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1 **Title:**
2 Linking lidar and forest modeling to assess biomass estimation across scales and disturbance states
3

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21

22 **Abstract**

23 Light detection and ranging (lidar) is currently the state-of-the-art remote sensing technology for
24 measuring the 3D structures of forests. Studies have shown that various lidar-derived metrics can be
25 used to predict forest attributes, such as aboveground biomass. However, finding out which metric
26 works best at which scale and under which conditions requires extensive field inventories as ground-
27 truth data. The goal of our study was to overcome the limitations of inventory data by complementing
28 field-derived data with virtual forest stands from a dynamic forest model. The simulated stands were
29 used to compare 29 different lidar metrics for their utility as predictors of tropical forest biomass at
30 different spatial scales. We used the process-based forest model FORMIND, developed a lidar simulation
31 model, based on the Beer-Lambert law of light extinction, and applied it to a tropical forest in Panama.
32 Simulation scenarios comprised undisturbed primary forests and stands exposed to logging and fire
33 disturbance regimes, resulting in mosaics of different successional stages, totaling 3.7 million trees on
34 4,200 ha. The simulated forest was sampled with the lidar model. Several lidar metrics, in particular
35 height metrics, showed good correlations with forest biomass, even for disturbed forest. Estimation
36 errors (nRMSE) increased with decreasing spatial scale from < 10% (200-m scale) to > 30% (20-m scale)
37 for the best metrics. At the often used 1-ha scale, the top-of-canopy height obtained from canopy height
38 models with fine to relatively coarse pixel resolutions (1 to 10 m) yielded the most accurate biomass
39 predictions, with nRMSE < 6% for undisturbed and nRMSE < 9% for disturbed forests. This study
40 represents the first time dynamic modeling of a tropical forest has been combined with lidar remote
41 sensing to systematically investigate lidar-to-biomass relationships for varying lidar metrics, scales and
42 disturbance states. In the future, this approach can be used to explore the potential of remote sensing of
43 other forest attributes, e.g., carbon dynamics, and other remote sensing systems, e.g., spaceborne lidar
44 and radar.

45 **Keywords:** aboveground biomass; tropical forest; disturbance; lidar simulation; forest modeling;
46 resolution; scale

47 **1. Introduction**

48
49 Due to their important role in the global carbon cycle and ongoing deforestation and degradation,
50 tropical forests are of particular interest to biomass remote sensing. Tropical forest carbon accounting
51 and monitoring of deforestation are important tasks in the context of REDD+ and global climate
52 modeling. In recent years, remote sensing has led to considerable improvements in this field (Gibbs et
53 al., 2007; De Sy et al., 2012; Pan et al., 2013). Airborne small-footprint lidar (light detection and ranging)
54 is currently the state-of-the-art technology for measuring the 3D structure of forests (Lefsky et al.,
55 2002b; Wulder et al., 2012; Mascaro et al., 2014). Various lidar metrics correlate well with different
56 forest attributes. In particular, lidar-derived height metrics have commonly been used to predict forest
57 aboveground biomass (AGB) and carbon density (ACD) (Drake et al., 2002; Asner et al., 2009; Dubayah et
58 al., 2010; Jubanski et al., 2013; Asner & Mascaro, 2014). The major challenges in biomass estimation
59 based on lidar data are that 1) the calibration of the prediction functions relies on field data that must be
60 collected manually in inventory plots; and 2) there are many different metrics available using different
61 spatial scales, and the task is to find the combination that provides accurate AGB predictions.

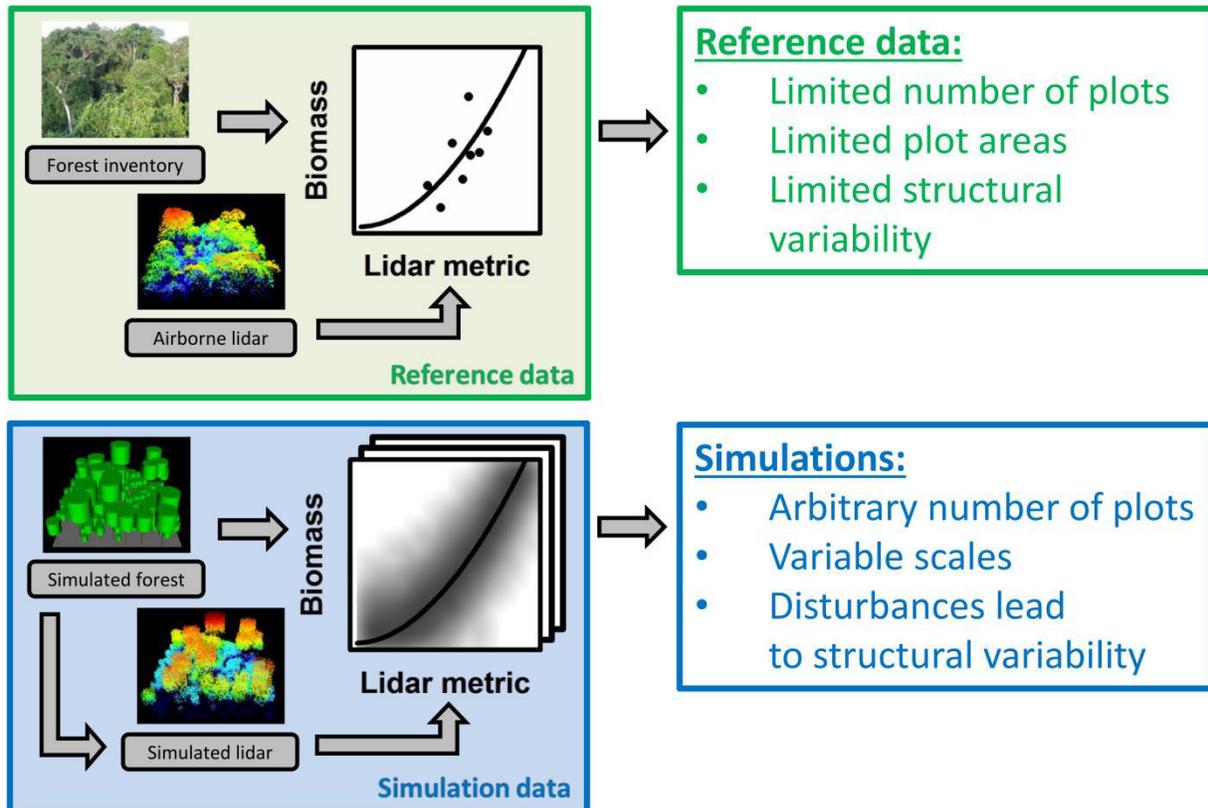
62 In inventory plots, tree diameters at breast height (DBH) are typically measured, from which AGB is
63 calculated via known allometric equations (e.g., Chave et al., 2005, 2014; Chen 2015). Lidar data are
64 acquired for the same inventory plots to build regression models between lidar-based structure metrics
65 and ground-based AGB. A wide range of metrics can be calculated from lidar data. To date, no standard
66 approach for AGB estimation from lidar has been established and different studies have applied different
67 metrics (Chen 2013; Lu et al. 2014). Several publications have compared metrics among each other for
68 different forest types (e.g., Lefsky et al., 1999, 2002a; Dubayah et al., 2010; Jubanski et al., 2013).
69 However, there has not been a comparison of a wide range of metrics on a single tropical forest dataset.
70 Lidar metrics can generally be divided into metrics which are based on the full 3D point cloud of lidar

71 returns and metrics which are based on canopy height models (CHM), i.e., the rasterized canopy surfaces
72 which are derived from the uppermost returns of the point clouds (Chen 2013). The full 3D point cloud
73 contains more information about the vertical canopy structure than the corresponding CHM. On the
74 other hand, the vertical distribution of lidar returns also depends on technical properties of the specific
75 sensor, making point-cloud-based metrics less robust and comparable between different studies than
76 CHM-based metrics (Næsset, 2009; Asner & Mascaro, 2014). Many commonly used metrics can be
77 calculated based on both types of data. Those metrics include mean heights (Lefsky et al., 2002a; Asner
78 & Mascaro, 2014), relative height quantiles (the heights below which a certain percentage of returns or
79 pixels falls) (Patenaude et al., 2004; Dubayah et al., 2010; Meyer et al., 2013), and metrics of
80 heterogeneity such as the standard deviation of heights or the Shannon diversity index of the height
81 profiles (Stark et al., 2012). Other metrics, such as the ratio of above ground returns to total returns or
82 fractional canopy cover above a certain height, that can be derived either from point clouds or CHMs
83 describe relative vegetation cover.

84 An important aspect of AGB prediction from remote sensing is spatial resolution. Resolution means, first,
85 spatial resolution of the remote sensing data from which different metrics are calculated and, second,
86 the spatial resolution of the output map, i.e., the grain size of the units for which the metrics are
87 calculated to produce an AGB prediction. The resolution of the data is determined by the sensor's
88 technical specifications and the capacities to store and process data. The resolution of the mapping units
89 is influenced by the desired estimation accuracy and the desired spatial detail of the mapped product.
90 Köhler & Huth (2010), Mascaro et al. (2011b) and Chen et al. (2016) showed how errors in AGB
91 estimations from mean lidar heights decreased with increasing grain sizes and that a grain of
92 approximately 1 ha is required to achieve errors of < 10%.

93 Fitting any of the described lidar metrics to measured AGB relies on field inventory data. Forest
94 inventory plots are limited in number, size and structural variety. The collection of inventory data is

95 costly and laborious and most studies in the past made use of tens to a few hundred plots (Fassnacht et
96 al., 2014). Those plots are often located in old growth forests. Hence, available data sets might not cover
97 the full structural complexity of forests over their entire successional range (noteworthy exceptions are
98 e.g., Dubayah et al. 2010, Poorter et al. 2016). For lidar-to-AGB-calibration, a broad range of different
99 forest succession states that cover the range of all possible AGB stocks and associated forest structures is
100 preferable. To overcome this limitation, we propose a new approach in which we complement in situ
101 measurements with simulated forest stands (Fig. 1). We used an individual-based forest model
102 (FORMIND, Fischer et al., 2016) to simulate a large virtual inventory dataset, covering the full range of
103 succession stages by including forest disturbances in the simulations. The model was parameterized to
104 represent the well-studied lowland tropical rainforest of Barro Colorado Island, Panama (Condit et al.,
105 2001; Kazmierczak et al., 2014). We developed a lidar model to sample lidar data of simulated forest
106 stands.



107

108 Fig. 1: Workflow of the study. Reference data from field inventories and an airborne lidar campaign were used to
 109 parameterize and calibrate a forest model and a lidar model. With the models, large quantities of simulated inventory and
 110 simulated lidar data were generated, allowing for a systematic analysis of lidar-to-biomass relationships under different
 111 disturbance regimes and for various spatial scales.

112 The research goals of this study were 1) to establish a lidar simulation model that is able to produce
 113 synthetic lidar-like data for dynamic forest model output; 2) to test a wide variety of lidar metrics for
 114 their ability to predict AGB of a tropical rainforest at various spatial scales; and 3) to investigate the
 115 influence of disturbances on the lidar-to-biomass relationships.

116

117 **2. Material & Methods**

118

119 *2.1 Study area*

120 The study focused on the tropical forest on Barro Colorado Island (BCI), Panama (9.15° N, 79.85° W). BCI
121 is a 15 km² island located in Lake Gatun, an artificial water body created by the construction of the
122 Panama Canal (Condit et al., 2001). It is covered with semi-deciduous tropical lowland rainforest, the
123 minimum forest age is estimated to range from 300 to 1500 years (Bohlman & O'Brien, 2006; Meyer et
124 al., 2013; Lobo & Dalling, 2014). The climate is characterized by average daily maximum and minimum
125 temperatures of 30.8 and 23.4 °C and an annual precipitation sum of approximately 2600 mm, with a dry
126 season from January to April (Condit et al., 2001). A 50-ha rainforest observation plot is located on the
127 central plateau of the island, with terrain altitudes varying between 120 and 160 m above sea level (Lobo
128 & Dalling, 2014). Since the establishment of the plot in the early 1980s, each tree in the 1000 m × 500 m
129 area with a DBH ≥ 1 cm has been measured during censuses in five year intervals (Condit, 1998; Hubbell
130 et al., 1999, 2005). Estimates of the mean canopy height are 24.6 ± 8.2 m, and those of the mean AGB
131 are 281 ± 20 t/ha (Chave et al., 2003).

132

133 *2.2 Lidar data*

134 An airborne discrete point cloud lidar dataset was collected on BCI in August 2009 with a multi-pulse
135 scanning laser altimeter (Optech ALTM Gemini system; BLOM Sistemas Geoespaciales SLU, Madrid,
136 Spain, Lobo & Dalling, 2014). The terrain elevation was subtracted from the point cloud to obtain the
137 relative height above ground. Point densities ranged from 0 to 60 m⁻² with a median of 10 m⁻² and a 5th-
138 percentile of 4 m⁻². To avoid locally varying point densities, caused by flight swath overlaps, the point
139 clouds were thinned by random subsampling of 4 returns in each square meter. A 1-m resolution canopy

140 height model (CHM) was derived from the highest returns in each square meter. Data processing was
141 performed using LAStools (Isenburg, 2011) and R (R Development Core Team, 2014).

142

143 *2.3 Lidar model description*

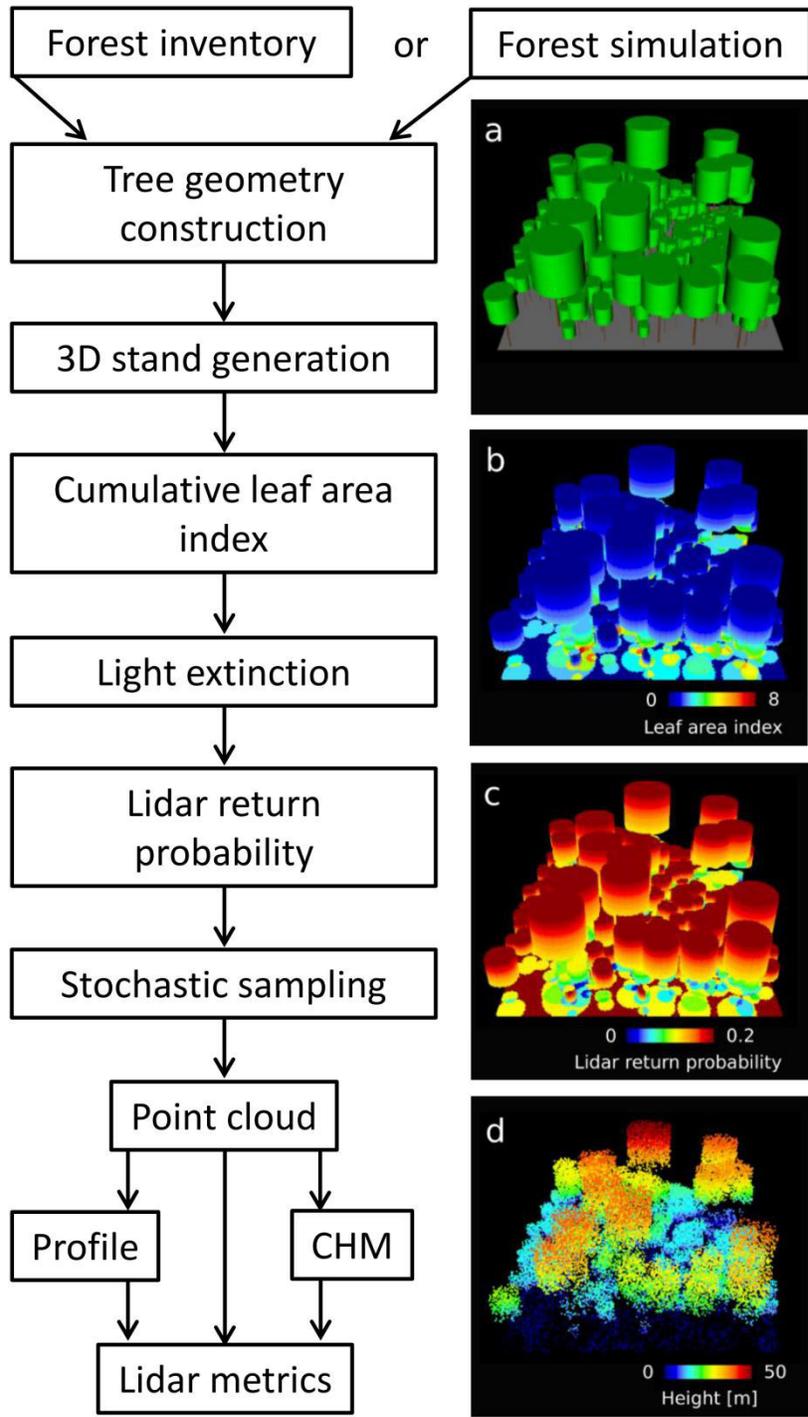
144 The purpose of the lidar model is the simulation of a lidar scan of a given forest stand. More specifically,
145 it generates point clouds of discrete returns as usually produced by small-footprint lidar systems. As
146 input, a tree list has to be provided. The list can either be real forest inventory data or data generated by
147 a forest model (Fig. 2a). The basic elements of the model are trees, lidar pulses and lidar returns. Trees
148 are characterized by their position (X- and Y-coordinate), height, crown length, crown radius, crown
149 shape and leaf area index (LAI). The model operates in a 3D space represented by an array of cuboid
150 voxels. Each vertical column of voxels represents one modeled lidar pulse. Lidar returns are points in 3D
151 space, characterized by their X-, Y- and Z-coordinates.

152 From the tree list, a voxel representation of the entire forest is created. Thus, voxels that could
153 potentially produce a lidar return, because they belong to a tree crown or the ground, are distinguished
154 from empty space voxels. The voxel forest is then scanned with a virtual lidar. The simulation follows a
155 probabilistic approach. Instead of explicitly simulating the branches and foliage and their interaction with
156 laser beams within the tree crowns, the model assumes that the tree crown space is a homogeneous,
157 turbid medium filled with a certain leaf area density (LAD). The probability of having a lidar return from a
158 certain point decreases as the distance the laser beam has to travel through the medium before reaching
159 the point increases. This relationship is analogous to the Beer-Lambert light-extinction law (Campbell &
160 Norman, 2012). Thus, the probability for a lidar return P for each tree and ground voxel (Fig. 2c) can be
161 calculated as a function of cumulative leaf area index LAI above the voxel (Fig. 2b).

162

$$P(LAI) = P_0 \cdot e^{-k \cdot LAI} \quad (1)$$

163 P_0 in Eq. (1) represents the probability of obtaining a return from the very upper voxel, where the laser
164 beam hits a tree or the ground for the first time. The parameter k is the exponential extinction
165 coefficient, which determines how fast the return probability decreases after entering the crown space.
166 The decision regarding whether each voxel will contain a return is taken stochastically, based on the
167 calculated return probability. Ultimately, this leads to a discrete point cloud (Fig. 2d). The voxel
168 resolution was set to 0.5 m \times 0.5 m along the horizontal direction and 1 m along the vertical direction.
169 The parameters P_0 and k were calibrated such that simulated point cloud profiles derived for subareas of
170 the 50-h inventory data set matched the airborne lidar profiles of those subareas (details see
171 supplements). The resulting value for $k = 0.2$ can be confirmed by literature (Campbell & Norman 2012,
172 Jones 2013). For P_0 we found 0.2 to be a good value, leading to simulated point densities that were
173 similar to the airborne reference point cloud. P_0 being smaller than 1 can be interpreted by the
174 heterogeneity of leafs, branches and empty space within the tree crown. This means that a laser beam
175 entering the idealized cylindrical tree crown does not necessarily trigger a return in the first voxel.



176
 177 **Fig. 2: Principle of the lidar model. Inputs to the workflow can either be forest model output or field inventory data. The**
 178 **pictures on the right side show intermediate products: a) Visualization of a forest stand; b) voxel representation with colors**
 179 **indicating the cumulative leaf area index; c) voxel representation with colors indicating the probability of containing a lidar**
 180 **return; d) simulated lidar point cloud with colors indicating height above ground.**

181

182 *2.4 Forest model description*

183 FORMIND belongs to the group of forest gap models (Botkin et al., 1972; Shugart, 1984; Bugmann,
184 2001). As such, the model simulates the processes of establishment, growth, competition and mortality
185 of trees on spatial patches with the dimensions of a typical treefall gap (20 m × 20 m). By combining
186 many patches, large forest areas of hundreds of hectares can be simulated. FORMIND is an individual-
187 based model (IBM) in which the individuals represent trees that belong to different plant functional
188 types (PFTs). One PFT may contain several species with similar ecological traits. FORMIND has been
189 applied to many tropical forest sites and has proven capable of accurately reproducing patterns
190 observed in these complex ecosystems (Fischer et al., 2016). The individual-based model architecture
191 allows for the inclusion of disturbances such as logging or forest fires in a structurally realistic way. A
192 detailed description of FORMIND including the modules for logging and fire disturbance can be found in
193 Fischer et al. (2016). The supplements contain descriptions of the parameterization of the lidar model
194 and the forest model (Tab. S1). Before using the forest model output for remote sensing analyses, the
195 structural validity of the simulated old growth stands was confirmed by visually comparing biomass
196 stocks (Fig. S1) and stem size distributions (Fig. S2) of all PFTs to the values obtained from the inventory
197 data.

198

199 *2.5 Simulation experiment*

200 Using FORMIND, we simulated the development of a 16 ha (400 m × 400 m) area of the BCI forest over
201 several thousands of years and stored the results at 20-yr intervals. The simulations were repeated with
202 different disturbance regimes. The first run comprised 2000 yr without any external disturbance,
203 simulating only natural gap dynamics. In the second run, forest fires were introduced as a source of
204 spatially heterogeneous disturbance to clear parts of the area regularly and enable natural succession
205 and regrowth. Fire occurrence was drawn from a Poisson distribution such that the mean interval

206 between two fire events was 25 yr. Fire size at each fire event was drawn from an exponential
207 distribution, such that on average 50% of the total area was affected. More information on the fire
208 module used is provided in Fischer (2013) and Fischer et al. (2016). The third scenario included selective
209 logging. At a logging cycle of 99 yr, all trees with DBH > 30 cm were felled and removed. More
210 information on the logging module used is provided in Huth et al. (2004). For all three runs, the first 200
211 yr were discarded as spin-up. For each of the remaining simulation years, a virtual lidar campaign using
212 the lidar model was conducted. The disturbance frequencies and intensities were not intended to
213 represent realistic disturbances scenarios in the study region. The intention was to sample many stands
214 at each stage along the full successional range, using the disturbance modules to regularly set the forest
215 back to an early stage. The selective logging acts on the whole area, while the fires move in a spatially
216 explicit way through the simulated area, causing mosaics of unaffected forest next to cleared areas
217 where succession starts over. Such patchy landscapes are typical for many forest regions, although the
218 reasons for the structures may be as diverse as clear cuts, wind blowdowns, fires or natural areas
219 without vegetation, e.g., grasslands or water bodies. Thus, these simulations produce landscapes that
220 can be used as general examples of heterogeneous landscapes.

221

222 *2.6 Lidar-based biomass prediction*

223 We analyzed forest plots measuring 20, 33, 50, 100 or 200 m (side length). At each spatial scale, a range
224 of 29 different lidar metrics (Tab. 1) were tested for their suitability as single predictors of AGB. Metrics
225 were either derived from point clouds (PC) or canopy height models (CHM). CHMs were constructed
226 from point clouds by rasterizing the highest lidar returns in each pixel of a given pixel size.

227 Point-cloud-based metrics comprised the mean canopy profile height (MCH), which is the mean height of
228 all lidar returns, and the quadratic mean canopy profile height (QMCH), where high returns receive a

229 larger weighting than low returns. For a given point cloud profile p_{PC} that consists of lidar return counts
 230 at height bins h_i , MCH and QMCH can be calculated from Eq. (2) and (3), respectively.

$$231 \quad MCH = \frac{\sum_{i=1}^{i_{max}} (p_{PC,i} \cdot h_i)}{\sum_{i=1}^{i_{max}} p_{PC,i}} \quad (2)$$

$$232 \quad QMCH = \sqrt{\frac{\sum_{i=1}^{i_{max}} (p_{PC,i} \cdot h_i^2)}{\sum_{i=1}^{i_{max}} p_{PC,i}}} \quad (3)$$

233 where $p_{PC,i}$ is the lidar return counts in height bin h_i . A metric similar to MCH can be derived from the
 234 vertical CHM profile instead of the point cloud profile. This metric corresponds to the mean of all pixel
 235 values of the CHM, and is commonly referred to as the mean top-of-canopy height (TCH, Eq. (4)).

$$236 \quad TCH = \frac{\sum_{i=1}^{i_{max}} (p_{CHM,i} \cdot h_i)}{\sum_{i=1}^{i_{max}} p_{CHM,i}} \quad (4)$$

237 Because a CHM can be derived from a point cloud at variable pixel resolutions, by taking the height of
 238 the highest return that falls into each pixel, TCH always depends on the pixel size used. We calculated
 239 TCH from CHMs with pixel side lengths of 1, 5, 10, 20, 33, 50 and 100 m. Note that, once the pixel size
 240 equals the plot size for which AGB is calculated, TCH is equal to the maximal height in the plot, which is
 241 also referred to as H_{max} or RH100 in the literature. Another method for measuring forest height from
 242 lidar data is by using relative height quantiles of either the point cloud or the CHM. These quantiles
 243 represent the heights below which a certain percentage of the returns or CHM pixels fall. We calculated
 244 RH25, RH50 and RH75 for the point clouds and 1-m resolution CHMs.

245 Other metrics, however, capture the vertical heterogeneity of the forest. Those metrics include the
 246 standard deviation (SD) of heights (point-cloud- or CHM-based), the coefficient of variation (CV, Eq. (5)
 247 and (6)), the skewness of the vertical point cloud profile (Eq. (7), where N is the total number of points
 248 and h_i is the height of each point i), the Shannon Index (Eq. (8), where i_{max} is the number of height layers
 249 and p_i is the count of points in the layer i) as a measure of entropy of the profile and the P:H ratio (Eq.
 250 (9), where i_{max} is the number of height layers, p_i is the count of points in the layer i and h_i is height of

251 layer i), which describes the height of the densest part of the point cloud (peak in the profile) relative to
 252 the maximal height (Marvin et al., 2014).

$$253 \quad CV_{PC} = \frac{SD_{PC}}{MCH} \quad (5)$$

$$254 \quad CV_{CHM} = \frac{SD_{CHM}}{TCH} \quad (6)$$

$$255 \quad Skewness = \frac{1}{N} \cdot \sum_{i=1}^N \left(\frac{h_i - MCH}{SD_{PC}} \right)^3 \quad (7)$$

$$256 \quad Shannon\ Index = - \sum_{i=1}^{i_{max}} p_i \cdot \ln(p_i) \quad (8)$$

$$257 \quad P:H\ ratio = \frac{h(\max_{i \in [1, i_{max}]}(p_i))}{\max_{i \in [1, i_{max}]}(h_i)} \quad (9)$$

258 Furthermore, we calculated vegetation density metrics. Based on the point clouds, the count of
 259 aboveground returns divided by either the count of ground returns N_{AGR}/N_{GR} or the count of total returns
 260 N_{AGR}/N_{TR} was calculated. Based on the CHMs, the fractional canopy cover (FCC) was derived by defining
 261 different height thresholds below which a CHM-pixel was considered a canopy gap. We calculated FCC0,
 262 FCC10 and FCC20 using the forest floor, 10 m and 20 m as height thresholds, respectively.

263 **Tab. 1: List of the lidar metrics and the underlying data (PC = point cloud, CHM = canopy height model). CHM usually refers to**
 264 **1-m resolution rasters, except for TCH where various resolutions were tested.**

Lidar metric	Description	Data
MCH	Mean canopy profile height	PC
QMCH	Quadratic mean canopy profile height	PC
TCH	Mean top-of-canopy height (at variable CHM pixel resolutions), e.g., TCH5 is based on 5-m pixels	CHM
RH	Relative height quantile, e.g., RH50 is the 50-percentile of heights	PC or CHM
SD	Standard deviation of heights	PC or CHM
CV	Coefficient of variation of heights (normalized SD)	PC or CHM
Skewness	Skewness of the vertical profile	PC
Shannon Index	Entropy of the vertical profile	PC
P:H ratio	Relative height of the peak in the vertical profile	PC
N_{AGR}/N_{GR}	Ratio of aboveground returns to ground returns	PC
N_{AGR}/N_{TR}	Ratio of aboveground returns to total returns	PC
FCC	Fractional canopy cover, e.g., FCC10 is the relative share of pixels higher than 10 m	CHM

265

266 Each lidar metric LM was fit to the dependent variable AGB using a power law model (Eq. (10)) and
267 maximum likelihood estimation in R.

$$268 \qquad \qquad \qquad AGB = a \cdot LM^b \qquad \qquad \qquad (10)$$

269 If possible, such relationships were derived for plots with side lengths of 20, 33, 50, 100 and 200 m.
270 Relationships could not be derived in cases where pixel size exceeded plot size or where the maximum
271 likelihood estimation did not provide a parameter b different from zero. The AGB-prediction accuracy for
272 the different power law functions was quantified as the normalized root mean square error ($nRMSE$) [%].
273 The measure was calculated as the RMSE of n AGB predictions against n observations, normalized by the
274 mean observed AGB (Eq. (11)).

$$275 \qquad \qquad \qquad nRMSE = \sqrt{\frac{\sum_{i=1}^n (predAGB_i - obsAGB_i)^2}{n}} \cdot \frac{1}{\overline{obsAGB}} \qquad \qquad \qquad (11)$$

276 The power law parameters and additional statistics (mean, RMSE, bias, R^2 , slope and intercept of linear
277 fits between predictions and observations) for all metrics, scales and datasets (672 models) can be found
278 in Tab. S2.

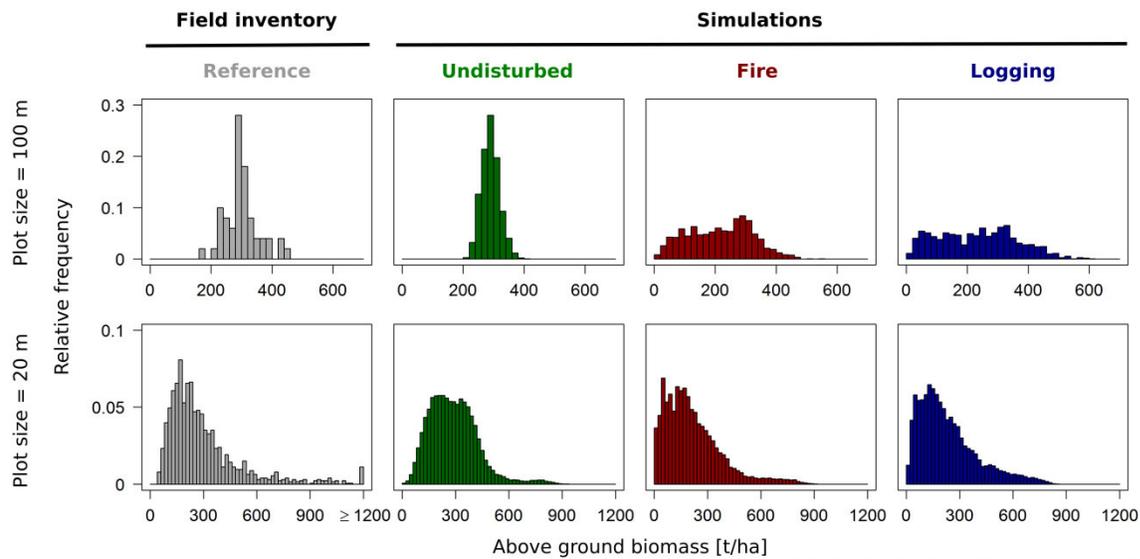
279

280 **3. Results**

281

282 *3.1 Forest and lidar simulation results*

283 The forest simulations could reproduce AGB succession over time for the four PFTs. An overshoot of total
284 AGB around a forest age of 100 yr was observed (Fig. S1). The duration of the primary succession and the
285 biomass overshoot are consistent with observations by Mascaro et al. (2012). Furthermore, the stem size
286 distributions for all four PFTs matched well between the model and reference data (Fig. S2). The AGB
287 distributions of reference data and undisturbed and disturbed FORMIND runs can be found in Fig. 3, and
288 for the undisturbed case, the simulated distributions are in good agreement with previously reported
289 distributions based on field data (Chave et al., 2003). At all scales the range of AGB in undisturbed
290 simulations was smaller than the observed range of AGB in the field reference data. In the disturbance
291 scenarios, the range of AGB values increased. At the small 20 m × 20 m scale, the real forest contained
292 extremely high local AGB values (max. 2022 t/ha) caused by single large trees. Such extreme values were
293 not reached in the simulations.



294

295 **Fig. 3: Relative frequency distributions of aboveground biomass (AGB).** Columns represent the BCI field data (50 ha) and
296 output of FORMIND simulations from different disturbance scenarios (1,400 ha each). Rows represent different spatial
297 resolutions. Notice the different axis scaling in each row.

298

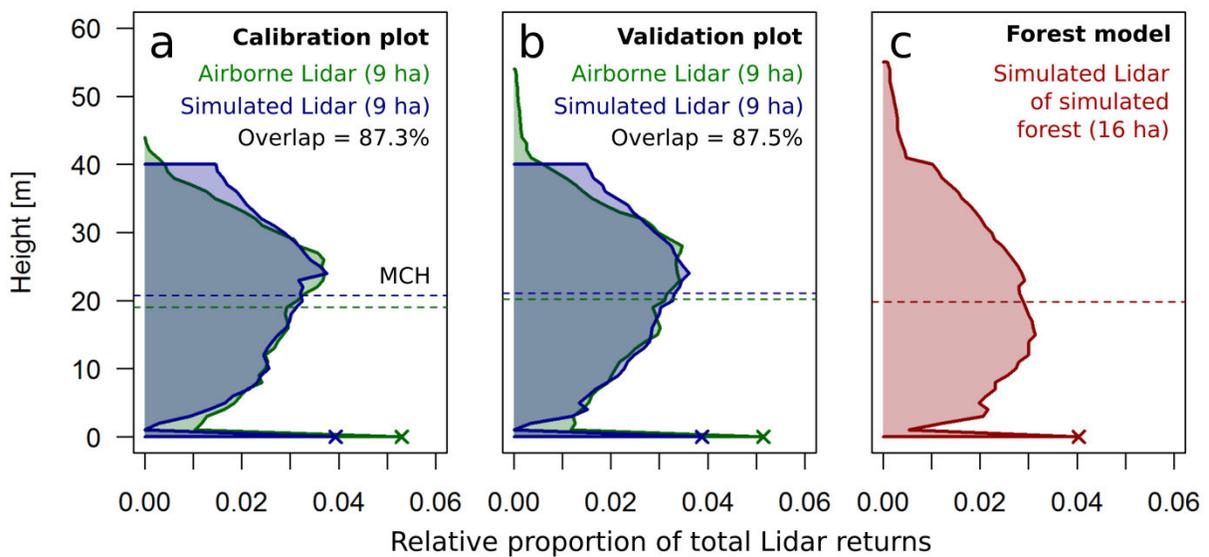
299 Using the lidar simulation approach, synthetic lidar data were generated for the simulated forest stands.

300 Lidar simulation outputs, such as the vertical point cloud profile (Fig. 4) and CHMs, closely resembled

301 their airborne equivalents. In the supplements we present how alternative assumptions about the tree

302 geometry affect the simulated lidar profiles and metrics (Fig. S15 to S18).

303



304

305 **Fig. 4:** Vertical lidar profiles of a) the 9 ha in the southwestern corner of the BCI megaplot, airborne and simulated based on
306 inventory data; b) the same for the 9 ha in the northeastern corner of the BCI megaplot; and c) the simulated lidar profile of
307 16 ha simulated forest in FORMIND in the old growth stage (age 500 yr). Dashed lines mark the mean canopy profile height
308 (MCH), and 'x' symbols mark the ground return peaks.

309

310 3.2 Biomass prediction from top-of-canopy height

311 Based on the simulated stands, we analyzed 4,200 ha of forest (3.7 million trees with DBH \geq 3 cm) with

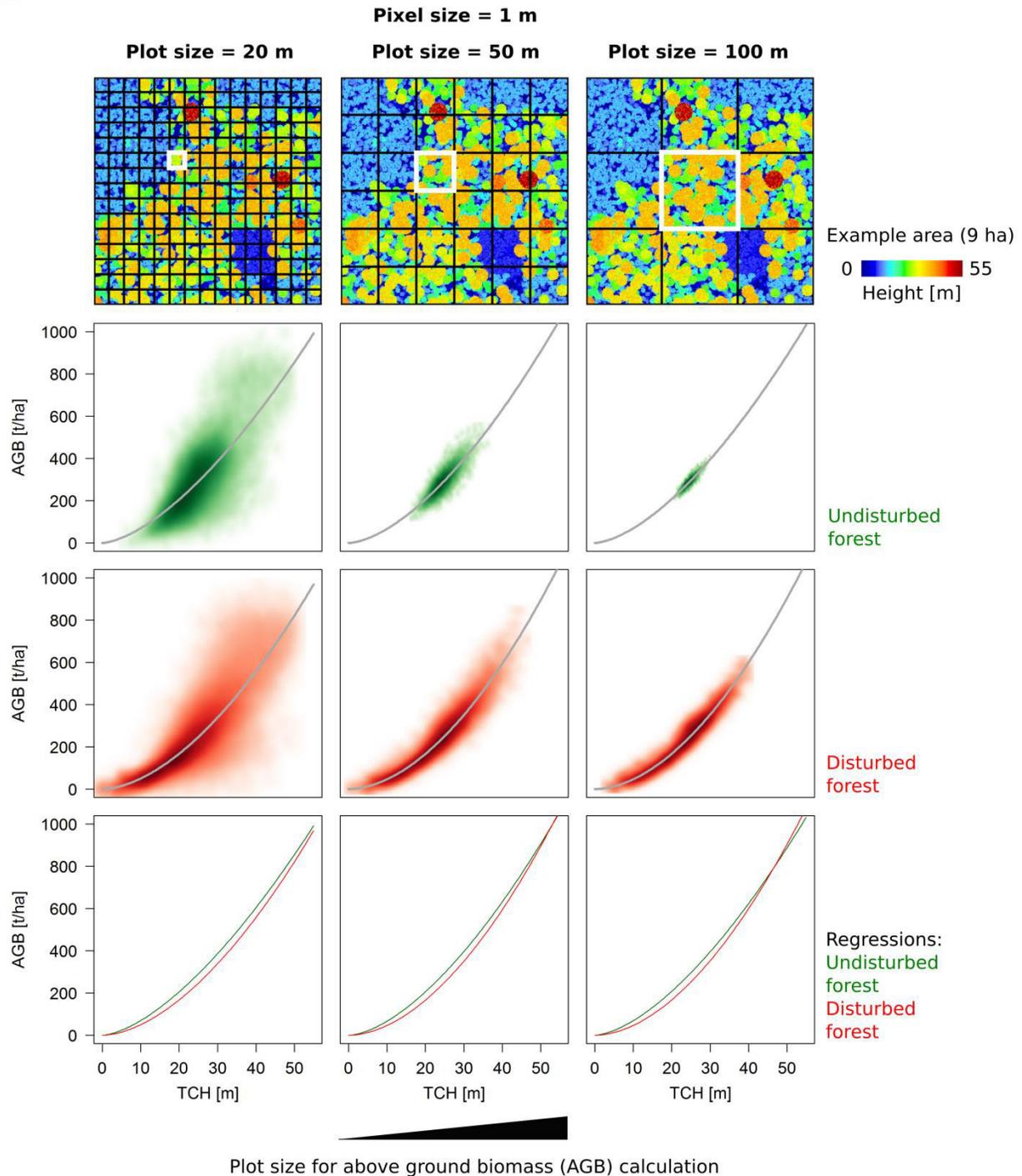
312 respect to the relationships between forest height (TCH) and biomass (AGB). We generated undisturbed

313 (1,400 ha), fire-disturbed (1,400 ha) and logging-disturbed (1,400 ha) stands. Fig. 5 shows the

314 relationships observed for different plot sizes (20 to 100 m) assuming a fine resolution (pixel size = 1 m).

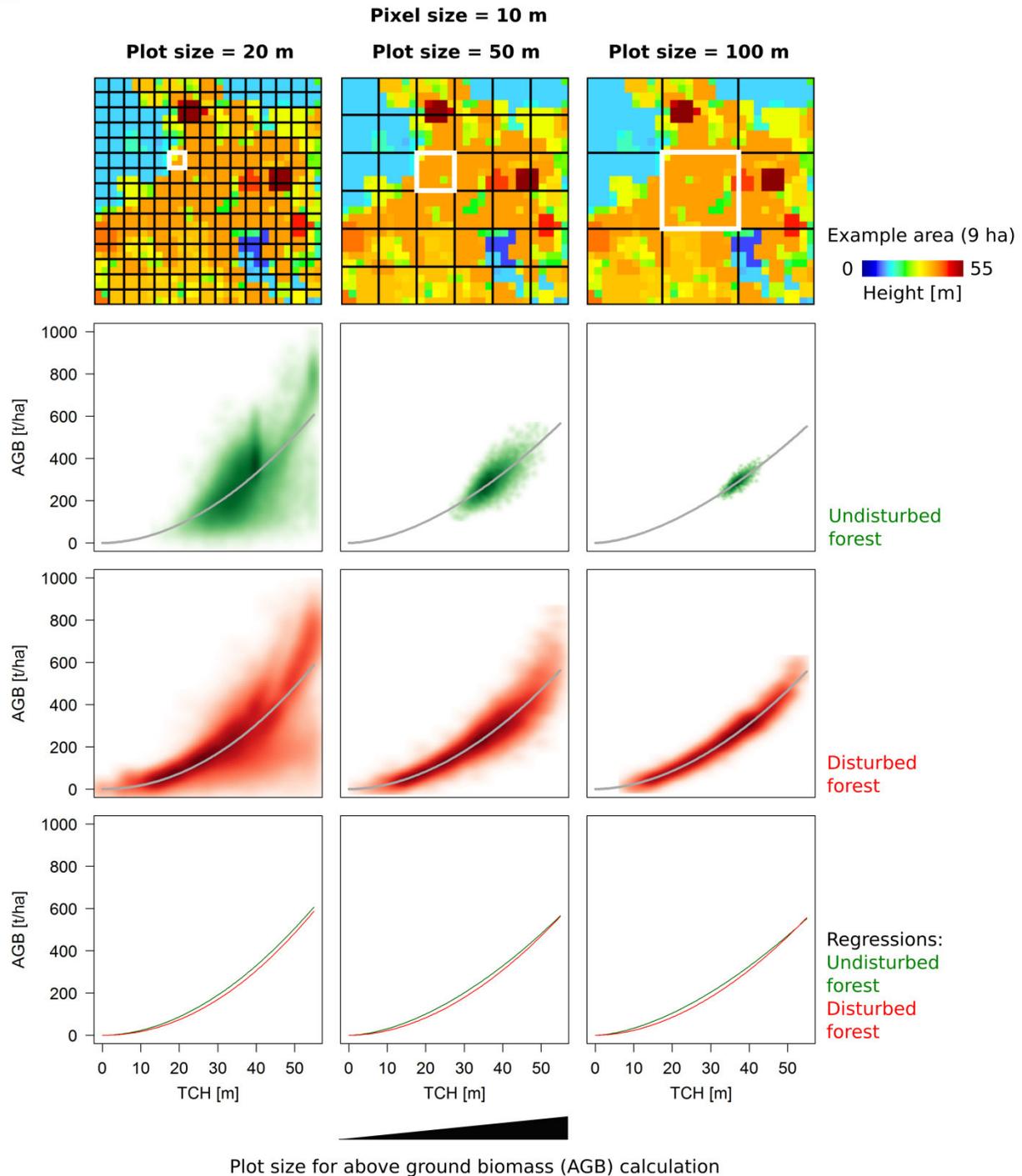
315 The disturbed stands (fire and logging were pooled) cover a wider range of TCH and AGB values than the

316 undisturbed stands. The fitted relationships for undisturbed and disturbed forest stands are similar. The
317 scattering around the regression lines decreases with increasing plot size. If we decrease the pixel
318 resolution from 1 to 10 m (Fig. 6), we observe a change in the TCH-to-AGB relationship. Curves become
319 flatter because averaging over lidar point height maxima in 10 m × 10 m pixels leads to higher TCH-
320 values than averaging over the lidar point height maxima in all 1 m × 1 m pixels. Thus, the coarser the
321 pixel resolution is, the higher the TCH value for a given stand becomes. For the 1-m and the 10-m pixel
322 resolution, we observe similar relations for disturbed and undisturbed forests, respectively. More
323 extensive analyses and graphics that consider the BCI reference data and treat the different disturbance
324 regimes separately can be found in the supplementary material (Fig. S4 and following).



325

326 **Fig. 5: Aboveground biomass (AGB) as a function of top-of-canopy height (TCH) from 1-m pixel resolution (CHM) for different**
 327 **plot sizes. All data was derived from FORMIND and lidar simulations. 1) The first row demonstrates the sampling approach.**
 328 **Shown is a scene of 9 ha simulated forest with different stages of succession. The following rows show the TCH-to-AGB**
 329 **relationship with each record representing one 20-m, 50-m or 100-m plot, respectively, for 2) 1,400 ha of undisturbed**
 330 **simulated forest (green), 3) 1,400 ha of fire-disturbed and 1,400 ha of regularly logged simulated forest (red) and 4) the**
 331 **curves of the best power law fits.**

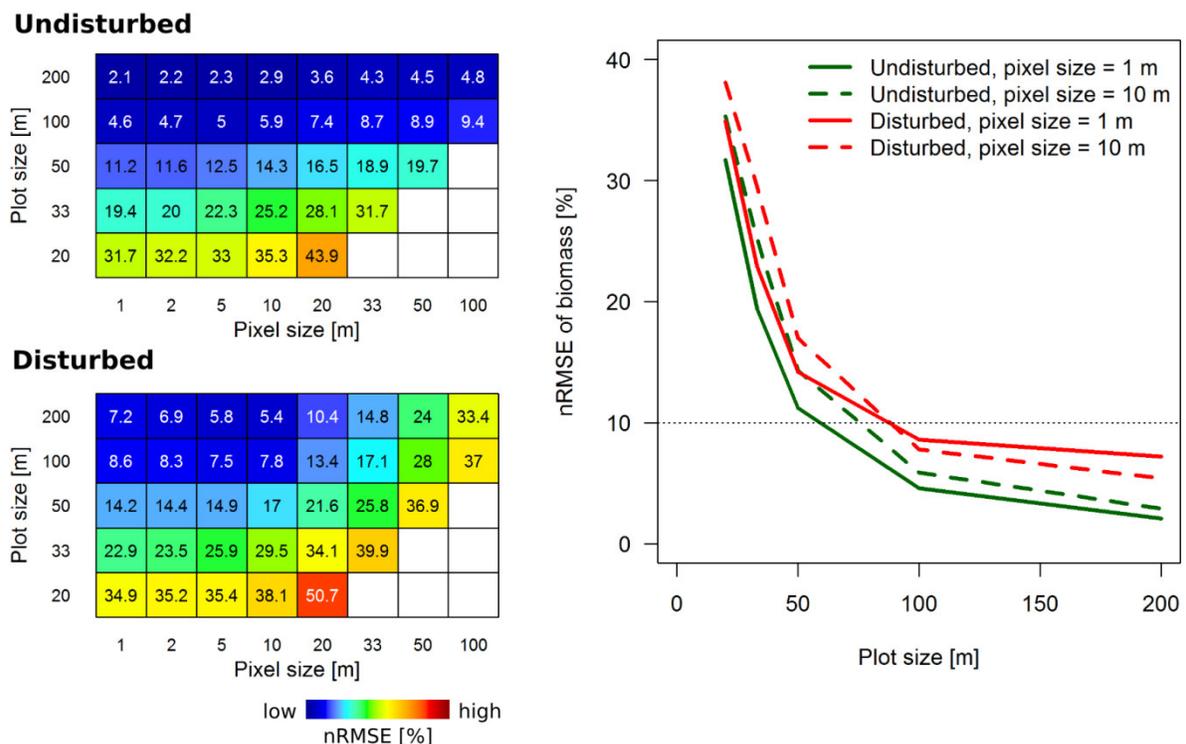


332

333 Fig. 6: Aboveground biomass (AGB) as a function of top-of-canopy height (TCH) from 10-m pixel resolution (CHM) for different
 334 plot sizes. All data was derived from FORMIND and lidar simulations. 1) The first row demonstrates the sampling approach.
 335 Shown is a scene of 9 ha simulated forest with different stages of succession. The following rows show the TCH-to-AGB
 336 relationship with each record representing one 20-m, 50-m or 100-m plot, respectively, for 2) 1,400 ha of undisturbed
 337 simulated forest (green), 3) 1,400 ha of fire-disturbed and 1,400 ha of regularly logged simulated forest (red) and 4) the
 338 curves of the best power law fits.

339

340 The general trends were that the nRMSE of the TCH-based AGB predictions increased with decreasing
 341 plot size and with increasing pixel size (Fig. 7). The prediction accuracy at each scale was better for the
 342 undisturbed forest dataset than for the disturbed forest dataset, indicated by generally lower nRMSE for
 343 each plot size and pixel size combination for the undisturbed forest as compared to the disturbed forest
 344 (Fig. 7). For the disturbed dataset and large plot sizes (100 and 200 m), we observed slightly better
 345 prediction accuracies at medium pixel resolutions (5 and 10 m) than at fine pixel resolutions (1 and 2 m).
 346 The analysis shows that to achieve, a plot-level biomass estimation error < 10%, plot sizes of ≥ 100 m are
 347 required. At such plot sizes, any pixel size would be sufficient to predict AGB for undisturbed forests with
 348 the desired accuracy, but for disturbed forests, the errors exceed 10% and increase strongly at pixel sizes
 349 ≥ 20 m.

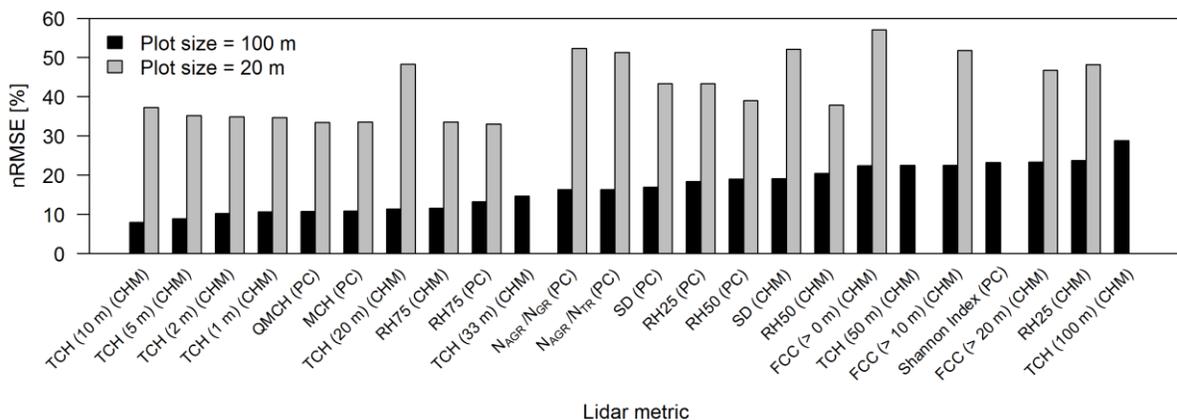


350
 351 **Fig. 7: Normalized root mean square errors (nRMSE) [%] of power law models that describe the relationship between**
 352 **aboveground biomass (AGB) and top-of-canopy height (TCH) at different plot scales and different pixel resolutions for**
 353 **undisturbed and disturbed simulated forest. For pixel sizes of 1 and 10 m, the decrease in nRMSE with increasing plot size is**
 354 **shown on the right side.**

355

356 3.3 Biomass prediction based on various lidar metrics

357 In addition to TCH, we analyzed 21 other metrics concerning their capability to predict biomass using
 358 power law equations. For this analysis, we no longer distinguished between the different disturbance
 359 regimes and pooled all forest stands. Fig. 8 shows nRMSE values for all lidar metrics, for which it was
 360 possible to fit a power law model, at the plot scales of 100 and 20 m. From left to right, the metrics are
 361 sorted by increasing nRMSE at the 100-m plot size. The figure shows that the best ten metrics are all
 362 measures of forest height. Vegetation density metrics (e.g., N_{AGR}/N_{GR} and FCC) and vertical heterogeneity
 363 metrics (e.g., SD and Shannon Index) were less accurate AGB predictors than height metrics. The best
 364 predictions at large plot scales were achieved by TCH (10 m) and TCH (5 m), whereas at small plot scales
 365 RH75, MCH, QMCH and TCH (1 m) were the most accurate predictors. We could not find any relationship
 366 between AGB and CV of height, profile skewness or P:H ratio. The Shannon Index of the profiles only
 367 showed a relationship with AGB for plot sizes ≥ 50 m. Scatter plots of a selection of metrics against AGB
 368 can be found in Fig. S12, nRMSE values for all metrics at all plot scales are displayed in Fig. S13 and
 369 detailed statistics and the coefficients of all fit power laws are listed in Tab. S2.



370
 371 **Fig. 8: Normalized root mean square errors (nRMSE) [%] of power law models that describe the relationship between**
 372 **aboveground biomass (AGB) and various lidar metrics (for explanations of the abbreviations, please refer to the main text**
 373 **and Tab. 1) at plot scales of 100 and 20 m, respectively. From left to right, the metrics are sorted by increasing nRMSE at the**
 374 **100-m plot size. Whether certain metrics were derived from point clouds (PC) or from canopy-height-models (CHM) is**
 375 **indicated in brackets. This analysis was based on pooled (undisturbed and disturbed) simulated forest data and lidar**
 376 **simulations. Missing bars indicate that no power law model could be fit at the 20-m plot size.**

377

378 4. Discussion

379
380 This study demonstrated a new approach for simulating 3D lidar point clouds of forest stands and for
381 investigating structural lidar metrics for their relationship with AGB of a tropical forest using forest
382 simulations. We explored the accuracy of AGB predictions based on various lidar metrics, spatial scales
383 and considering undisturbed and disturbed forest plots.

384 385 4.1 Lidar simulations

386 Unlike other lidar simulation approaches that use detailed radiative transfer theory (Sun et al., 1993; Ni-
387 Meister et al., 2001; Kotchenova et al., 2003; Goodwin et al., 2007) or explicit 3D models of trees and ray
388 tracing (Disney et al., 2010; Endo et al., 2012), our method requires only a minimal parameter set to
389 efficiently compute synthetic lidar point clouds for large areas. Under simple assumptions, e.g., one DBH-
390 to-height and DBH-to-crown-diameter allometry, a constant crown length proportion, cylindrical crowns
391 shapes and a homogeneous leaf area density within crowns, the lidar model was able to reproduce the
392 vertical lidar profiles of different 9-ha subplots within the 50-ha BCI megaplot to an overlap of 87%. An
393 extinction factor k_{NIR} of approximately 0.2 was suggested by empirical measurements (Jones, 2013) and
394 theoretical considerations (Campbell & Norman, 2012; Tang et al., 2012) and could be confirmed by our
395 inverse modeling tests.

396 Airborne and simulated profiles for the 9-ha subplots matched well in general. They diverged most in the
397 upper canopy, where the DBH-to-height allometry led to an overestimation of high trees. Frequencies of
398 ground returns of simulated profiles were approximately 25% lower than for the airborne data, which
399 could be adjusted by choosing another lidar return probability P_0 for ground voxels. Because the exact
400 size of the ground return peak does not affect most of the lidar metrics, we did not treat ground voxels
401 differently than canopy voxels in this study. It should also be noted that simulated lidar profiles

402 (inventory- and FORMIND-based) contain only returns from trees and ground. Non-woody vegetation
403 such as shrubs and lianas may contribute to the airborne lidar profiles, particularly near ground, whereas
404 they are absent in the simulations.

405

406 *4.2 Biomass prediction from lidar height*

407 For the simulated BCI lidar dataset, TCH at various pixel resolutions performed better than any other
408 lidar metric for biomass predictions. The lowest AGB prediction errors (< 10%) were found for large
409 mapping units (plot sizes of 100 and 200 m) with TCH derived from CHMs with pixel sizes of 5 to 20 m.
410 For the smaller mapping units of 50 m, 33 m and 20 m, the minimal achievable errors from any metric
411 were 15%, 23% and 33%, respectively. At those scales, the high pixel resolution TCH, RH75 or point-
412 cloud-based MCH and QMCH led to slightly smaller errors than TCH of medium pixel resolution. The
413 finding that medium pixel resolution CHMs are sufficient to make highly accurate AGB predictions at the
414 1-ha scale is encouraging for spaceborne biomass mapping efforts on the global scale. The generation of
415 high-resolution information (e.g., pixel size of 1 m) requires airborne laser scanning campaigns, whereas
416 medium resolutions can be derived from satellites. The synthetic aperture radar satellite system
417 TanDEM-X can provide forest heights closely correlated to TCH at a resolution of 10 m (referred to as
418 H100 in the radar literature; Kugler et al., 2014; Lee & Fatoyinbo, 2015). Future sensors, such as GEDI
419 (<http://science.nasa.gov/missions/gedi/>) and Tandem-L (<https://www.tandem-l.de/>), will provide data of
420 similar horizontal resolution (20 to 50 m) and improved vertical resolution. Thus, TCH as well as MCH and
421 RH75 of the vertical profiles are promising metrics for estimating AGB using these sensors. The analysis
422 also showed that sensors that only provide maximum height at the coarse resolution of 100 m lead to
423 AGB estimation errors of > 25%. It appears highly plausible that CHMs with pixels sizes around 10 m that
424 correspond to the dimensions of the objects of interest, namely crowns of medium to large trees, which
425 contribute most to the total AGB, are a good data source for AGB inference. High-resolution data such as

426 1-m pixel CHMs or the full point cloud have the advantage of providing detailed information on crown
427 architecture and small gaps, but this information might only be additional noise in the signal for stand
428 level AGB and may not be necessary for large-scale mapping.

429

430 *4.3 The role of structural metrics*

431 Metrics of vertical heterogeneity (e.g., standard deviation or Shannon Index) and vegetation density
432 (e.g., N_{AGR}/N_{GR} or FCC) showed weaker relationships with AGB than most of the height metrics. Hence,
433 these metrics might not be the optimal choice as single AGB predictors. However, considering vegetation
434 structure in addition to mean height could potentially improve AGB estimations. Several approaches
435 have been suggested to improve power-law-based lidar-to-AGB models by considering additional
436 predictors. These predictors include horizontal and vertical structure indices (Tello et al., 2015) and
437 texture metrics of the CHM (Abdullahi et al., 2016). Finally, when thinking beyond AGB stock prediction
438 and towards the study of forest dynamics and disturbances based on remote sensing, structural metrics
439 may become very important. The Shannon Index of the lidar profile has been previously associated with
440 productivity and mortality (Stark et al., 2012), and gap fraction and size distribution may provide
441 information about disturbances (Lobo & Dalling, 2014).

442

443 *4.4 Prediction errors*

444 For all tested lidar metrics, we observed the tendency for the prediction errors to decrease with
445 increasing plot scale. This pattern has been reported and quantified previously for MCH (Asner et al.,
446 2010; Mascaro et al., 2011b), QMCH (Chen et al. 2016) and TCH (Köhler & Huth, 2010; Asner & Mascaro,
447 2014) and in general for the situation in which remote sensing footprints and ground plot extents do not
448 fully match (Réjou-Méchain et al., 2014). In our analysis, the spatial locations and extents of ground plots
449 and remote sensing data matched perfectly, because they were based on simulations. Also there was no

450 displacement of crowns from stem locations. Thus, our dataset is free of geolocation errors and the
451 observed residuals in the lidar-to-AGB relationships can be attributed to the following sources of
452 uncertainty: 1) the highly clumped biomass distribution on the ground, i.e., the majority of biomass is
453 localized in tree trunks at specific positions with empty space in between, whereas remote sensing
454 signals capture the tree crowns, which are spread around the trunk positions; 2) edge effects of
455 overhanging tree crowns with trunk positions and thus biomass being located outside the focal plot area;
456 3) the general variability among trees with respect to their geometries and wood densities; and 4) the
457 undergrowth vegetation that is obscured by the upper canopy and not detected by the remote sensing
458 sensor. The error caused by 1) should decrease with increasing plot size due to the decrease in biomass
459 variability (Fig. 3) and the decreasing influence of single large trees. The error caused by 2) should
460 decrease with increasing core area to edge length ratio. The error caused by 3) should decrease because
461 differences at the individual tree level average out with increasing plot size. Only errors caused by 4) can
462 be expected to be scale-independent. Using a crown-distributed instead of a stem-localized biomass
463 distribution as ground truth has been shown to reduce estimation errors (Mascaro et al., 2011b).
464 However, the actual biomass distribution in a forest is expected to be closer to being stem-localized than
465 (uniformly) crown-distributed. Thus, reducing errors by assuming crown-distributed biomass does not
466 necessarily lead to more accurate biomass maps. Our modeling approach may allow future studies to
467 gain a closer look at the contributions of the separate error sources by switching them off one at a time.
468 Different lidar metrics showed different changes in errors across scales: e.g., in moving from large to
469 small plots, the errors of TCH20, TCH33 and the Shannon Index increased much faster than for other
470 metrics with similar errors at the 200-m scale (Fig. 8 and S13). For the Shannon Index, the relationship
471 with AGB was entirely lost at scales smaller than 50 m.

472

473 *4.5 Linking remote sensing with dynamic forest models*

474 Despite the great potential of the proposed approach, relatively few studies have linked remote sensing
475 and forest modeling. Applications include model initialization (Ranson et al., 2001; Hurtt et al., 2004),
476 model parameterization (Falkowski et al., 2010), remote sensing calibration (Köhler & Huth, 2010; Palace
477 et al., 2015), error quantification (Hurtt et al., 2010; Frazer et al., 2011) and the understanding of large-
478 scale ecosystem patterns and processes (Shugart et al., 2015). Our study is the first to demonstrate how
479 remote sensing simulations combined with a dynamic forest model can provide remote sensing metrics
480 over the full range of disturbance-induced successional stages, which is particularly useful for tropical
481 forests where available field data is limited. The lidar-to-AGB relationships can differ between
482 disturbance types because one type (e.g., fire) might cause mosaics of surviving trees and bare ground,
483 whereas another type (e.g., selective logging) might cause a height degradation throughout the entire
484 study area. Horizontal heterogeneities, such as those caused by fires, are particularly problematic when
485 lidar metrics are aggregated over larger areas. Thus, the disturbance regime of a region and the presence
486 of the described phenomena should be taken into account when deciding which metric and resolution to
487 choose for biomass mapping. Modeling can be one way to explore these effects in greater detail.

488 An important condition for combining a forest model and remote sensing is the structural realism of the
489 model in the relevant aspects. Overall, our model was able to reproduce forest attributes and literature
490 values well. Previous studies on BCI that linked AGB at the 1-ha scale to MCH derived from airborne lidar
491 scans reported RMSE values of $17 \text{ t}_{\text{Carbon}}/\text{ha}$ (Mascaro et al., 2011a) and $28.9 \text{ t}_{\text{AGB}}/\text{ha}$ (Meyer et al., 2013)
492 in agreement with the value of $27.1 \text{ t}_{\text{AGB}}/\text{ha}$ we obtained for the pooled simulated dataset (Tab. S2). A
493 noteworthy deviation between the simulation data and reference data was that for comparable AGB
494 values the simulated TCH was higher than the airborne TCH, particularly at the upper end of the AGB and
495 TCH ranges (described in detail in supplements). We believe that this deviation was primarily caused by
496 the simple tree geometries used in the forest model. Using only one general DBH-to-height allometry for
497 all trees might be suboptimal if the aim is to reproduce the natural height heterogeneity of the upper

498 canopy at all scales. In our simulations, too many trees reached the maximum possible height of 55 m,
499 which is an exceptional height on BCI observed for only one tree in the airborne lidar CHM. Hurtt et al.
500 (2004) encountered a similar problem with large trees. In their case, model-derived canopy heights were
501 restrained to a maximum, whereas observed lidar heights exceeded that limit. Therefore, one potential
502 improvement for future model parameterizations would be to consider asymptotic instead of power law
503 DBH-to-height allometries and allow for a certain plasticity of modeled heights and crown diameters. The
504 sensitivity analysis about model assumptions showed that the alternative scenario using an asymptotic
505 tree height allometry led to slight increases in R^2 and decreases in nRMSE of the stand height to biomass
506 relationship (S16-S18). Recent advances in individual tree delineation from airborne lidar (Duncanson et
507 al., 2014; Ferraz et al., 2016) and terrestrial laser scanning (Raumonen et al., 2013) have the potential to
508 improve our understanding of tree allometries and the structural realism of forest models. When models
509 are able to reproduce observed patterns in the relationship between remote sensing metrics and static
510 biomass stocks, we can move forward using the presented methodology to explore dynamic changes of
511 biomass stocks.

512

513 **5. Conclusion**

514

515 This study introduced a novel approach for coupling remote sensing simulations with a dynamic forest
516 model to derive structure-to-biomass relationships for a tropical forest, including disturbed stands. The
517 lidar model was validated successfully with airborne and census reference data from Barro Colorado
518 Island. The model proved its capacity for efficient and realistic lidar point cloud simulations for large,
519 simulated forest stands. Virtual forest inventory datasets were generated with a forest model and
520 sampled with the lidar simulation model. The results provide a comprehensive overview of biomass

521 estimation errors for a wide range of lidar metrics and spatial scales and may guide decisions on which
522 metric to choose for a given remote sensing data structure (e.g., point clouds, vertical profiles, canopy
523 height models). It was found that height-to-biomass relationships were similar for undisturbed and
524 disturbed forest, but errors were larger for the latter. Furthermore, we found that top-of-canopy height
525 was an accurate biomass predictor even if pixel resolutions were only 10 to 20 m. Such resolutions could
526 be derived at large scale from spaceborne sensors.

527

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529

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539

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754 **LIST OF FIGURE CAPTIONS**

755 Fig. 1: Workflow of the study. Reference data from field inventories and an airborne lidar campaign were
756 used to parameterize and calibrate a forest model and a lidar model. With the models, large quantities of
757 simulated inventory and simulated lidar data were generated, allowing for a systematic analysis of lidar-
758 to-biomass relationships under different disturbance regimes and for various spatial scales.

759 Fig. 2: Principle of the lidar model. Inputs to the workflow can either be forest model output or field
760 inventory data. The pictures on the right side show intermediate products: a) Visualization of a forest
761 stand; b) voxel representation with colors indicating the cumulative leaf area index; c) voxel
762 representation with colors indicating the probability of containing a lidar return; d) simulated lidar point
763 cloud with colors indicating height above ground.

764 Fig. 3: Relative frequency distributions of aboveground biomass (AGB). Columns represent the BCI field
765 data (50 ha) and output of FORMIND simulations from different disturbance scenarios (1,400 ha each).
766 Rows represent different spatial resolutions. Notice the different axis scaling in each row.

767 Fig. 4: Vertical lidar profiles of a) the 9 ha in the southwestern corner of the BCI megaplot, airborne and
768 simulated based on inventory data; b) the same for the 9 ha in the northeastern corner of the BCI
769 megaplot; and c) the simulated lidar profile of 16 ha simulated forest in FORMIND in the old growth
770 stage (age 500 yr). Dashed lines mark the mean canopy profile height (MCH), and 'x' symbols mark the
771 ground return peaks.

772 Fig. 5: Aboveground biomass (AGB) as a function of top-of-canopy height (TCH) from 1-m pixel resolution
773 (CHM) for different plot sizes. All data was derived from FORMIND and lidar simulations. 1) The first row
774 demonstrates the sampling approach. Shown is a scene of 9 ha simulated forest with different stages of
775 succession. The following rows show the TCH-to-AGB relationship with each record representing one 20-
776 m, 50-m or 100-m plot, respectively, for 2) 1,400 ha of undisturbed simulated forest (green), 3) 1,400 ha
777 of fire-disturbed and 1,400 ha of regularly logged simulated forest (red) and 4) the curves of the best
778 power law fits.

779 Fig. 6: Aboveground biomass (AGB) as a function of top-of-canopy height (TCH) from 10-m pixel
780 resolution (CHM) for different plot sizes. All data was derived from FORMIND and lidar simulations. 1)
781 The first row demonstrates the sampling approach. Shown is a scene of 9 ha simulated forest with
782 different stages of succession. The following rows show the TCH-to-AGB relationship with each record
783 representing one 20-m, 50-m or 100-m plot, respectively, for 2) 1,400 ha of undisturbed simulated forest
784 (green), 3) 1,400 ha of fire-disturbed and 1,400 ha of regularly logged simulated forest (red) and 4) the
785 curves of the best power law fits.

786 Fig. 7: Normalized root mean square errors (nRMSE) [%] of power law models that describe the
787 relationship between aboveground biomass (AGB) and top-of-canopy height (TCH) at different plot
788 scales and different pixel resolutions for undisturbed and disturbed simulated forest. For pixel sizes of 1
789 and 10 m, the decrease in nRMSE with increasing plot size is shown on the right side.

790 Fig. 8: Normalized root mean square errors (nRMSE) [%] of power law models that describe the
791 relationship between aboveground biomass (AGB) and various lidar metrics (for explanations of the
792 abbreviations, please refer to the main text and Tab. 1) at plot scales of 100 and 20 m, respectively. From
793 left to right, the metrics are sorted by increasing nRMSE at the 100-m plot size. Whether certain metrics
794 were derived from point clouds (PC) or from canopy-height-models (CHM) is indicated in brackets. This
795 analysis was based on pooled (undisturbed and disturbed) simulated forest data and lidar simulations.
796 Missing bars indicate that no power law model could be fit at the 20-m plot size.

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798 **LIST OF TABLE CAPTIONS**

799 Tab. 1: List of the lidar metrics and the underlying data (PC = point cloud, CHM = canopy height model).
800 CHM usually refers to 1-m resolution rasters, except for TCH where various resolutions were tested.

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