisier, J.P., Ciais, P., Ducharne, A., Guimberteau, M., 2015. Projected strengthening of
- 1013 Amazonian dry season by constrained climate model simulations. Nat. Clim. Chang.
- 1014 5, 656–660. https://doi.org/10.1038/nclimate2658
- 1015 Bohn, F.J., Huth, A., 2017. The importance of forest structure to biodiversity-productivity
- 1016 relationships. R. Soc. Open Sci. 4, 160521. https://doi.org/10.1098/rsos.160521
- 1017 Calders, K., Newnham, G., Burt, A., Murphy, S., Raumonen, P., Herold, M., Culvenor, D.,

- 1018 Avitabile, V., Disney, M., Armston, J., Kaasalainen, M., 2015. Nondestructive
- 1019 estimates of above-ground biomass using terrestrial laser scanning. Methods Ecol.
- 1020 Evol. 6, 198–208. https://doi.org/10.1111/2041-210X.12301
- 1021 Calders, K., Origo, N., Burt, A., Disney, M., Nightingale, J., Raumonen, P., Åkerblom, M.,
- 1022 Malhi, Y., Lewis, P., 2018. Realistic forest stand reconstruction from terrestrial
- 1023 LiDAR for radiative transfer modelling. Remote Sens. 10, 933.
- 1024 https://doi.org/10.3390/rs10060933
- 1025 Cano, I.M., Muller-Landau, H.C., Joseph Wright, S., Bohlman, S.A., Pacala, S.W., 2019.
- 1026 Tropical tree height and crown allometries for the Barro Colorado Nature
- 1027 Monument, Panama: A comparison of alternative hierarchical models incorporating
- 1028 interspecific variation in relation to life history traits. Biogeosciences 16, 847–862.
- 1029 https://doi.org/10.5194/bg-16-847-2019
- 1030 Chalom, A., Mandai, C., Prado, P., 2013. Sensitivity analyses: a brief tutorial with
- 1031 Rpackage pse. Cran.Rstudio.Com 1–14.
- 1032 Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a
- 1033 worldwide wood economics spectrum. Ecol. Lett. 12, 351–366.
- 1034 https://doi.org/10.1111/j.1461-0248.2009.01285.x
- 1035 Chave, J., Olivier, J., Bongers, F., Châtelet, P., Forget, P.-M., van der Meer, P., Norden, N.,
- 1036 Riéra, B., Charles-Dominique, P., 2008a. Above-ground biomass and productivity in
- a rain forest of eastern South America. J. Trop. Ecol. 24, 355–366.
- 1038 https://doi.org/10.1017/s0266467408005075
- 1039 Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C.,
- 1040 Duque, A., Eid, T., Fearnside, P.M., Goodman, R.C., Henry, M., Martínez-Yrízar, A.,
- 1041 Mugasha, W.A., Muller-Landau, H.C., Mencuccini, M., Nelson, B.W., Ngomanda, A.,
- 1042 Nogueira, E.M., Ortiz-Malavassi, E., Pélissier, R., Ploton, P., Ryan, C.M., Saldarriaga,

- 1043 J.G., Vieilledent, G., 2014. Improved allometric models to estimate the aboveground
- 1044 biomass of tropical trees. Glob. Chang. Biol. 20, 3177–3190.
- 1045 https://doi.org/10.1111/gcb.12629
- 1046 Chazdon, R.L., Broadbent, E.N., Rozendaal, D.M.A., Bongers, F., Zambrano, A.M.A., Aide,
- 1047 T.M., Balvanera, P., Becknell, J.M., Boukili, V., Brancalion, P.H.S., Craven, D., Almeida-
- 1048 Cortez, J.S., Cabral, G.A.L., De Jong, B., Denslow, J.S., Dent, D.H., DeWalt, S.J., Dupuy,
- 1049 J.M., Durán, S.M., Espírito-Santo, M.M., Fandino, M.C., César, R.G., Hall, J.S.,
- 1050 Hernández-Stefanoni, J.L., Jakovac, C.C., Junqueira, A.B., Kennard, D., Letcher, S.G.,
- 1051 Lohbeck, M., Martínez-Ramos, M., Massoca, P., Meave, J.A., Mesquita, R., Mora, F.,
- 1052 Muñoz, R., Muscarella, R., Nunes, Y.R.F., Ochoa-Gaona, S., Orihuela-Belmonte, E.,
- 1053 Peña-Claros, M., Pérez-García, E.A., Piotto, D., Powers, J.S., Rodríguez-Velazquez, J.,
- 1054 Romero-Pérez, I.E., Ruíz, J., Saldarriaga, J.G., Sanchez-Azofeifa, A., Schwartz, N.B.,
- 1055 Steininger, M.K., Swenson, N.G., Uriarte, M., Van Breugel, M., Van Der Wal, H., Veloso,
- 1056 M.D.M., Vester, H., Vieira, I.C.G., Bentos, T.V., Williamson, G.B., Poorter, L., 2016.
- 1057 Carbon sequestration potential of second-growth forest regeneration in the Latin
- 1058 American tropics. Sci. Adv. 2, e1501639. https://doi.org/10.1126/sciadv.1501639
- 1059 Condit, R., 1998. Tropical Forest Census Plots, Tropical Forest Census Plots.
- 1060 https://doi.org/10.1007/978-3-662-03664-8
- 1061 Coomes, D.A., Asner, G.P., Lewis, S.L., Dalponte, M., Phillips, O.L., Qie, L., Nilus, R., Phua,
- 1062 M.-H., Banin, L.F., Burslem, D.F.R.P., Jucker, T., 2017. Area-based vs tree-centric
- 1063 approaches to mapping forest carbon in Southeast Asian forests from airborne laser
- scanning data. Remote Sens. Environ. 194, 77–88.
- 1065 https://doi.org/10.1016/j.rse.2017.03.017
- 1066 Coomes, D.A., Duncan, R.P., Allen, R.B., Truscott, J., 2003. Disturbances prevent stem size-
- 1067 density distributions in natural forests from following scaling relationships. Ecol.

- 1068 Lett. 6, 980–989. https://doi.org/10.1046/j.1461-0248.2003.00520.x
- 1069 Csilléry, K., Blum, M.G.B., Gaggiotti, O.E., François, O., 2010. Approximate Bayesian
- 1070 Computation (ABC) in practice. Trends Ecol. Evol.
- 1071 https://doi.org/10.1016/j.tree.2010.04.001
- 1072 Csilléry, K., François, O., Blum, M.G.B., 2012. Abc: An R package for approximate Bayesian
- 1073 computation (ABC). Methods Ecol. Evol. 3, 475–479.
- 1074 https://doi.org/10.1111/j.2041-210X.2011.00179.x
- 1075 Dalponte, M., Coomes, D.A., 2016. Tree-centric mapping of forest carbon density from
- 1076 airborne laser scanning and hyperspectral data. Methods Ecol. Evol. 7, 1236–1245.
- 1077 https://doi.org/10.1111/2041-210X.12575
- 1078 Davis, K.T., Dobrowski, S.Z., Holden, Z.A., Higuera, P.E., Abatzoglou, J.T., 2019.
- 1079 Microclimatic buffering in forests of the future: the role of local water balance.
- 1080 Ecography (Cop.). 42, 1–11. https://doi.org/10.1111/ecog.03836
- 1081 DeRose, R.J., Long, J.N., 2014. Resistance and Resilience: A Conceptual Framework for
- 1082 Silviculture. For. Sci. 60, 1205–1212. https://doi.org/10.5849/forsci.13-507
- 1083 Disney, M., 2019. Terrestrial LiDAR: a three-dimensional revolution in how we look at
- 1084 trees. New Phytol. 222, 1736–1741. https://doi.org/10.1111/nph.15517
- 1085 Dassot, M., Constant, T., Fournier, M., 2011. The use of terrestrial LiDAR technology in
- 1086 forest science: Application fields, benefits and challenges. Ann. For. Sci. 68, 959–
- 1087 974. https://doi.org/10.1007/s13595-011-0102-2
- 1088 Dowle, M., Srinivasan, A., 2018. data.table: Extension of "data.frame". R package version
- 1089 1.11.2. https://cran.r-project.org/package=data.table.
- 1090 Dubayah, R., Blair, J.B., Goetz, S., Fatoyinbo, L., Hansen, M., Healey, S., Hofton, M., Hurtt, G.,
- 1091 Kellner, J., Luthcke, S., Armston, J., Tang, H., Duncanson, L., Hancock, S., Jantz, P.,
- 1092 Marselis, S., Patterson, P., Qi, W., Silva, C., 2020. The Global Ecosystem Dynamics

- 1093 Investigation: High-resolution laser ranging of the Earth's forests and topography.
- 1094 Sci. Remote Sens. 100002. https://doi.org/10.1016/j.srs.2020.100002
- 1095 Duncanson, L., Armston, J., Disney, M., Avitabile, V., Barbier, N., Calders, K., Carter, S.,
- 1096 Chave, J., Herold, M., Crowther, T.W., Falkowski, M., Kellner, J.R., Labrière, N., Lucas,
- 1097 R., MacBean, N., McRoberts, R.E., Meyer, V., Næsset, E., Nickeson, J.E., Paul, K.I.,
- 1098 Phillips, O.L., Réjou-Méchain, M., Román, M., Roxburgh, S., Saatchi, S.,
- 1099 Schepaschenko, D., Scipal, K., Siqueira, P.R., Whitehurst, A., Williams, M., 2019. The
- 1100 Importance of Consistent Global Forest Aboveground Biomass Product Validation.
- 1101 Surv. Geophys. 40, 979–999. https://doi.org/10.1007/s10712-019-09538-8
- 1102 Engone Obiang, N.L., Kenfack, D., Picard, N., Lutz, J.A., Bissiengou, P., Memiaghe, H.R.,
- 1103 Alonso, A., 2019. Determinants of spatial patterns of canopy tree species in a
- tropical evergreen forest in Gabon. J. Veg. Sci. 30, 929–939.
- 1105 https://doi.org/10.1111/jvs.12778
- 1106 Farrior, C.E., Bohlman, S.A., Hubbell, S., Pacala, S.W., 2016. Dominance of the suppressed:
- 1107 Power-law size structure in tropical forests. Science 351, 155–157.
- 1108 https://doi.org/10.1126/science.aad0592
- 1109 Fassnacht, F.E., Latifi, H., Hartig, F., 2018. Using synthetic data to evaluate the benefits of
- 1110 large field plots for forest biomass estimation with LiDAR. Remote Sens. Environ.
- 1111 213, 115–128. https://doi.org/10.1016/j.rse.2018.05.007
- 1112 Fatoyinbo, L., Pinto, N., Hofton, M., Simard, M., Blair, B., Saatchi, S., Lou, Y., Dubayah, R.,
- 1113 Hensley, S., Armston, J., Duncanson, L., Lavalle, M., 2017. The 2016 NASA AfriSAR
- 1114 campaign: Airborne SAR and Lidar measurements of tropical forest structure and
- biomass in support of future satellite missions, in: International Geoscience and
- 1116 Remote Sensing Symposium (IGARSS). pp. 4286–4287.
- 1117 https://doi.org/10.1109/IGARSS.2017.8127949

1118	Feldpausch, T.R., Lloyd, J., Lewis, S.L., Brienen, R.J.W., Gloor, M., Monteagudo Mendoza, A.,
1119	Lopez-Gonzalez, G., Banin, L., Abu Salim, K., Affum-Baffoe, K., Alexiades, M., Almeida,
1120	S., Amaral, I., Andrade, A., Aragão, L.E.O.C., Araujo Murakami, A., Arets, E.J.M.,
1121	Arroyo, L., Aymard C., G.A., Baker, T.R., Bánki, O.S., Berry, N.J., Cardozo, N., Chave, J.,
1122	Comiskey, J.A., Alvarez, E., De Oliveira, A., Di Fiore, A., Djagbletey, G., Domingues,
1123	T.F., Erwin, T.L., Fearnside, P.M., França, M.B., Freitas, M.A., Higuchi, N., Honorio C.,
1124	E., Iida, Y., Jiménez, E., Kassim, A.R., Killeen, T.J., Laurance, W.F., Lovett, J.C., Malhi, Y.,
1125	Marimon, B.S., Marimon-Junior, B.H., Lenza, E., Marshall, A.R., Mendoza, C., Metcalfe,
1126	D.J., Mitchard, E.T.A., Neill, D.A., Nelson, B.W., Nilus, R., Nogueira, E.M., Parada, A., S
1127	H. Peh, K., Pena Cruz, A., Peñuela, M.C., Pitman, N.C.A., Prieto, A., Quesada, C.A.,
1128	Ramírez, F., Ramírez-Angulo, H., Reitsma, J.M., Rudas, A., Saiz, G., Salomão, R.P.,
1129	Schwarz, M., Silva, N., Silva-Espejo, J.E., Silveira, M., Sonké, B., Stropp, J., Taedoumg,
1130	H.E., Tan, S., Ter Steege, H., Terborgh, J., Torello-Raventos, M., Van Der Heijden,
1131	G.M.F., Vásquez, R., Vilanova, E., Vos, V.A., White, L., Willcock, S., Woell, H., Phillips,
1132	O.L., 2012. Tree height integrated into pantropical forest biomass estimates.
1133	Biogeosciences 9, 3381–3403. https://doi.org/10.5194/bg-9-3381-2012
1134	Ferraz, A., Saatchi, S., Mallet, C., Meyer, V., 2016. Lidar detection of individual tree size in
1135	tropical forests. Remote Sens. Environ. 183, 318–333.
1136	https://doi.org/10.1016/j.rse.2016.05.028
1137	Fischer, F.J., Maréchaux, I., Chave, J., 2019. Improving plant allometry by fusing forest
1138	models and remote sensing. New Phytol. 223, 1159–1165.
1139	https://doi.org/10.1111/nph.15810
1140	Fischer, R., Knapp, N., Bohn, F., Shugart, H.H., Huth, A., 2019. The Relevance of Forest
1141	Structure for Biomass and Productivity in Temperate Forests: New Perspectives for
1142	Remote Sensing. Surv. Geophys. 1–26. https://doi.org/10.1007/s10712-019-

1143 09519-x

1144	Garnier, S., 2018. viridis: Default Color Maps from "matplotlib." R Packag. version 0.5.1.

- 1145 Goetz, S.J., Steinberg, D., Betts, M.G., Holmes, R.T., Doran, P.J., Dubayah, R., Hofton, M.,
- 1146 2010. Lidar remote sensing variables predict breeding habitat of a Neotropical
- 1147 migrant bird. Ecology 91, 1569–1576. https://doi.org/10.1890/09-1670.1
- 1148 Goodbody, T.R.H., Coops, N.C., White, J.C., 2019. Digital Aerial Photogrammetry for
- 1149 Updating Area-Based Forest Inventories: A Review of Opportunities, Challenges,
- and Future Directions. Curr. For. Reports. https://doi.org/10.1007/s40725-019-
- 1151 00087-2
- 1152 Grassi, G., House, J., Dentener, F., Federici, S., Den Elzen, M., Penman, J., 2017. The key
- role of forests in meeting climate targets requires science for credible mitigation.

1154 Nat. Clim. Chang. 7, 220–226. https://doi.org/10.1038/nclimate3227

- 1155 Hartig, F., Calabrese, J.M., Reineking, B., Wiegand, T., Huth, A., 2011. Statistical inference
- for stochastic simulation models theory and application. Ecol. Lett. 14, 816–827.
- 1157 https://doi.org/10.1111/j.1461-0248.2011.01640.x
- 1158 Hartig, F., Dislich, C., Wiegand, T., Huth, A., 2014. Technical note: Approximate bayesian
- 1159 parameterization of a process-based tropical forest model. Biogeosciences 11,

1160 1261–1272. https://doi.org/10.5194/bg-11-1261-2014

- 1161 Henry, H.A.L., Aarssen, L.W., 1999. The interpretation of stem diameter-height allometry
- in trees: Biomechanical constraints, neighbour effects, or biased regressions? Ecol.
- 1163 Lett. 2, 89–97. https://doi.org/10.1046/j.1461-0248.1999.22054.x
- Hijmans, R.J., 2016. raster: Geographic Data Analysis and Modeling. R package version2.5-8. R Packag.
- 1166 Hill, R.W., Holland, P.W., 1977. Two Robust Alternatives to Least-Squares Regression. J.
- 1167 Am. Stat. Assoc. 72, 828–833. https://doi.org/10.2307/2286469

- 1168 Hurtt, G.C., Dubayah, R., Drake, J., Moorcroft, P.R., Pacala, S.W., Blair, J.B., Fearon, M.G.,
- 1169 2004. Beyond potential vegetation: Combining lidar data and a height-structured
- 1170 model for carbon studies. Ecol. Appl. 14, 873–883. https://doi.org/10.1890/02-
- 1171 5317
- Hyyppä, J., Inkinen, M., 1999. Detecting and estimating attributes for single trees using
 laser scanner. Photogramm. J. Finl. 16, 27–42.
- 1174 Inman, H.F., Bradley, E.L., 1989. The Overlapping Coefficient as a Measure of Agreement
- 1175 Between Probability Distributions and Point Estimation of the Overlap of two
- 1176 Normal Densities. Commun. Stat. Theory Methods 18, 3851–3874.
- 1177 https://doi.org/10.1080/03610928908830127
- 1178 Isenburg, M., 2018. LAStools efficient LiDAR processing software.
- 1179 Jucker, T., Bouriaud, O., Coomes, D.A., 2015. Crown plasticity enables trees to optimize
- 1180 canopy packing in mixed-species forests. Funct. Ecol. 29, 1078–1086.
- 1181 https://doi.org/10.1111/1365-2435.12428
- 1182 Jucker, T., Caspersen, J., Chave, J., Antin, C., Barbier, N., Bongers, F., Dalponte, M., van
- 1183 Ewijk, K.Y., Forrester, D.I., Haeni, M., Higgins, S.I., Holdaway, R.J., Iida, Y., Lorimer, C.,
- 1184 Marshall, P.L., Momo, S., Moncrieff, G.R., Ploton, P., Poorter, L., Rahman, K.A.,
- 1185 Schlund, M., Sonké, B., Sterck, F.J., Trugman, A.T., Usoltsev, V.A., Vanderwel, M.C.,
- 1186 Waldner, P., Wedeux, B.M.M., Wirth, C., Wöll, H., Woods, M., Xiang, W., Zimmermann,
- 1187 N.E., Coomes, D.A., 2017. Allometric equations for integrating remote sensing
- imagery into forest monitoring programmes. Glob. Chang. Biol. 23, 177–190.
- 1189 https://doi.org/10.1111/gcb.13388
- 1190 Kattge, J., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönisch, G., Garnier, E., Westoby,
- 1191 M., Reich, P.B., Wright, I.J., Cornelissen, J.H.C., Violle, C., Harrison, S.P., Van Bodegom,
- 1192 P.M., Reichstein, M., Enquist, B.J., Soudzilovskaia, N.A., Ackerly, D.D., Anand, M.,

1193	Atkin, O., Bahn, M., Baker, T.R., Baldocchi, D., Bekker, R., Blanco, C.C., Blonder, B.,
1194	Bond, W.J., Bradstock, R., Bunker, D.E., Casanoves, F., Cavender-Bares, J., Chambers,
1195	J.Q., Chapin, F.S., Chave, J., Coomes, D., Cornwell, W.K., Craine, J.M., Dobrin, B.H.,
1196	Duarte, L., Durka, W., Elser, J., Esser, G., Estiarte, M., Fagan, W.F., Fang, J., Fernández-
1197	Méndez, F., Fidelis, A., Finegan, B., Flores, O., Ford, H., Frank, D., Freschet, G.T.,
1198	Fyllas, N.M., Gallagher, R. V., Green, W.A., Gutierrez, A.G., Hickler, T., Higgins, S.I.,
1199	Hodgson, J.G., Jalili, A., Jansen, S., Joly, C.A., Kerkhoff, A.J., Kirkup, D., Kitajima, K.,
1200	Kleyer, M., Klotz, S., Knops, J.M.H., Kramer, K., Kühn, I., Kurokawa, H., Laughlin, D.,
1201	Lee, T.D., Leishman, M., Lens, F., Lenz, T., Lewis, S.L., Lloyd, J., Llusià, J., Louault, F.,
1202	Ma, S., Mahecha, M.D., Manning, P., Massad, T., Medlyn, B.E., Messier, J., Moles, A.T.,
1203	Müller, S.C., Nadrowski, K., Naeem, S., Niinemets, Ü., Nöllert, S., Nüske, A., Ogaya, R.,
1204	Oleksyn, J., Onipchenko, V.G., Onoda, Y., Ordoñez, J., Overbeck, G., Ozinga, W.A.,
1205	Patiño, S., Paula, S., Pausas, J.G., Peñuelas, J., Phillips, O.L., Pillar, V., Poorter, H.,
1206	Poorter, L., Poschlod, P., Prinzing, A., Proulx, R., Rammig, A., Reinsch, S., Reu, B.,
1207	Sack, L., Salgado-Negret, B., Sardans, J., Shiodera, S., Shipley, B., Siefert, A., Sosinski,
1208	E., Soussana, J.F., Swaine, E., Swenson, N., Thompson, K., Thornton, P., Waldram, M.,
1209	Weiher, E., White, M., White, S., Wright, S.J., Yguel, B., Zaehle, S., Zanne, A.E., Wirth,
1210	C., 2011. TRY - a global database of plant traits. Glob. Chang. Biol. 17, 2905–2935.
1211	https://doi.org/10.1111/j.1365-2486.2011.02451.x
1212	Khosravipour, A., Skidmore, A.K., Isenburg, M., Wang, T., Hussin, Y.A., 2014. Generating
1213	Pit-free Canopy Height Models from Airborne Lidar. Photogramm. Eng. Remote
1214	Sens. 80, 863–872. https://doi.org/10.14358/PERS.80.9.863

1215 King, D.A., 1996. Allometry and life history of tropical trees. J. Trop. Ecol. 12, 25–44.

1216 https://doi.org/10.1017/s0266467400009299

1217 Knapp, N., Fischer, R., Huth, A., 2018. Linking lidar and forest modeling to assess

- 1218 biomass estimation across scales and disturbance states. Remote Sens. Environ.
- 1219 205, 199–209. https://doi.org/10.1016/j.rse.2017.11.018
- 1220 Labriere, N., Tao, S., Chave, J., Scipal, K., Toan, T. Le, Abernethy, K., Alonso, A., Barbier, N.,
- 1221 Bissiengou, P., Casal, T., Davies, S.J., Ferraz, A., Herault, B., Jaouen, G., Jeffery, K.J.,
- 1222 Kenfack, D., Korte, L., Lewis, S.L., Malhi, Y., Memiaghe, H.R., Poulsen, J.R., Rejou-
- 1223 Mechain, M., Villard, L., Vincent, G., White, L.J.T., Saatchi, S., 2018. In Situ Reference
- 1224 Datasets from the TropiSAR and AfriSAR Campaigns in Support of Upcoming
- 1225 Spaceborne Biomass Missions. IEEE J. Sel. Top. Appl. Earth Obs. Remote Sens. 11,
- 1226 3617–3627. https://doi.org/10.1109/JSTARS.2018.2851606
- 1227 Lau, A., Martius, C., Bartholomeus, H., Shenkin, A., Jackson, T., Malhi, Y., Herold, M.,
- 1228 Bentley, L.P., 2019. Estimating architecture-based metabolic scaling exponents of
- tropical trees using terrestrial LiDAR and 3D modelling. For. Ecol. Manage. 439,
- 1230 132–145. https://doi.org/10.1016/j.foreco.2019.02.019
- 1231 Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A., Ribeiro, J.E.L.S., Giraldo,
- 1232 J.P., Lovejoy, T.E., Condit, R., Chave, J., Harms, K.E., D'Angelo, S., 2006. Rapid decay of
- 1233 tree-community composition in Amazonian forest fragments. Proc. Natl. Acad. Sci.
- 1234 U. S. A. 103, 19010–19014. https://doi.org/10.1073/pnas.0609048103
- 1235 Le Toan, T., Quegan, S., Davidson, M.W.J., Balzter, H., Paillou, P., Papathanassiou, K.,
- 1236 Plummer, S., Rocca, F., Saatchi, S., Shugart, H., Ulander, L., 2011. The BIOMASS
- 1237 mission: Mapping global forest biomass to better understand the terrestrial carbon
- 1238 cycle. Remote Sens. Environ. 115, 2850–2860.
- 1239 https://doi.org/10.1016/j.rse.2011.03.020
- 1240 Levick, S.R., Asner, G.P., 2013. The rate and spatial pattern of treefall in a savanna
- 1241 landscape. Biol. Conserv. 157, 121–127.
- 1242 https://doi.org/10.1016/j.biocon.2012.07.009

1243	Lewis, S.L., Edwards, D.P., Galbraith, D., 2015. Increasing human dominance of tropical
1244	forests. Science 349, 827 – 832. https://doi.org/10.1126/science.aaa9932
1245	Lines, E.R., Zavala, M.A., Purves, D.W., Coomes, D.A., 2012. Predictable changes in
1246	aboveground allometry of trees along gradients of temperature, aridity and
1247	competition. Glob. Ecol. Biogeogr. 21, 1017–1028. https://doi.org/10.1111/j.1466-
1248	8238.2011.00746.x
1249	Lutz, J.A., Furniss, T.J., Johnson, D.J., Davies, S.J., Allen, D., Alonso, A., Anderson-Teixeira,
1250	K.J., Andrade, A., Baltzer, J., Becker, K.M.L., Blomdahl, E.M., Bourg, N.A.,
1251	Bunyavejchewin, S., Burslem, D.F.R.P., Cansler, C.A., Cao, K., Cao, M., Cárdenas, D.,
1252	Chang, L.W., Chao, K.J., Chao, W.C., Chiang, J.M., Chu, C., Chuyong, G.B., Clay, K.,
1253	Condit, R., Cordell, S., Dattaraja, H.S., Duque, A., Ewango, C.E.N., Fischer, G.A.,
1254	Fletcher, C., Freund, J.A., Giardina, C., Germain, S.J., Gilbert, G.S., Hao, Z., Hart, T., Hau,
1255	B.C.H., He, F., Hector, A., Howe, R.W., Hsieh, C.F., Hu, Y.H., Hubbell, S.P., Inman-
1256	Narahari, F.M., Itoh, A., Janík, D., Kassim, A.R., Kenfack, D., Korte, L., Král, K., Larson,
1257	A.J., Li, Y. De, Lin, Y., Liu, S., Lum, S., Ma, K., Makana, J.R., Malhi, Y., McMahon, S.M.,
1258	McShea, W.J., Memiaghe, H.R., Mi, X., Morecroft, M., Musili, P.M., Myers, J.A., Novotny,
1259	V., de Oliveira, A., Ong, P., Orwig, D.A., Ostertag, R., Parker, G.G., Patankar, R., Phillips,
1260	R.P., Reynolds, G., Sack, L., Song, G.Z.M., Su, S.H., Sukumar, R., Sun, I.F., Suresh, H.S.,
1261	Swanson, M.E., Tan, S., Thomas, D.W., Thompson, J., Uriarte, M., Valencia, R.,
1262	Vicentini, A., Vrška, T., Wang, X., Weiblen, G.D., Wolf, A., Wu, S.H., Xu, H., Yamakura,
1263	T., Yap, S., Zimmerman, J.K., 2018. Global importance of large-diameter trees. Glob.
1264	Ecol. Biogeogr. 27, 849–864. https://doi.org/10.1111/geb.12747
1265	Lutz, J.A., Larson, A.J., Freund, J.A., Swanson, M.E., Bible, K.J., 2013. The importance of
1266	large-diameter trees to forest structural heterogeneity. PLoS One 8.

1267 https://doi.org/10.1371/journal.pone.0082784

- 1268 Maréchaux, I., Chave, J., 2017. An individual-based forest model to jointly simulate
- 1269 carbon and tree diversity in Amazonia: description and applications. Ecol. Monogr.

1270 87, 632–664. https://doi.org/10.1002/ecm.1271

- 1271 Mascaro, J., Detto, M., Asner, G.P., Muller-Landau, H.C., 2011. Evaluating uncertainty in
- 1272 mapping forest carbon with airborne LiDAR. Remote Sens. Environ. 115, 3770–
- 1273 3774. https://doi.org/10.1016/j.rse.2011.07.019
- 1274 Malhi, Y., Adu-Bredu, S., Asare, R.A., Lewis, S.L., Mayaux, P., 2013. African rainforests:

1275 Past, present and future. Philos. Trans. R. Soc. B Biol. Sci.

- 1276 https://doi.org/10.1098/rstb.2012.0312
- 1277 Memiaghe, H.R., Lutz, J.A., Korte, L., Alonso, A., Kenfack, D., 2016. Ecological Importance
- 1278 of Small-Diameter Trees to the Structure, Diversity and Biomass of a Tropical
- 1279 Evergreen Forest at Rabi, Gabon. PLoS One 11.
- 1280 https://doi.org/10.1371/journal.pone.0154988
- 1281 Meyer, V., Saatchi, S., Clark, D.B., Keller, M., Vincent, G., Ferraz, A., Espírito-Santo, F.,
- 1282 D'Oliveira, M.V.N., Kaki, D., Chave, J., 2018. Canopy Area of Large Trees Explains
- 1283 Aboveground Biomass Variations across Nine Neotropical Forest Landscapes.
- 1284 Biogeosciences Discuss. 1–38. https://doi.org/10.5194/bg-2017-547
- 1285 Molto, Q., Hérault, B., Boreux, J.J., Daullet, M., Rousteau, A., Rossi, V., 2014. Predicting tree
- 1286 heights for biomass estimates in tropical forests -A test from French Guiana.
- 1287 Biogeosciences 11, 3121–3130. https://doi.org/10.5194/bg-11-3121-2014
- 1288 Momo Takoudjou, S., Ploton, P., Sonké, B., Hackenberg, J., Griffon, S., Coligny, F., Kamdem,
- 1289 N.G., Libalah, M., Mofack, G.I.I., Le Moguédec, G., Pélissier, R., Barbier, N., 2017. Using
- 1290 terrestrial laser scanning data to estimate large tropical trees biomass and calibrate
- allometric models: A comparison with traditional destructive approach. Methods
- 1292 Ecol. Evol. 9, 905–916. https://doi.org/10.1111/2041-210X.12933

- 1293 Morsdorf, F., Meier, E., Kötz, B., Itten, K.I., Dobbertin, M., Allgöwer, B., 2004. LIDAR-based
- 1294 geometric reconstruction of boreal type forest stands at single tree level for forest
- and wildland fire management, in: Remote Sensing of Environment. pp. 353–362.

1296 https://doi.org/10.1016/j.rse.2004.05.013

- 1297 Muller-Landau, H.C., Condit, R.S., Harms, K.E., Marks, C.O., Thomas, S.C., Bunyavejchewin,
- 1298 S., Chuyong, G., Co, L., Davies, S., Foster, R., Gunatilleke, S., Gunatilleke, N., Hart, T.,
- 1299 Hubbell, S.P., Itoh, A., Kassim, A.R., Kenfack, D., LaFrankie, J. V., Lagunzad, D., Lee,
- 1300 H.S., Losos, E., Makana, J.R., Ohkubo, T., Samper, C., Sukumar, R., Sun, I.F., Nur
- 1301 Supardi, M.N., Tan, S., Thomas, D., Thompson, J., Valencia, R., Vallejo, M.I., Muñoz,
- 1302 G.V., Yamakura, T., Zimmerman, J.K., Dattaraja, H.S., Esufali, S., Hall, P., He, F.,
- 1303 Hernandez, C., Kiratiprayoon, S., Suresh, H.S., Wills, C., Ashton, P., 2006. Comparing
- 1304 tropical forest tree size distributions with the predictions of metabolic ecology and
- 1305 equilibrium models. Ecol. Lett. 9, 589–602. https://doi.org/10.1111/j.1461-
- 1306 0248.2006.00915.x
- 1307 Næsset, E., 2002. Predicting forest stand characteristics with airborne scanning laser
- 1308 using a practical two-stage procedure and field data. Remote Sens. Environ. 80, 88–
- 1309 99. https://doi.org/10.1016/S0034-4257(01)00290-5

1310 Newnham, G.J., Armston, J.D., Calders, K., Disney, M.I., Lovell, J.L., Schaaf, C.B., Strahler,

- 1311 A.H., Mark Danson, F., 2015. Terrestrial laser scanning for plot-scale forest
- 1312 measurement. Curr. For. Reports 1, 239–251. https://doi.org/10.1007/s40725-
- 1313 015-0025-5
- Niklas, K.J., 1994. Plant allometry: the scaling of form and process. University of ChicagoPress.
- 1316 Niklas, K.J., 2007. Maximum plant height and the biophysical factors that limit it, in: Tree
- 1317 Physiology. pp. 433–440. https://doi.org/10.1093/treephys/27.3.433

- 1318 Niklas, K.J., Midgley, J.J., Enquist, B.J., 2003. A general model for mass-growth-density
- relations across tree-dominated communities. Evol. Ecol. Res. 5, 459–468.
- 1320 Nobre, C.A., Sampaio, G., Borma, L.S., Castilla-Rubio, J.C., Silva, J.S., Cardoso, M., 2016.
- 1321 Land-use and climate change risks in the amazon and the need of a novel
- 1322 sustainable development paradigm. Proc. Natl. Acad. Sci. U. S. A. 113, 10759–10768.
- 1323 https://doi.org/10.1073/pnas.1605516113
- Nunes, M., Prangle, D., 2015. abctools : An R Package for Tuning Approximate Bayesian
 Computation Analyses. R J. 7, 1–16.
- 1326 Oldeman, R., 1974. The architecture of the forest of French Guiana. L'architecture de la
- 1327 foret Guyanaise, Memoires-ORSTOM. ORSTOM.
- 1328 Palace, M.W., Sullivan, F.B., Ducey, M.J., Treuhaft, R.N., Herrick, C., Shimbo, J.Z., Mota-E-
- 1329 Silva, J., 2015. Estimating forest structure in a tropical forest using field
- 1330 measurements, a synthetic model and discrete return lidar data. Remote Sens.
- 1331 Environ. 161, 1–11. https://doi.org/10.1016/j.rse.2015.01.020
- 1332 Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L.,
- 1333 Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire,
- 1334 A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A Large and Persistent Carbon
- 1335 Sink in the World's Forests. Science (80-.). 333, 988 LP 993.
- 1336 https://doi.org/10.1126/science.1201609
- 1337 Pan, Y., Birdsey, R.A., Phillips, O.L., Jackson, R.B., 2013. The Structure, Distribution, and
- Biomass of the World's Forests. Annu. Rev. Ecol. Evol. Syst. 44, 593–622.
- 1339 https://doi.org/10.1146/annurev-ecolsys-110512-135914
- 1340 Poncy, O., Sabatier, D., Prévost, M.F., Hardy, I., 2001. The Lowland High Rainforest:
- 1341 Structure and Tree Species Diversity, in: Bongers, F., Charles-Dominique, P., Forget,
- 1342 P.M., Théry, M. (Eds.), Nouragues. Monographiae Biologicae, Vol 80. Springer,

1343 Dordrecht, pp. 31–46.

- Poorter, L., Bongers, L., Bongers, F., 2006. Architecture of 54 moist-forest tree species:
 Traits, trade-offs, and functional groups. Ecology 87, 1289–1301.
- 1346 Pretzsch, H., 2014. Canopy space filling and tree crown morphology in mixed-species
- 1347 stands compared with monocultures. For. Ecol. Manage. 327, 251–264.
- 1348 https://doi.org/10.1016/j.foreco.2014.04.027
- 1349 Pretzsch, H., Dieler, J., 2012. Evidence of variant intra- and interspecific scaling of tree
- 1350 crown structure and relevance for allometric theory. Oecologia 169, 637–649.
- 1351 https://doi.org/10.1007/s00442-011-2240-5
- 1352 Purves, D.W., Lichstein, J.W., Strigul, N., Pacala, S.W., 2008. Predicting and understanding
- 1353 forest dynamics using a simple tractable model. Proc. Natl. Acad. Sci. 105, 17018–
- 1354 17022. https://doi.org/10.1073/pnas.0807754105
- 1355 Pyörälä, J., Saarinen, N., Kankare, V., Coops, N.C., Liang, X., Wang, Y., Holopainen, M.,
- 1356 Hyyppä, J., Vastaranta, M., 2019. Variability of wood properties using airborne and
- 1357 terrestrial laser scanning. Remote Sens. Environ. 235.
- 1358 https://doi.org/10.1016/j.rse.2019.111474
- 1359 R Development Core Team, 2019. R: A Language and Environment for Statistical
- 1360 Computing. R Found. Stat. Comput. https://doi.org/10.1007/978-3-540-74686-7
- 1361 Réjou-Méchain, M., Muller-Landau, H.C., Detto, M., Thomas, S.C., Le Toan, T., Saatchi, S.S.,
- 1362 Barreto-Silva, J.S., Bourg, N.A., Bunyavejchewin, S., Butt, N., Brockelman, W.Y., Cao,
- 1363 M., Cárdenas, D., Chiang, J.M., Chuyong, G.B., Clay, K., Condit, R., Dattaraja, H.S.,
- 1364 Davies, S.J., Duque, A., Esufali, S., Ewango, C., Fernando, R.H.S., Fletcher, C.D., N.
- 1365 Gunatilleke, I.A.U., Hao, Z., Harms, K.E., Hart, T.B., Hérault, B., Howe, R.W., Hubbell,
- 1366 S.P., Johnson, D.J., Kenfack, D., Larson, A.J., Lin, L., Lin, Y., Lutz, J.A., Makana, J.R.,
- 1367 Malhi, Y., Marthews, T.R., Mcewan, R.W., Mcmahon, S.M., Mcshea, W.J., Muscarella,

- 1368 R., Nathalang, A., Noor, N.S.M., Nytch, C.J., Oliveira, A.A., Phillips, R.P.,
- 1369 Pongpattananurak, N., Punchi-Manage, R., Salim, R., Schurman, J., Sukumar, R.,
- 1370 Suresh, H.S., Suwanvecho, U., Thomas, D.W., Thompson, J., Uríarte, M., Valencia, R.,
- 1371 Vicentini, A., Wolf, A.T., Yap, S., Yuan, Z., Zartman, C.E., Zimmerman, J.K., Chave, J.,
- 1372 2014. Local spatial structure of forest biomass and its consequences for remote
- 1373 sensing of carbon stocks. Biogeosciences 11, 6827–6840.
- 1374 https://doi.org/10.5194/bg-11-6827-2014
- 1375 Réjou-Méchain, M., Tanguy, A., Piponiot, C., Chave, J., Hérault, B., 2017. Biomass: an R
- 1376 Package for Estimating Above-Ground Biomass and Its Uncertainty in Tropical
- 1377 Forests. Methods Ecol. Evol. 8, 1163–1167. https://doi.org/10.1111/2041-
- 1378 210X.12753
- 1379 Réjou-Méchain, M., Tymen, B., Blanc, L., Fauset, S., Feldpausch, T.R., Monteagudo, A.,
- 1380 Phillips, O.L., Richard, H., Chave, J., 2015. Using repeated small-footprint LiDAR
- 1381 acquisitions to infer spatial and temporal variations of a high-biomass Neotropical
- 1382 forest. Remote Sens. Environ. 169, 93–101.
- 1383 https://doi.org/10.1016/j.rse.2015.08.001
- 1384 Riaño, D., Valladares, F., Condés, S., Chuvieco, E., 2004. Estimation of leaf area index and
- 1385 covered ground from airborne laser scanner (Lidar) in two contrasting forests.
- 1386 Agric. For. Meteorol. 124, 269–275.
- 1387 https://doi.org/10.1016/j.agrformet.2004.02.005
- 1388 Rosette, J.A.B., North, P.R.J., Suárez, J.C., 2008. Vegetation height estimates for a mixed
- 1389 temperate forest using satellite laser altimetry, in: International Journal of Remote
- 1390 Sensing. pp. 1475–1493. https://doi.org/10.1080/01431160701736380
- 1391 Rubner, Y., Tomasi, C., Guibas, L.J., 2000. Earth mover's distance as a metric for image
- 1392 retrieval. Int. J. Comput. Vis. 40, 99–121.

- 1393 https://doi.org/10.1023/A:1026543900054
- 1394 Schimel, D., Pavlick, R., Fisher, J.B., Asner, G.P., Saatchi, S., Townsend, P., Miller, C.,
- 1395 Frankenberg, C., Hibbard, K., Cox, P., 2015. Observing terrestrial ecosystems and the
- 1396 carbon cycle from space. Glob. Chang. Biol. https://doi.org/10.1111/gcb.12822
- 1397 Seidl, R., Rammer, W., Spies, T.A., 2014. Disturbance legacies increase the resilience of
- 1398 forest ecosystem structure, composition, and functioning. Ecol. Appl. 24, 2063–
- 1399 2077. https://doi.org/10.1890/14-0255.1
- 1400 Shugart, H.H., Asner, G.P., Fischer, R., Huth, A., Knapp, N., Le Toan, T., Shuman, J.K., 2015.
- 1401 Computer and remote-sensing infrastructure to enhance large-scale testing of
- individual-based forest models. Front. Ecol. Environ. 13, 503–511.
- 1403 https://doi.org/10.1890/140327
- 1404 Shugart, H.H., Saatchi, S., Hall, F.G., 2010. Importance of structure and its measurement
- in quantifying function of forest ecosystems. J. Geophys. Res. Biogeosciences 115,
- 1406 G2. https://doi.org/10.1029/2009JG000993
- 1407 Spriggs, R.A., Vanderwel, M.C., Jones, T.A., Caspersen, J.P., Coomes, D.A., 2019. A critique
- 1408 of general allometry-inspired models for estimating forest carbon density from
- airborne LiDAR. PLoS One 14, e0215238.
- 1410 https://doi.org/10.1371/journal.pone.0215238
- 1411 Spriggs, R.A., Vanderwel, M.C., Jones, T.A., Caspersen, J.P., Coomes, D.A., 2015. A simple
- 1412 area-based model for predicting airborne LiDAR first returns from stem diameter
- 1413 distributions: An example study in an uneven-aged, mixed temperate forest. Can. J.
- 1414 For. Res. 45, 1338–1350. https://doi.org/10.1139/cjfr-2015-0018
- 1415 Sterck, F.J., Bongers, F., 2001. Crown development in tropical rain forest trees: Patterns
- 1416 with tree height and light availability. J. Ecol. 89, 1–13.
- 1417 https://doi.org/10.1046/j.1365-2745.2001.00525.x

- 1418 Stovall, A.E.L., Anderson-Teixeira, K.J., Shugart, H.H., 2018. Assessing terrestrial laser
- scanning for developing non-destructive biomass allometry. For. Ecol. Manage. 427,
- 1420 217–229. https://doi.org/10.1016/j.foreco.2018.06.004
- 1421 Stovall, A.E.L., Shugart, H., Yang, X., 2019. Tree height explains mortality risk during an
- 1422 intense drought. Nat. Commun. 10. https://doi.org/10.1038/s41467-019-12380-6
- 1423 Strigul, N., Pristinski, D., Purves, D., Dushoff, J., Pacala, S., 2008. Scaling from trees to
- 1424 forests: Tractable macroscopic equations for forest dynamics. Ecol. Monogr. 78,

1425 523–545. https://doi.org/10.1890/08-0082.1

- 1426 Sullivan, M.J.P., Lewis, S.L., , W., Qie, L., Baker, T.R., Banin, L.F., Chave, J., Cuni-Sanchez, A.,
- 1427 Feldpausch, T.R., Lopez-Gonzalez, G., Arets, E., Ashton, P., Bastin, J.F., Berry, N.J.,
- 1428 Bogaert, J., Boot, R., Brearley, F.Q., Brienen, R., Burslem, D.F.R.P., de Canniere, C.,
- 1429 Chudomelová, M., Dančák, M., Ewango, C., Hédl, R., Lloyd, J., Makana, J.R., Malhi, Y.,
- 1430 Marimon, B.S., Junior, B.H.M., Metali, F., Moore, S., Nagy, L., Vargas, P.N., Pendry, C.A.,
- 1431 Ramírez-Angulo, H., Reitsma, J., Rutishauser, E., Salim, K.A., Sonké, B., Sukri, R.S.,
- 1432 Sunderland, T., Svátek, M., Umunay, P.M., Martinez, R.V., Vernimmen, R.R.E., Torre,
- 1433 E.V., Vleminckx, J., Vos, V., Phillips, O.L., 2018. Field methods for sampling tree
- height for tropical forest biomass estimation. Methods Ecol. Evol. 9, 1179–1189.
- 1435 https://doi.org/10.1111/2041-210X.12962
- 1436 Swain, M.J., Ballard, D.H., 1991. Color indexing. Int. J. Comput. Vis. 7, 11–32.
- 1437 https://doi.org/10.1007/BF00130487
- 1438 Tanskanen, H., Venäläinen, A., Puttonen, P., Granström, A., 2005. Impact of stand
- structure on surface fire ignition potential in Picea abies and Pinus sylvestris
- 1440 forests in southern Finland. Can. J. For. Res. 35, 410–420.
- 1441 https://doi.org/10.1139/x04-188
- 1442 Taubert, F., Jahn, M.W., Dobner, H.-J., Wiegand, T., Huth, A., 2015. The structure of

tropical forests and sphere packings. Proc. Natl. Acad. Sci. 112, 15125–15129.

1444 https://doi.org/10.1073/pnas.1513417112

1445 Tebaldini, S., Ho Tong Minh, D., Mariotti d'Alessandro, M., Villard, L., Le Toan, T., Chave,

- 1446 J., 2019. The Status of Technologies to Measure Forest Biomass and Structural
- 1447 Properties: State of the Art in SAR Tomography of Tropical Forests. Surv. Geophys.
- 1448 https://doi.org/10.1007/s10712-019-09539-7
- 1449 Ter Steege, H., Pitman, N.C.A., Phillips, O.L., Chave, J., Sabatier, D., Duque, A., Molino, J.F.,
- 1450 Prévost, M.F., Spichiger, R., Castellanos, H., Von Hildebrand, P., Vásquez, R., 2006.
- 1451 Continental-scale patterns of canopy tree composition and function across
- 1452 Amazonia. Nature 443, 444–447. https://doi.org/10.1038/nature05134
- 1453 Thomas, S.C., 1996. Asymptotic height as a predictor of growth and allometric
- 1454 characteristics in Malaysian rain forest trees. Am. J. Bot. 83, 556–566.
- 1455 https://doi.org/10.2307/2445913
- 1456 Vaglio Laurin, G., Chen, Q., Lindsell, J.A., Coomes, D.A., Frate, F. Del, Guerriero, L., Pirotti,
- 1457 F., Valentini, R., 2014. Above ground biomass estimation in an African tropical
- 1458 forest with lidar and hyperspectral data. ISPRS J. Photogramm. Remote Sens. 89,
- 1459 49–58. https://doi.org/10.1016/j.isprsjprs.2014.01.001
- 1460 Van Leeuwen, M., Hilker, T., Coops, N.C., Frazer, G., Wulder, M.A., Newnham, G.J.,
- 1461 Culvenor, D.S., 2011. Assessment of standing wood and fiber quality using ground
- and airborne laser scanning: A review. For. Ecol. Manage.
- 1463 https://doi.org/10.1016/j.foreco.2011.01.032
- 1464 Vincent, G., Antin, C., Laurans, M., Heurtebize, J., Durrieu, S., Lavalley, C., Dauzat, J., 2017.
- 1465 Mapping plant area index of tropical evergreen forest by airborne laser scanning. A
- 1466 cross-validation study using LAI2200 optical sensor. Remote Sens. Environ. 198,
- 1467 254–266. https://doi.org/10.1016/j.rse.2017.05.034

- 1468 West, G.B., Brown, J.H., Enquist, B.J., 1999. A general model for the structure and
- allometry of plant vascular systems. Nature 400, 664–667.
- 1470 https://doi.org/10.1038/23251
- 1471 West, G.B., Enquist, B.J., Brown, J.H., 2009. A general quantitative theory of forest
- structure and dynamics. Proc. Natl. Acad. Sci. U. S. A. 106, 7040–7045.
- 1473 https://doi.org/10.1073/pnas.0812294106
- 1474 Wickham, H., 2011. ggplot2. Wiley Interdiscip. Rev. Comput. Stat.
- 1475 https://doi.org/10.1002/wics.147
- 1476 Zanne, A.E., Lopez-Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., Miller, R.B.,
- 1477 Swenson, N.G., Wiemann, M.C., Chave, J., 2009. Data from: Global wood density
- 1478 database. Dryad Digit. Repos. https://doi.org/10.5061/dryad.234
- 1479 Zolkos, S.G., Goetz, S.J., Dubayah, R., 2013. A meta-analysis of terrestrial aboveground
- 1480 biomass estimation using lidar remote sensing. Remote Sens. Environ. 128, 289–
- 1481 298. https://doi.org/10.1016/j.rse.2012.10.017
- 1482

1483 List of Figure Captions

1484 **Figure 1: The two-step procedure of the Canopy Constructor algorithm.** Step 1 uses

1485 tree inventory data, and a canopy height model (CHM). To infer the position and size of

1486 each tree, the algorithm creates an initial reconstruction drawing randomly dimensions

1487 from allometric relationships between tree dimensions. In ill-fitting regions (red),

1488 deviations from the allometric means are swapped between trees until a good spatial fit

is obtained (green). Step 2 extrapolates the results of step 1 and creates virtual

1490 inventories across thousands of hectares, following the same fitting algorithm as in step

1491 1, but with fitted trees drawn from a distribution (see main text for details).

1492

1493 **Figure 2: Example of canopy reconstruction at the Petit Plateau plot, Nouragues.**

1494 Shown are the initial canopy height model (CHM) where tree dimensions are randomly

1495 drawn from site-specific allometries (a), the ALS-derived CHM (b), and the final

1496 reconstruction of the Canopy Constructor (c).

1497

1498 Figure 3: Inferred allometries at Nouragues and Rabi (step 1). The panels show 1499 height allometries (top row) and crown allometries (bottom row), as inferred by the 1500 Canopy Constructor, for Nouragues (a,d), Rabi (b,e) and both sites combined (c,f). The 1501 grey background indicates the prior range. Mean and 75% highest density intervals are 1502 given for each plot separately, i.e. for Grand Plateau (orange) and Petit Plateau (dark 1503 red) at Nouragues, and for the 10ha (light blue) and 15ha (dark blue) plot at Rabi. As 1504 comparison, we have plotted empirical height allometries measured from in the field for 1505 both Grand Plateau (dotted) and Petit Plateau (dashed) in the top panels, as well as a 1506 single ground-inferred allometry at Rabi (dotted). Results for same inference procedure, 1507 but with a lower number of simulation runs, are provided in Figure S8.

1508

1509 Figure 4: Aboveground biomass predictions for ALS campaign at Nouragues and 1510 Rabi (step 2). Maps show the mean aboveground biomass values (t ha-1) predicted 1511 with the Canopy Constructor approach across 2,016 ha at Nouragues (panel a) and 832 1512 ha at Rabi (panel d), as well as the respective coefficient of variation across 100 1513 simulations (panels b and e, dimensionless). Also given are the overall distributions of 1514 aboveground biomass (panels c and f, red distributions, in t ha-1) and previously 1515 obtained estimates (panels c and f, yellow) from a pooled regression-model (Labrière et 1516 al. 2018). Clearly evident is the shrinkage towards the mean in the regression-based 1517 approach, as opposed to much stronger variation in the Canopy Constructor approach. 1518 Please note that the geographic extent of the maps has been rescaled for visualization 1519 purposes.

1520

1521 Figure 5: Evaluation of aboveground biomass predictions in extrapolation (step

1522 2). Shown are the predictions of aboveground biomass (median of 100 posterior

1523 simulations, given in t ha⁻¹) at the 1 ha scale (a, b) and 0.25 ha scale (c, d). The left

1524 column shows the results when the space-filling approach is applied at the calibration

1525 plot from which allometries and packing densities were derived ("Model fit"), the right

1526 column the results when the approach is transferred between plots ("Cross-

1527 validation"). The Nouragues results are plotted in red/orange, and for Rabi in dark/light

1528 green. Goodness of fit values are provided in the bottom-right corner of the panels. MBE

does not change between 0.25 and 1 ha scales and is thus only given in the top panels.

1530 For visualization purposes, we only plot error bars at the hectare scale, representing the

1531 interquartile ranges of estimates from 100 posterior simulations.