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Using repeated small-footprint LiDAR acquisitions to infer spatial and temporal variations of a high-biomass Neotropical forest

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3

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21 **Abstract**

22

23 In recent years, LiDAR technology has provided accurate forest aboveground biomass (AGB) maps

24 in several forest ecosystems, including tropical forests. However, its ability to accurately map forest

25 AGB changes in high-biomass tropical forests has seldom been investigated. Here, we assess the

26 ability of repeated LiDAR acquisitions to map AGB stocks and changes in an old-growth

27 Neotropical forest of French Guiana. Using two similar aerial small-footprint LiDAR campaigns

28 over a four year interval, spanning ca. 20 km², and concomitant ground sampling, we constructed a

29 model relating median canopy height and AGB at a 0.25-ha and 1-ha resolution. This model had an

30 error of 14% at a 1-ha resolution (RSE=54.7 Mg ha⁻¹) and of 23% at a 0.25-ha resolution

31 (RSE=86.5 Mg ha⁻¹). This uncertainty is comparable with values previously reported in other

32 tropical forests and confirms that aerial LiDAR is an efficient technology for AGB mapping in

33 high-biomass tropical forests. Our map predicts a mean AGB of 340 Mg ha⁻¹ within the landscape.

34 We also created an AGB change map, and compared it with ground-based AGB change estimates.

35 The correlation was weak but significant only at the 0.25-ha resolution. One interpretation is that

36 large natural tree-fall gaps that drive AGB changes in a naturally regenerating forest can be picked

37 up at fine spatial scale but are veiled at coarser spatial resolution. Overall, both field-based and

38 LiDAR-based estimates did not reveal a detectable increase in AGB stock over the study period, a

39 trend observed in almost all forest types. Small footprint LiDAR is a powerful tool to dissect the

40 fine-scale variability of AGB and to detect the main ecological controls underpinning forest

41 biomass variability both in space and time.

42

43 **Keywords:** LiDAR; Aboveground biomass; Forest carbon; Tropical forest; Forest dynamic.

44 **1. Introduction**

45 Tropical forests play an important role in the terrestrial carbon cycle. Tropical deforestation and
46 degradation are a large source of carbon (C) emissions into the atmosphere, contributing some 7-
47 15% to the total anthropogenic C emissions since the early 2000s (Pan *et al.* 2011; Harris *et al.*
48 2012). This carbon loss from the terrestrial biosphere is thought to be approximately balanced by
49 forest regrowth and by an increase in terrestrial ecosystem carbon storage ability through time
50 related to global or regional forcings, such as CO₂ fertilization, temperature increase, or rainfall
51 fluctuations (Lewis *et al.* 2009; Pan *et al.* 2011). An effective strategy for mitigating anthropogenic
52 CO₂ emissions is to implement national and international governance agreements that will help curb
53 deforestation and forest degradation (Agrawal *et al.* 2011). To meet this challenge, it is essential to
54 implement robust techniques for the quantification of carbon stocks and changes in tropical forests
55 (Chave *et al.* 2005; Saatchi *et al.* 2011; Le Toan *et al.* 2011; Clark & Kellner 2012).

56 Light detection and ranging sensors (LiDAR), a technology dating back to the early 1980s (Arp
57 & Tranarg 1982; Aldred & Bonner 1985), has now made impressive progress and is being routinely
58 used to determine forest structural characteristics (Lefsky *et al.* 2002). The high spatial resolution of
59 current airborne LiDAR systems and their ability to cover large remote areas make it an attractive
60 option for conservation and/or management programs and for the implementation of landscape-
61 scale GHG emission mitigation strategies (Agrawal *et al.* 2011). In mixed-species, closed-canopy
62 tropical forests, studies using a LiDAR system to infer forest structural parameters date back at least
63 to the early 2000s (Drake *et al.* 2002, 2003), and they have since been applied broadly in the
64 Neotropics (e.g. d'Oliveira *et al.* 2012; Vincent *et al.* 2012; Asner *et al.* 2013a; b), in South-East
65 Asia (Englhart *et al.* 2013; Jubanski *et al.* 2013) and in Africa (Asner *et al.* 2012a; b; Vaglio Laurin
66 *et al.* 2014). Zolkos *et al.* (2013) have conducted a meta-analysis including over 70 studies that used
67 LiDAR for forest aboveground biomass (AGB) retrieval. Of these, 10 studies were conducted in
68 forests with a mean AGB > 300 Mg ha⁻¹, and only one of these studies was in the tropics (Hawaii;
69 Asner *et al.* 2009). In light of the fast pace of publications on this research theme, two challenges

70 appear to be outstanding.

71 First, it is important to document the errors associated with LiDAR-AGB models in the high-
72 biomass forested areas of the tropics, notably because the absolute errors associated with LiDAR-
73 AGB models are expected to be significantly higher in such high-biomass areas (Zolkos *et al.*
74 2013). Second, the direct monitoring of changes in AGB in tropical forests is a crucial challenge in
75 carbon accounting programs, and it appears to be now possible from remotely sensed instruments at
76 least in areas undergoing deforestation and degradation (Asner *et al.* 2005). However, the ability of
77 this technique to describe the natural dynamics of old-growth forests is still outstanding.

78 Encouraging results have been obtained in temperate and in boreal forests (Hudak *et al.* 2012;
79 Bollandsås *et al.* 2013; Næsset *et al.* 2013; Skowronski *et al.* 2014). However, tests in tropical
80 forests have thus far been less conclusive. To our knowledge, only two published studies have
81 sought to compare the performance of LiDAR and ground-based data to measure the AGB
82 dynamics of tropical forests. The first study was conducted at La Selva, Costa Rica, and used large-
83 footprint airborne LiDAR data (Dubayah *et al.* 2010). The second study was conducted at Barro
84 Colorado Island, Panama, and used a combination of small- and large-footprint LiDAR (Meyer *et*
85 *al.* 2013). Both studies found a weak relationship between changes in LiDAR metrics and field-
86 measured AGB changes. One possible interpretation is that the signature of natural forest dynamics
87 is too subtle to be detectable by change in LiDAR metrics (Dubayah *et al.* 2010). However, the use
88 of large footprint sensors or systematic differences in accuracy across LiDAR sensors may also
89 explain these results (Zolkos *et al.* 2013).

90 Forests of the Guiana Shield hold the highest AGB values and the tallest forests of the
91 Neotropics (Feldpausch *et al.* 2011, 2012; Saatchi *et al.* 2011). Their AGB stock is comparable to
92 that reported in central Africa and in some forests of South-East Asia (Slik *et al.* 2013). Using two
93 LiDAR campaigns conducted at four-year intervals combined with intensive and concomitant
94 ground sampling (15,438 trees monitored over almost 30 ha), we infer the spatial and temporal
95 variation of AGB in an old growth tropical forest landscape of French Guiana (Fig. 1). We

96 specifically ask the two following questions: i) Can the spatial variation in AGB be detected
97 accurately using LiDAR in tall, high-biomass, tropical forests?; ii) How do LiDAR-derived
98 temporal changes in AGB compare with field-derived estimates?

99

100 **2. Materials and methods**

101 *2.1. Study area*

102 Our study was carried out in the lowland rain forest of French Guiana at the Nouragues Ecological
103 Research Station (Fig. 1 and 2). The landscape corresponds to a succession of hills, ranging
104 between 26-280 m asl, with a granitic outcrop (inselberg) reaching 430 m asl. Rainfall is 2861 mm
105 y^{-1} (average 1992-2012), with a 2-mo dry season ($< 100 \text{ mm month}^{-1}$) during September and
106 October, and a shorter dry season in March. Human activity is unlikely to have induced major
107 disturbances in recent history: now extinct Nouragues Amerindians are reported to have inhabited
108 this area during the eighteenth century, but departed further south some 200 years ago. The forest
109 around the station harbours a diverse flora (Sabatier & Prévost 1990; van der Meer & Bongers
110 1996), with over 1700 angiosperm species recorded in the Natural Reserve.

111

112 *2.2. LiDAR data acquisition*

113 Two acquisitions of small footprint discrete return LiDAR were conducted in the Nouragues
114 research area. The first coverage was conducted in two steps, in November 2007 and November
115 2008 for a total area of 1,900 ha (Fig. S1a). This first acquisition was based on a portable Riegl
116 laser rangefinder (LMS6Q140i-60) positioned on a helicopter flying at about 30 m s^{-1} ca 150 m
117 above the ground. This rangefinder system is a time-of-flight measurement of 30 kHz laser pulse in
118 the infrared wavelength region ($0.9 \mu\text{m}$) with a footprint of 0.45 m and a scan angle of 60° . The
119 average laser point density was ca. 4 imp/m^2 and acquisitions were all conducted in last return mode
120 to maximise penetration (the system used did not have multiple return registering capacity). The
121 second acquisition occurred in March 2012 and covered an area of 2,400 ha (Fig. S1b). Acquisition

122 was based on a portable Riegl laser rangefinder (LMS-Q560) embarked on a Falcon aircraft at a
123 speed ca 45 m s⁻¹ about 400 m above the ground. It used a 200 kHz laser pulse in the infrared
124 wavelength region (1.5 μm) with a footprint of 0.25 m and a scan angle of 45°. The average laser
125 point density was ca. 20 imp/m² (the system had multiple returns registering capacity). This pulse
126 density is much higher than most previous studies, ensuring a good canopy penetration rate and thus
127 an accurate digital elevation model. In both acquisitions, the systems included two dual-frequency
128 GPS receivers coupled to an inertial navigation system, ensuring that a sub-decimeter differential
129 position can be calculated at the post-processing stage. The area of overlap of the two acquisitions
130 was ca. 1,400 ha. The two LiDAR campaigns were contracted by a private company
131 (<http://www.altoa.fr/>).

132

133 2.3. LiDAR data processing

134 A major challenge, especially in dense tropical forests, is to identify the LiDAR echoes that lie on
135 the probable ground surface (i.e. bare-earth points). The number of bare-earth points directly affects
136 the accuracy of the digital elevation model (DEM), which itself determines the precision of the
137 canopy model (Dubayah *et al.* 2010). To maximize the accuracy of the DEM, we combined the
138 cloud data of the two acquisitions. Bare-earth points were identified in the global cloud data using
139 the TerraScan (TerraSolid, Helsinki) ‘ground’ routine, which classifies ground points by iteratively
140 building a triangulated surface model. We manually checked the cloud of points to assess possible
141 issues with this automatic procedure. This led to about 0.35 bare earth points/m² over the entire area
142 (out of c.a. 24 imp/m² combining the two acquisitions). A DEM grid was subsequently generated at
143 1-m resolution using the “GridSurfaceCreate” procedure implemented in FUSION v.3.2
144 (McGaughey 2012). This procedure computes the elevation of each grid cell using the average
145 elevation of all points within the cell (cells containing no bare-earth points are filled by the
146 weighted average of the closest grid points).

147 Two canopy elevation models were produced with the 2007/8 dataset and with the 2012

148 dataset. Canopy point outliers were removed automatically by the “FilterData” procedure
149 implemented in FUSION (McGaughey 2012). The canopy model was then constructed at 1-m
150 resolution using the 1-m resolution DEM and the “CanopyModel” procedure implemented in
151 FUSION. This procedure subtracts the elevation model from the return elevation and then uses the
152 highest return value to compute the canopy surface model. The last step consisted in applying a 3x3
153 neighbour window median filter to smooth the surface and thus avoid local unrealistic maxima or
154 minima. To construct the most recent canopy model, we only considered the last return points (12.5
155 points/m²), so as to avoid systematic biases when comparing the two LiDAR datasets. Median
156 canopy height (H_{50}) constructed with LiDAR first returns correlated strongly with that constructed
157 with the last returns (Pearson’s $r > 0.99$), and the mean difference was 0.89 m (median of 0.83).

158 The 2007/8 LiDAR dataset had a sparser and more heterogeneous coverage and a more
159 heterogeneous point density in space than the 2012 dataset (Fig. S1). To analyse changes in forest
160 structure and carbon stocks, we thus discarded all grid units in which more than 15% of the 1-m²
161 pixels contained less than 2 points/m² in the 2007/8 dataset (i.e. about half of the mean point
162 density). Exploratory analyses showed that this procedure removed all unrealistic grid values of
163 AGB change while preserving most of the grid units (90.3% of the pixels were kept in the analysis).

164

165 *2.4. Field data*

166 Seven permanent sampling plots covering a total area of 29.75 ha were established at the Nouragues
167 Ecological Research Station (Fig. 2). In these plots, all living trees ≥ 10 cm of diameter at breast
168 height (DBH) were mapped, censused, and botanically identified by experts during the last decade
169 (67.3% of the 15,438 individuals were identified to at least genus level). DBH was measured at 1.3
170 m above the ground and to the nearest 0.1 cm. For trees with buttresses, stilt roots or irregularities,
171 trunks were measured 30 cm above the highest irregularity, and the point of measurement was
172 marked with permanent paint. The procedure implemented in the case of a change in the DBH point
173 of measurement between two campaigns is fully described in the supplementary information. One

174 10-ha plot (called “grand plateau”) and one 12-ha plot (“petit plateau”) were remeasured at the end
175 of 2008, and then again at the end of 2012 (data available from forestplots.net; Lopez-Gonzalez *et*
176 *al.* 2009, 2011). These two plots are dominated by terra-firme forest, with small flooded forest
177 patches and a ca. 1-ha patch of liana-infested forest (B. Tymen *et al.*, in revision). In 2007, one 6-ha
178 terra-firme forest plot was inventoried ca. 7 km South (“Pararé”, Fig. 2). In 2012, smaller plots were
179 established to encompass the range of forest type variability: one 1-ha plot in an occasionally
180 flooded forest (“Ringler”), two 0.25-ha plots in swamp forest dominated by the palm *Euterpe*
181 *oleracea*, and one 0.25-ha plot in a low forest on shallow granitic bedrock.

182 In addition to DBH measurements, we measured the total height of all trees located in plots
183 ≤ 1 ha and in at least one 1-ha subplot in the three larger plots. For a few trees for which accurate
184 measurements were impossible, total height was estimated. In total 2,212 trees had total tree height
185 measured directly. Total tree height was measured by aiming at the tallest branches with a high-
186 resolution laser rangefinder (LaserAce 1000 rangefinder, Trimble, Sunnyvale CA). The built-in
187 inclinometer of this rangefinder has an accuracy of 0.2° , and its distance-measuring device an
188 accuracy of 10 cm at 75 m with a passive target, and a resolution of 1 cm. We targeted the top
189 leaves or branches, moving 180 degrees around the tree in order to locate the highest point, and we
190 also relied on the opinion of at least two trained operators. Total tree height was taken to be the
191 maximum value of several distance measurements. Cross-controls by different operators were
192 regularly conducted to assess the accuracy of our measurements, and these validation checks
193 indicate that our tree height data were on average accurate to the nearest 0.5 m. To infer total tree
194 height for the trees that were not directly measured, we defined plot-specific tree height-diameter
195 allometries of the form:

$$196 \quad (1) \quad \ln(H) = a + b \times \ln(D) + c \times \ln(D)^2 + \varepsilon$$

197 where H and D are total tree height and dbh, respectively, and ε is the error term, assumed to be
198 normally distributed with zero mean and residual standard error $\sigma_{\log\text{-log model}}$. Model (1) was trained
199 using the tree height ground measurements. The height of all trees was subsequently estimated

200 using Eq (1) and accounting for a known bias by applying the Baskerville correction (see
201 supplementary information; Baskerville 1972):

$$202 \quad (2) \quad \bar{H} = \exp(\sigma_{\log-\log model}^2/2 + a + b \ln(D) + c \ln(D)^2)$$

203 Model parameters are provided in the supplementary information (Fig. S2 and Table S1).

204

205 Ground plots were carefully geo-located by averaging several GPS points at the corners of
206 the plots. We selected one corner and calculated the location of the three other corners using the size
207 and orientation of the plot on the field. A deviation of 18° from the magnetic North Pole to the
208 geographic North Pole was assumed to account for the magnetic singularity over the Guiana Shield.
209 We cross-validated the geolocation using the location of large tree crowns clearly visible in the
210 LiDAR canopy model (Fig. S3).

211

212 2.5. Ground AGB estimation

213 In the recent literature, stand-scale AGB was often reported in carbon units and referred to as
214 aboveground carbon density (or ACD). Here we prefer to report values in oven dry biomass units,
215 but it should be borne in mind that 1 kg of dry biomass holds on average 0.48 kg of carbon (Thomas
216 & Martin 2012). Tree aboveground biomass (AGB_t) was estimated using the equation of Chave et al.
217 (2014):

$$218 \quad (3) \quad AGB_t = 0.0673 \times (\rho \times D^2 \times \bar{H})^{0.976}$$

219 where ρ is the wood density in g.cm^{-3} and where total height \bar{H} was either measured directly or
220 inferred from equation (2). Wood density ρ was inferred from the taxonomy using a global database
221 (Chave et al. 2009). We assigned a ρ value to each individual tree that corresponded to the mean ρ
222 for species found in the database. We considered only measures that were made in tropical region of
223 South America (n=4,182) in order to limit the bias due to regional variation of wood density
224 (Muller-Landau 2004; Chave et al. 2006). When no reliable species identification or no wood
225 density information at the species level was available, the mean wood density at higher taxonomic

226 level (i.e. genus, family) or at the plot level was assigned to the tree.

227 The palm *Euterpe oleracea* was dominant in flooded areas. We thus constructed a specific
228 biomass allometry from the destructive harvest data of Miranda et al. (2012) (See supplementary
229 information and Fig. S4 for details and for other error metrics):

230 (4) $AGB_t = \exp(-3.863 + 2.987 \times \ln(D))$ (n=13; $\sigma_{\log\text{-log model}}=0.292$)

231 or

232 (5) $AGB_t = \exp(-3.290 + 0.879 \times \ln(D^2 \times H))$ (n=13; $\sigma_{\log\text{-log model}}=0.205$)

233 AGB was then summed across trees, and normalized by plot area to obtain AGB in $Mg\ ha^{-1}$. To
234 estimate AGB in patches of bamboo forest, we conducted a destructive sampling in one 0.125-ha
235 plot of *Guadua sp.* bamboos. In one 10 m x 1 m subplot, we sampled all bamboos ≥ 0.8 cm
236 diameter (36 individuals). The above ground part (stem and leaves) of 13 individuals was oven-
237 dried and weighted, the total dry mass being 4.27 kg. This estimate was then extrapolated to the
238 0.125-ha plot and the AGB of an isolated tree of *Cecropia obtusa* was added to the estimate using
239 Equation (3).

240

241 2.6. Relating LiDAR metrics and stand-scale AGB estimates

242 We carefully coregistered the LiDAR cloud of points and the ground plots by using several GPS
243 datapoints per plot, and also by matching the ground position of emergent trees with the LiDAR
244 canopy model (Fig. S2). LiDAR metrics were calculated within the limits of the calibration plots,
245 ensuring the best spatial match between LiDAR and ground measurements. Stand-scale AGB
246 estimate was fitted against several LiDAR metrics at two different spatial resolutions: 1 ha (100 m x
247 100 m) and 0.25 ha (50 m x 50 m). To this end, we partitioned our large plots into subplots. We
248 found that median height of the LiDAR canopy model (H_{50}) provided the best fit to ground-based
249 AGB (Table S2). A model selection using H_{50} and any other of these additional LiDAR-based
250 metrics did not provide significantly better model fits than the model including H_{50} alone (Table
251 S3). At both spatial resolutions, we thus fitted independently a log-log linear ordinary least square

252 model of the form:

$$253 \quad (6) \quad \ln(\text{AGB}) = a + b \times \ln(H_{50}) + \varepsilon$$

254 where ε is an error term assumed to be normally distributed with zero mean. After the back-
255 transformation, accounting for the Baskerville correction, stand-scale AGB can thus be inferred
256 from H_{50} using the following model:

$$257 \quad (7) \quad \overline{\text{AGB}} = \exp\left(a + \frac{RSE^2}{2} + b \times \ln(H_{50})\right)$$

258 To facilitate the comparison with previous studies (e.g. Mascaro *et al.* 2011a; Asner *et al.* 2012b;
259 Asner & Mascaro 2014), we also provide equation (7) in the equivalent form:

$$260 \quad (8) \quad \overline{\text{AGB}} = A \times H_{50}^b$$

261 where $A = \exp\left(a + \frac{RSE^2}{2}\right)$. Such a power-law model has been shown to predict well AGB from
262 LiDAR metrics (Mascaro *et al.* 2011a). To fit this statistical model, stand-scale AGB was inferred
263 from the 2012 ground data while H_{50} was calculated from the 2012 LiDAR canopy model, except
264 for the “Pararé” plot where the field data were only available in 2007. In that special case, the
265 2007/8 LiDAR canopy model was used. We also tested whether AGB model construction based on
266 only the 2007/2008 data or based on only the 2012 data led to different results. We found that the
267 two statistical models relating H_{50} and AGB were very close and thus interchangeable: the mean
268 relative difference across model predictions was within 0.5% of the estimate, and both had the same
269 uncertainty (Fig. S5). We henceforth use only the model based on the 2012 data, thought to be the
270 more accurate.

271

272 2.7. LiDAR AGB change

273 To estimate AGB changes using multiple LiDAR acquisitions, we computed the difference of the
274 two AGB stock layers as derived from the LiDAR metrics and divided the difference by the time
275 elapsed between the two acquisitions, to obtain an annual change in AGB. This procedure was
276 conducted at the 0.25-ha and 1-ha scales. This approach is similar to the “indirect approach”

277 described in Meyer *et al.* (2013) and Skowronski *et al.* (2014), excepted that we used the same
278 LiDAR-AGB model to infer AGB from the two LiDAR datasets (see above; Fig. S5). To validate
279 these products, we compared AGB change as inferred from LiDAR and as measured within the
280 limits of the calibration plots at 0.25 and 1 ha scale using field plots that were surveyed both in
281 2008 and 2012 (22 ha). The comparison was done with a reduced major axis (RMA) regression that
282 minimizes the sum of squared distances both horizontally (accounting for the error in X) and
283 vertically (accounting for the error in Y) because neither the field-based nor the LiDAR-based AGB
284 changes can be considered as true measurements. Significance was assessed with a test based on the
285 Pearson's product moment correlation coefficient (function “cor.test” in the R statistical software).
286 A second approach would have been to model AGB change directly from change in LiDAR metrics
287 (Skowronski *et al.* 2014). However, because we used the same inversion model for the two datasets,
288 our approach has exactly the same associated error (i.e., the same residual standard error, RSE).

289

290 **3. Results**

291 *3.1. Landscape variation in canopy height*

292 Canopy height, as inferred by LiDAR, revealed a strong spatial structure at the landscape scale (Fig.
293 2b, Table S4). The maximum registered canopy height was of 67 m and 1% of the 1x1 m pixels had
294 a height > 50 m. A mosaic of low vegetation (<10 m), low forests (10-25 m) and tall forests (>25 m)
295 occurred within the landscape (Fig. 2b and 2c; mean canopy height per vegetation type is given in
296 Table S4). The large patches of low vegetation (2% of the surveyed scene) corresponded
297 predominantly to bamboo thickets or occasionally to Marantaceae or Heliconiaceae patches; low
298 forests correspond to liana forests (1%), flooded forests (13%) or hill-top forests (9%). Tall forests
299 are typical *terra firme* forests (72%).

300

301 *3.2. Relation between LiDAR metrics and field AGB*

302 Ground-based AGB was significantly predicted by H_{50} both at the 0.25-ha (ratio of the RSE to the

303 prediction mean, RSE_{rel}, of 22.3%; $P < 0.001$; Fig. 3) and the 1-ha scale (RSE_{rel} = 13.8%; $P < 0.001$).
304 Alternative models or alternative LiDAR-derived metrics did not display a better statistical
305 performance (table S2). The residuals of this model were not explained by forest type at the 0.25-ha
306 scale (Kruskall-Wallis test, $X^2=2.07$, $P=0.72$), or by variation in wood density across plots
307 (Pearson's $r=0.11$, $P=0.22$) but were spatially autocorrelated (Moran's $I=0.31$, $P < 0.001$). The
308 exponent b relating H_{50} to the AGB was close to 1 at the 1-ha scale, thus the relationship was found
309 to be nearly linear. At the 0.25-ha resolution, a few plots were outliers, displaying a much higher
310 ground-based AGB value than inferred using the LiDAR data (Fig. 3). These outlying plots were
311 characterized by a disproportionate number of large-diameter trees.

312 The AGB map revealed an important spatial structure (Fig. 4a), related to topographical
313 variation (Supplementary information ; Fig. S6). Over the study area, AGB showed a bimodal
314 distribution (Fig. 4b). The first mode corresponded to about 7 % of the total area, and was
315 characteristic of low-vegetation patches, bamboo thickets and of the bare ground of the Inselberg
316 top. The second represented a continuum of closed-canopy forest types. At landscape-scale, mean
317 AGB was estimated to be 344 Mg ha⁻¹ (excluding the granitic outcrop). In comparison, mean AGB
318 across plots was 388 Mg ha⁻¹, hence permanent plots tend to be biased towards high-AGB forests
319 (tall forests have a mean landscape AGB of 382 Mg ha⁻¹; Table S4). Mean AGB per forest type
320 within the scene is provided in Table S4.

321

322 *3.3. Relation between LiDAR metrics and field AGB change*

323 We first compared ground-based AGB change measures and LiDAR-derived ones in the survey
324 plots. We found a significant correlation at 0.25-ha scale, but not at 1-ha scale (Fig. 5). In both
325 cases, the relationship was poor. Across the study area, the LiDAR-derived AGB change map
326 showed that the median change was slightly positive during the study period (median of +0.13 Mg
327 ha⁻¹ yr⁻¹), indicating that most patches were accumulating carbon (Fig. 6). However mean AGB
328 change was slightly negative (mean of -0.79 Mg ha⁻¹ yr⁻¹). Together, these results suggest that the

329 forest landscape has not increased in AGB during the study period due to some localized large
330 losses of carbon (defined as losses of $> 25 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ in localized pixels). The slight negative
331 trend was observed in all forest types with the exception of the granitic outcrop (Table S4). To
332 verify that our results were not influenced by the difference in sensor type from one survey to the
333 next, we constructed independent LiDAR-AGB models using the two LiDAR datasets and showed
334 that they provided undistinguishable predictions (mean relative difference to within 0.5%) with the
335 same associated error (Fig. S5).

336

337 **4. Discussion**

338 We used two small-footprint LiDAR campaigns to construct a detailed map of canopy structure in
339 an old-growth, high-carbon stock, tropical forest of the Guiana Shield. The landscape was
340 surprisingly heterogeneous, with frequent occurrences of low vegetation patches (liana-infested
341 forests, palm-dominated swamps, bamboo-dominated patches) interspersed within the high-canopy
342 forest matrix. We constructed and validated a statistical model to infer aboveground biomass (AGB)
343 stocks from LiDAR data and we compared the field and LiDAR estimates of AGB changes over a
344 four-year period.

345

346 *4.1. Inferring AGB from LiDAR*

347 Small footprint LiDAR technology was able to detect the fine-grained spatial variation in AGB
348 across a 2,400-ha landscape characterized by both high AGB values (344 Mg ha^{-1} on average in our
349 study area, excluding the granitic outcrop) and a range of tropical forest types. Recently, Taylor et
350 al. (2015) also found that LiDAR was appropriate to map AGB in closed-canopy forests on the Osa
351 Peninsula, Costa Rica, but their mean AGB was much lower than the value reported here (mean of
352 $150\text{-}200 \text{ Mg ha}^{-1}$ depending on the soil type, see their Figure 3A). In our study, the average AGB
353 stock in permanent plots was 388 Mg ha^{-1} , higher than the landscape-scale average inferred from
354 LiDAR, suggesting that our permanent plots are predominantly established in the dominant high-

355 canopy vegetation type, which has a mean landscape AGB of 382 Mg ha⁻¹. The presence of a
356 mosaic of forest types has a direct bearing on carbon accounting programs. An accurate estimate of
357 carbon storage at the landscape scale critically depends on the representativeness of carbon
358 sampling units. In our study area, topographical elevation was the main driver of forest carbon
359 stocks variation (see also Réjou-Méchain *et al.* (2014) for a global cross-site analysis). Caution
360 should be thus exercised when regional-scale carbon stocks are inferred from permanent sampling
361 plots without assimilating any remote sensing observations or without explicitly taking into account
362 topographical variations (e.g. Malhi *et al.* 2006).

363 The potential of LiDAR for tropical forest AGB mapping is not novel but most published
364 studies to date have been carried out in tropical forests with AGB typically < 300 Mg/ha (Zolkos *et al.*
365 *al.* 2013). The relative error of our LiDAR-AGB model was 13.8% at the 1-ha scale, only slightly
366 higher than previous studies (10-12%; Mascaro *et al.* 2011a; Meyer *et al.* 2013), and 22.3% at the
367 0.25-ha scale. This confirms that small-footprint LiDAR can be used to infer AGB even in high-
368 biomass tropical forests. A common interpretation of the IPCC measuring reporting and verification
369 (MRV) guidelines is that AGB uncertainty should be no more than 20% of the mean (Zolkos *et al.*
370 2013). Even in our high-biomass forest landscape, the error at 1-ha scale meets these requirements
371 with small footprint LiDAR.

372 We also attempted to improve the predictive power of this model by exploring its
373 dependence to plot-average wood density or to forest type. The residuals of our models were not
374 explained by either of these factors. However, we found that these residuals were spatially
375 autocorrelated, probably because trees strongly vary in their height-diameter allometric
376 relationships from one area to another one at the landscape scale (Fig. S2). Such spatial
377 autocorrelation in the residuals suggests that the subplots are not independent. Thus the error
378 associated with our LiDAR-AGB model may have been underestimated and using several subplots
379 from a larger field plots is not an optimal strategy from this standpoint.

380 The performance of our power-law models were similar to that obtained by Mascaro *et al.*

381 (2011a; b) and Asner *et al.* (2012b, 2013b), lending some credence to the view that universal
382 features in the LiDAR-AGB allometry may exist, in spite of the substantial variation in the power
383 law exponent across forest types (Asner *et al.* 2012). To account for this cross-site variation of
384 model exponents, Asner *et al.* (2012b) and Asner & Mascaro (2014) developed generic models
385 where field data are used to account for cross-site variation in wood density and height-diameter
386 relationships. Asner & Mascaro (2014) found that their model accounted for the variation in the
387 LiDAR-AGB relationship across five contrasted tropical forests (Hawaii, Panama, Madagascar,
388 Colombia and Peru). To further test their generic model, we tested whether it yielded correct results
389 in our study site, and found that it underestimated the stand-scale AGB by 16% (Fig. S7). Because
390 the generic model was originally calibrated with the AGB of trees ≥ 5 cm DBH, and validated in
391 our study with the AGB of trees ≥ 10 cm DBH, the underestimation is probably closer to
392 20%. Taylor *et al.* (2015) used the approach developed by Asner & Mascaro (2014) but they refitted
393 the parameters of the generic model with their local field data, showing that this model could be
394 applied in other forests but shedding no light on the issue of parameter universality in Asner &
395 Mascaro (2014)'s model. For the sake of completeness, we also conducted the same approach as
396 Taylor *et al.* (2015) at our study site. We found that Asner & Mascaro (2014)'s reparameterized
397 model gave a RMSE of 53.5 Mg.ha⁻¹ at the 1-ha scale, higher than with our model reported in
398 Equation 8 (RMSE=52.8 Mg.ha⁻¹). The strategy of seeking a universal predictive equation relating
399 LiDAR metrics and AGB is an important step forward, so that Asner and Mascaro (2014)'s model
400 would benefit from including more sites, such as our high-carbon stock forest site. The present
401 study contributes one more study site to this endeavor (raw data are available in Table S5-6).

402

403 4.2. *Inferring AGB change from repeated LiDAR acquisitions*

404 We also compared the ability of repeated LiDAR coverages to detect AGB change due to natural
405 vegetation turnover with ground-based estimate. In our old-growth tropical forest, characterized by
406 a relatively slow dynamics, we showed that LiDAR was able to model, but with very large

407 uncertainties, the fine-scale patterns of variation in AGB change as measured from the ground.
408 Indeed, ground-based AGB change was significantly correlated to LiDAR AGB change at the 0.25-
409 ha scale, but not at the 1-ha scale.

410 Our study was conducted in a remote forest landscape that is unlikely to have been exposed
411 to significant localized anthropogenic forest disturbances in the past two centuries. Thus, most of
412 the detected changes are likely related to the natural dynamics of the ecosystem. Scaling the
413 estimated LiDAR-AGB change to the study area did not reveal a detectable increase in AGB stock
414 over the study period. Most pixels increased in canopy height (median was positive) but the pixels
415 that lost height had larger losses than the gains. Thus, most forest types were predicted to be a slight
416 source of atmospheric CO₂ during the study period. We emphasize that our LiDAR-AGB change
417 map is highly uncertain, and that given this uncertainty the null hypothesis of no net change cannot
418 be rejected. That said, our result may still be contrasted with a previous study conducted in the same
419 forest but based on tree plots only. Chave *et al.* (2008) found a modest forest carbon sink in the Petit
420 Plateau plot for the period 1992-2000 (+ 0.40 Mg ha⁻¹ yr⁻¹), and a larger sink in the Grand Plateau
421 plot (+2.29 Mg ha⁻¹ yr⁻¹), and this supported the hypothesis of an increase in AGB in tropical rain
422 forests (Lewis *et al.* 2009). A reanalysis of the same field dataset for the period 2008-2012 gave a
423 very modest sink of + 0.47 Mg ha⁻¹ yr⁻¹ (Fig. 6), confirming that the area has not significantly
424 increased its AGB stock, as found with the LiDAR-based approach. A similar LiDAR-based
425 approach has been done recently in the Barro Colorado Island (BCI, Panama) where the old growth
426 part of the forest was found to have lost a significant amount of AGB between 1998 and 2009
427 (Meyer *et al.* 2013). A recent field-based approach confirmed that the old growth forests from BCI
428 have not significantly increased in AGB during the same period (Cushman *et al.* 2014). Together,
429 these observations are in line with the recent findings of Brien *et al.* (2015), who found a long-
430 term decreasing trend of carbon accumulation in 321 Amazonian field plots.

431 The AGB changes estimated with repeated LiDAR acquisitions was poorly related to the
432 changes estimated from the field. It suggests that ground-based and LiDAR-based measurements

433 measure different components of forest dynamics and this may be due to several reasons. One
434 interpretation is that natural canopy dynamics is typically dominated by many small-scale events at
435 the top of the canopy, which are associated with branchfalls, rather than treefalls (Kellner & Asner
436 2009). In our study area, van der Meer and Bongers (1996) previously conducted a careful survey of
437 canopy openings and they found that only a third of natural canopy gaps were larger than 4 m²,
438 many such events being caused by branch-falls. A LiDAR sensor will probably pick up these
439 changes in canopy structure but they cannot be detected in ground-based surveys, which generally
440 focus on tree diameter. Such canopy dynamics thus probably contributes to increasing the
441 uncertainty in the comparison between field-based AGB change estimates and LiDAR-based AGB
442 changes (Fig. 5). However, it is unlikely that this effect was the main driver of uncertainties
443 because, contrary to our results, a larger mismatch between field- and LiDAR- AGB change
444 estimates would have been expected at smaller scales, where branch-damage constitute a large
445 fraction of AGB change, than at larger scales. Another source of possible mismatch between the
446 field and LiDAR's field of view is that canopy dynamics, sensed by LiDAR, does not correlate
447 simply with AGB change because woody biomass regenerates more slowly than leaf biomass after a
448 disturbance (Asner *et al.* 2006). Canopy closure following disturbance may also be faster in more
449 disturbed areas (Asner, Keller & Silva 2004), blurring the effect of disturbance on AGB stocks from
450 a canopy field of view. Further, those trees which fall but are alive have lost their canopy position
451 but not their woody biomass, while stand-level wood density can change due to stochastic and
452 deterministic shifts in species composition. Such changes are generally accounted for by ground-
453 based tree-by-tree surveys but not by LiDAR measurements. Finally, even small errors in co-
454 registration between LiDAR maps and ground data or temporal mismatch between the LiDAR and
455 the field campaigns, are likely to weaken the relationship between LiDAR and natural vegetation
456 turnover. In our study, the temporal mismatch between the LiDAR and the field campaigns was of
457 38% and thus probably increased the mismatch between field- and LiDAR- AGB change estimates.

458 In natural forests, a major natural cause of AGB change is the large and infrequent gaps

459 formed by multiple tree falls ($> 100 \text{ m}^2$ in area). Such rare events are accurately captured by LiDAR
460 at the 0.25-ha resolution but are likely to be averaged out at the 1-ha resolution. In theory, any
461 random change at the pixel scale that is lower than the LiDAR-AGB model RSErel (in our case
462 13.8% at the 1-ha scale) cannot be detected. However, if changes are concerted across large spatial
463 scales, as is often the case in anthropogenic forest degradation or regrowth, effects of smaller
464 amplitude may be detected (Asner *et al.* 2005). Note also that the eastern and central Amazonia is
465 characterized by a tree turnover that is about half as that measured in southern and western
466 Amazonia (Phillips *et al.* 2004). In western Amazonia, large changes in AGB are thus more frequent
467 than in our study area and we therefore speculate that AGB change may thus be easier to detect by
468 LiDAR in these areas. Finally, in forests exposed to logging activities and/or forest conversion,
469 LiDAR technology is certainly able to map disturbances to a high accuracy (Englhart *et al.* 2013;
470 Andersen *et al.* 2014).

471

472 **5. Conclusion**

473 Building on the outstanding advances of LiDAR-based technology, we were able to map forest
474 types and estimate AGB stocks of an old-growth tropical forest of French Guiana. Our results show
475 that AGB can be mapped even in a high biomass tropical forest. Given the continuous improvement
476 in LiDAR technology, as well as the decay in the associated operational costs, LiDAR technology
477 will soon provide highly accurate carbon maps over large areas in the tropics (Mascaro *et al.* 2014).
478 This will considerably improve our ability to quantify the carbon stored in the biosphere and thus
479 reduce the uncertainties in the global carbon budget. From an ecological point of view, these fine-
480 scale AGB maps may be used to detect the main ecological controls underpinning forest biomass
481 variability both in space and time. We also showed that the dynamics of old-growth forests is seen
482 differently from a ground or a LiDAR perspective but that the landscape estimate of those two
483 approaches gave consistent conclusions about the overall forest carbon budget. Hence, forest
484 dynamics monitoring would clearly benefit from combining the complementary strengths and

485 insights gained from a top-down and bottom-up views.

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506

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731 **List of Figure Captions**

732

733 **Figure 1:** Geographic location of the study area in South America (top right) and in French Guiana
734 (left). The study area of 2,400 ha (bottom right) is illustrated by a hillshade model.

735

736 **Figure 2: Study area. (a)** LiDAR elevation model constructed from combining bare-earth points in
737 the 2007/8 and 2012 LiDAR datasets. A scale bar is given within the panel. **(b)** LiDAR canopy
738 height model (top of canopy height) constructed at a 5-m resolution from the 2012 LiDAR dataset.
739 The dotted lines delineate the 2007/8 LiDAR campaign. (c) Vegetation map obtained by height
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741 truthing. All areas smaller than 1000 m² were eliminated by removing the longest boundary with an
742 adjacent area (rmarea tool in the v.clean procedure of GRASS). Flooded areas were arbitrarily
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745

746 **Figure 3: Relationship between the aboveground biomass density (AGB) and LiDAR H_{50}** for
747 **(a)** 119 plots of 0.25-ha and 1 plot of 0.125 ha (bamboo forest), and **(b)** 29 plots of 1 ha. The
748 residual standard error (RSE) and the coefficients of the power-law model of equation (8) (see
749 methods) are provided in the bottom-right insets.

750

751 **Figure 4: Biomass stocks in the Nouragues forests. (a)** Map and **(b)** histogram of the AGB
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753 metrics is displayed in equation (8); for parameters, see figure 4. The landscape mean and standard
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756

757 **Figure 5: Relationship between AGB change estimated from the field and from the LiDAR**
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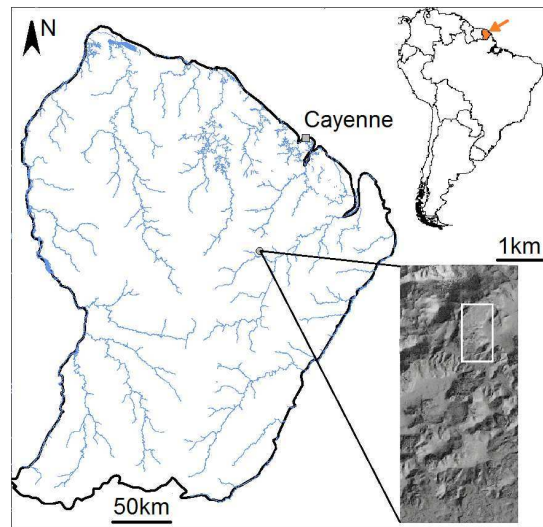
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765 **Figure 6: AGB change inferred from the LiDAR model at 50-m resolution.** (a) Map over the
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771

772 **FIGURES**

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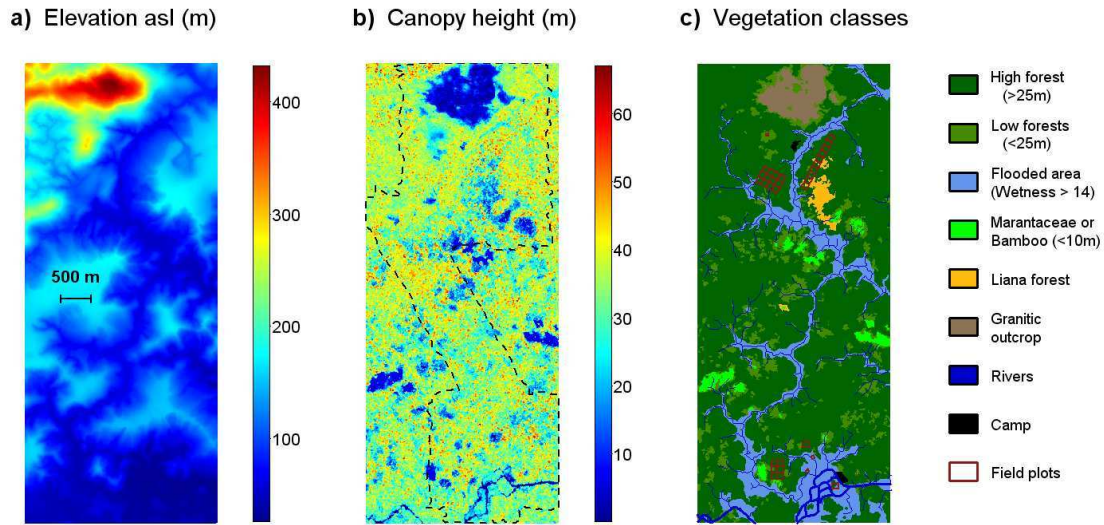


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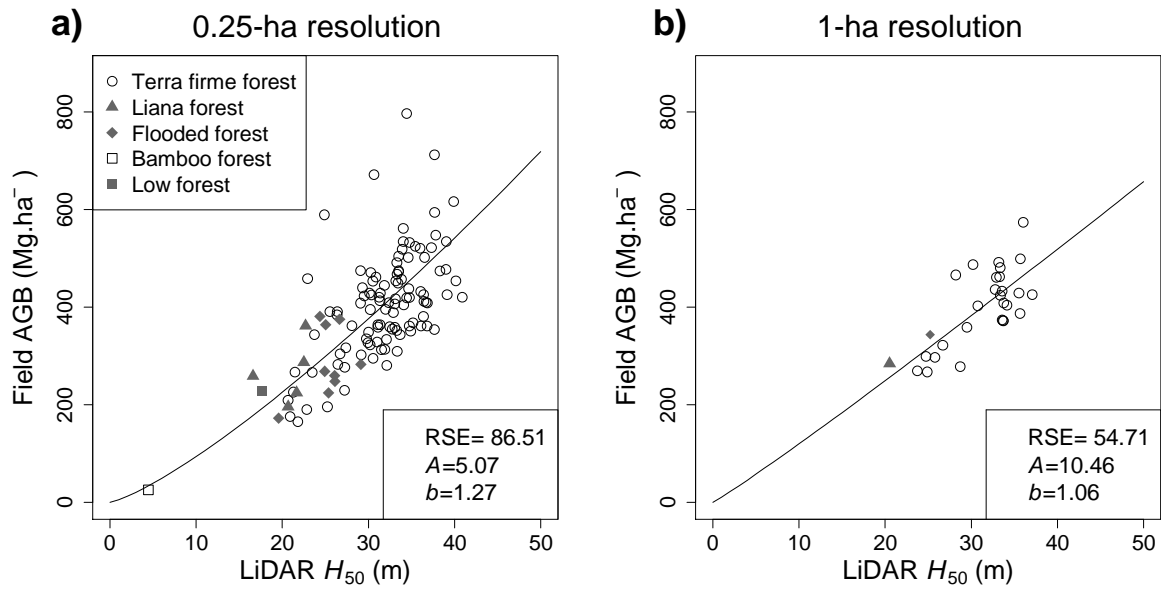
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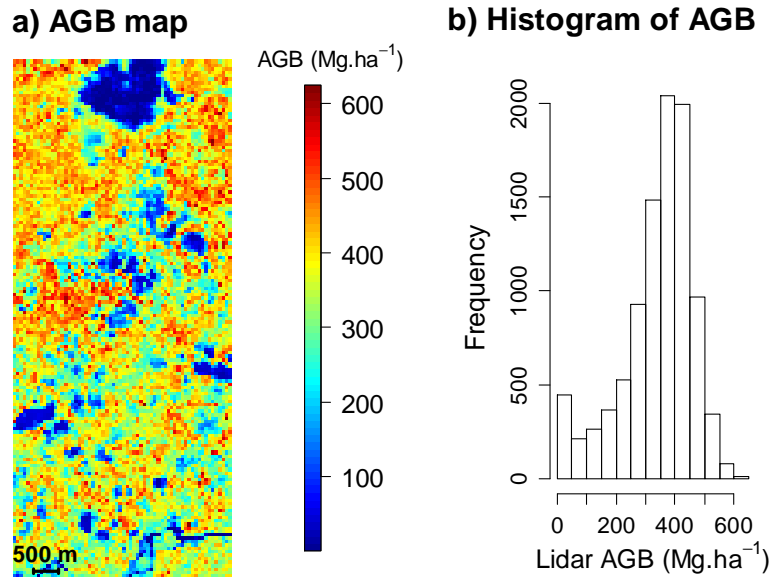
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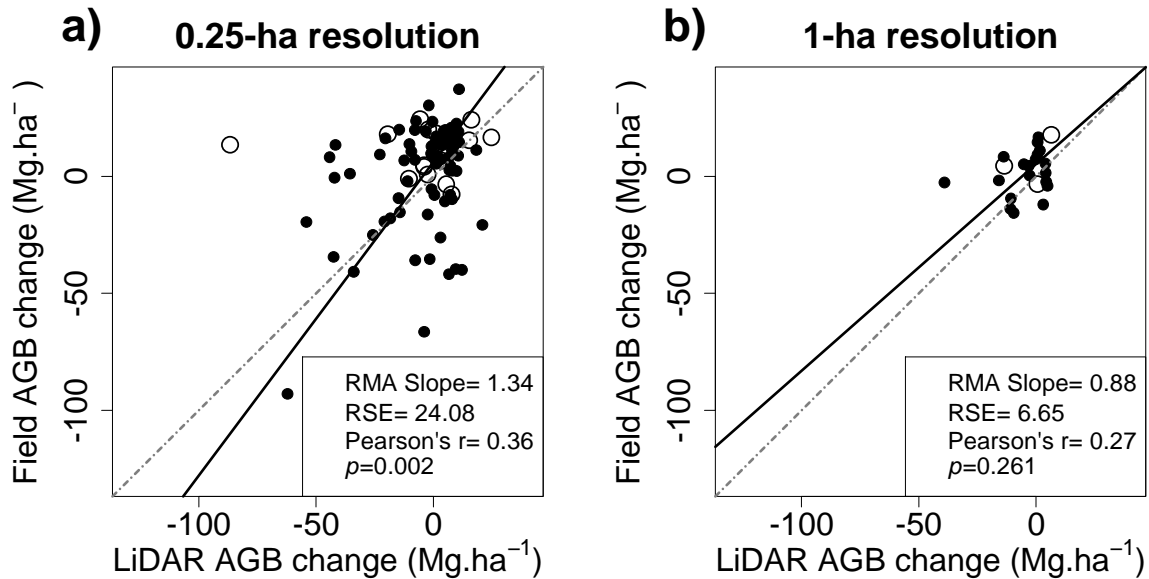
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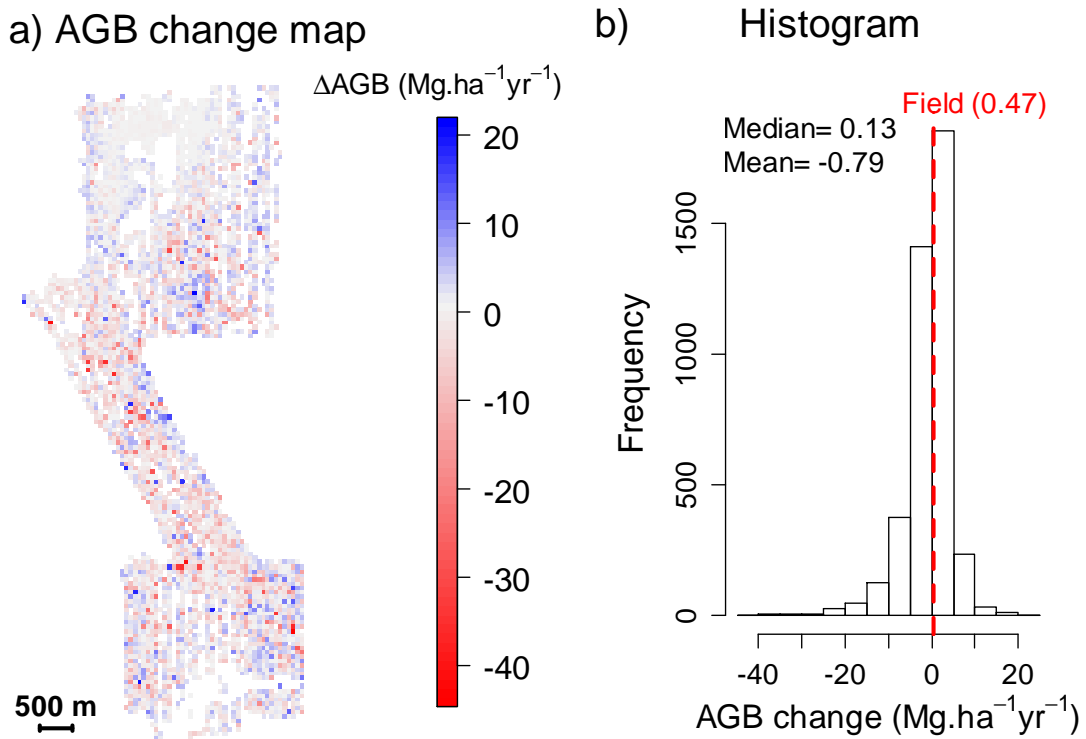
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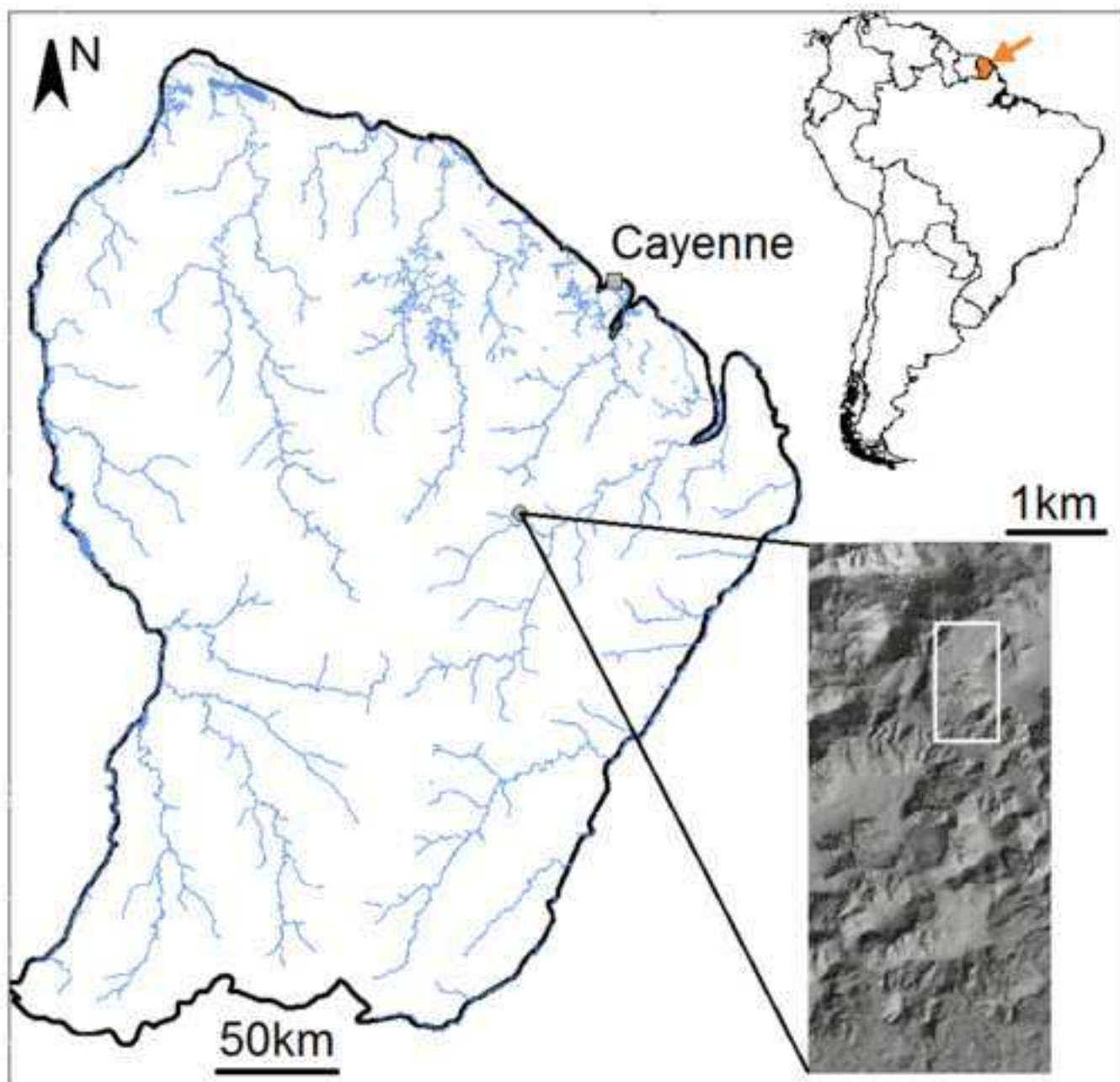
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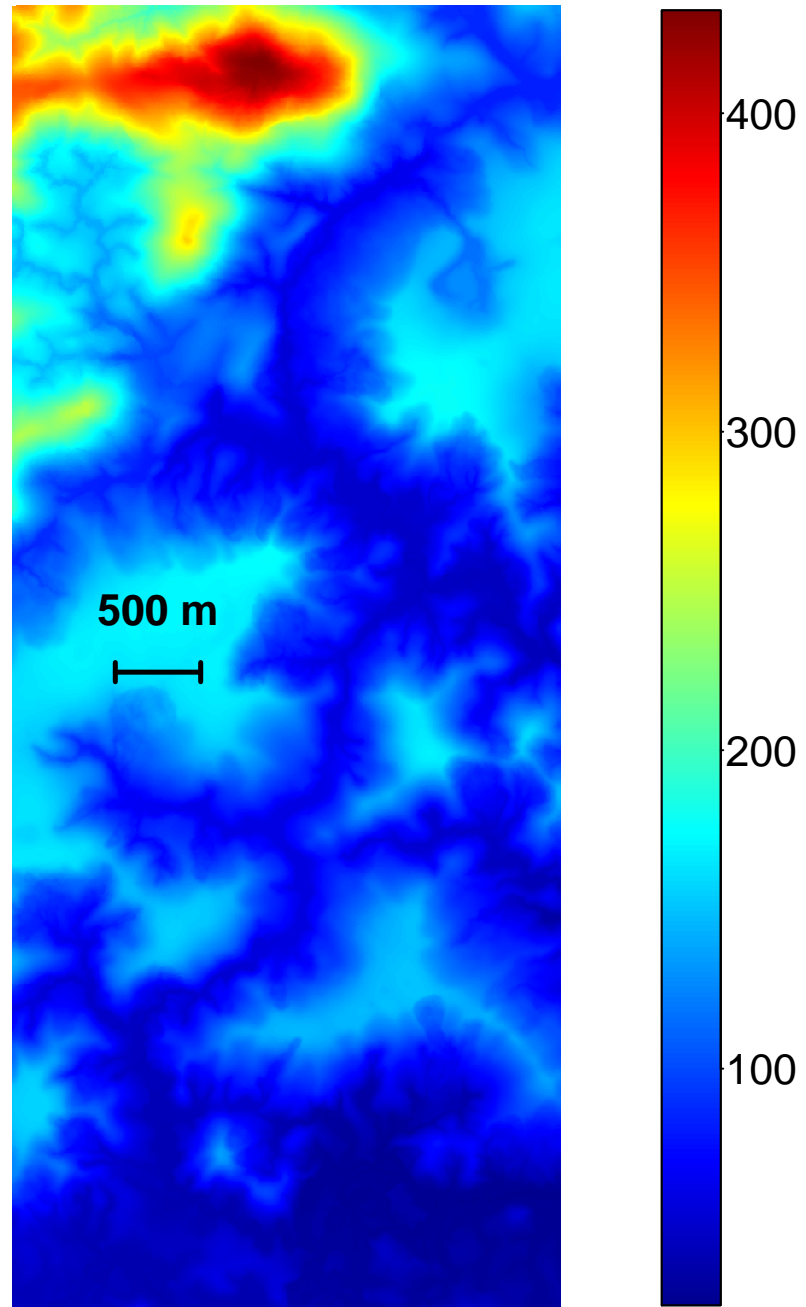
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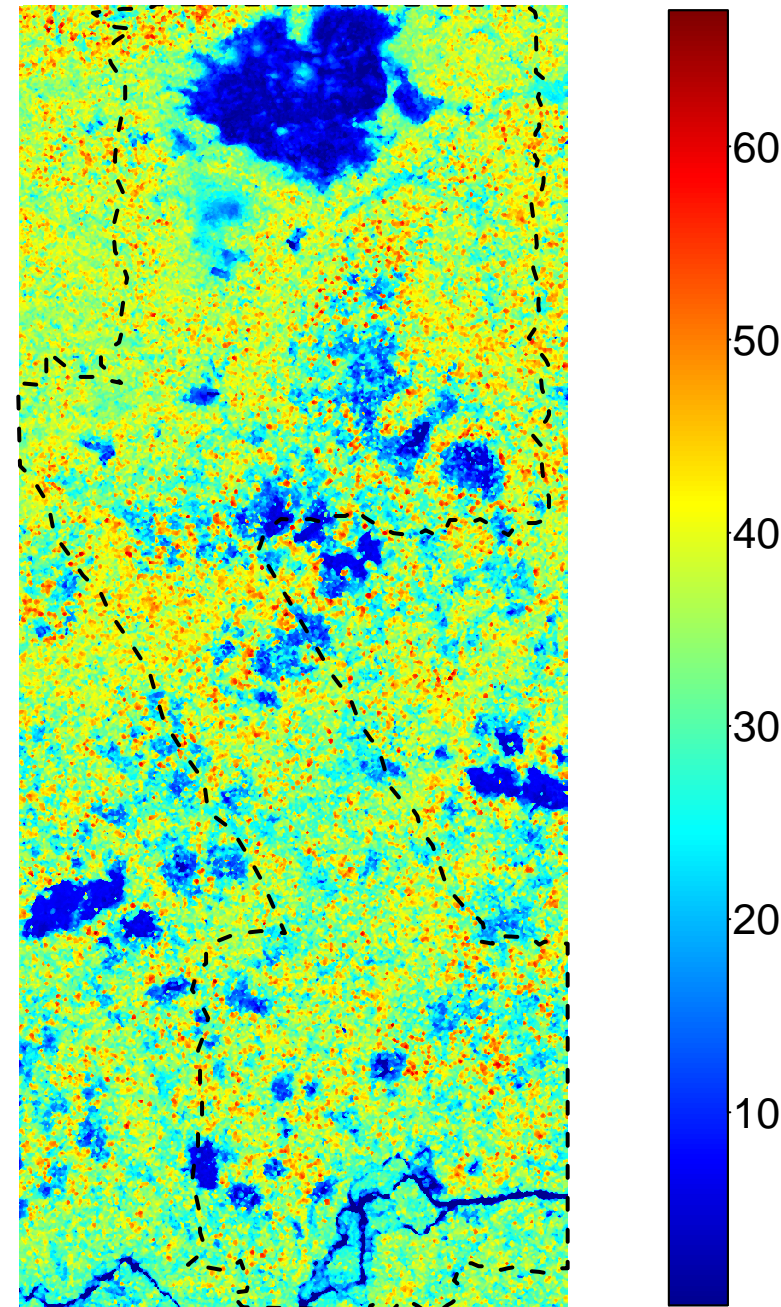
Figure 1
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a) Elevation asl (m)



b) Canopy height (m)



c) Vegetation classes

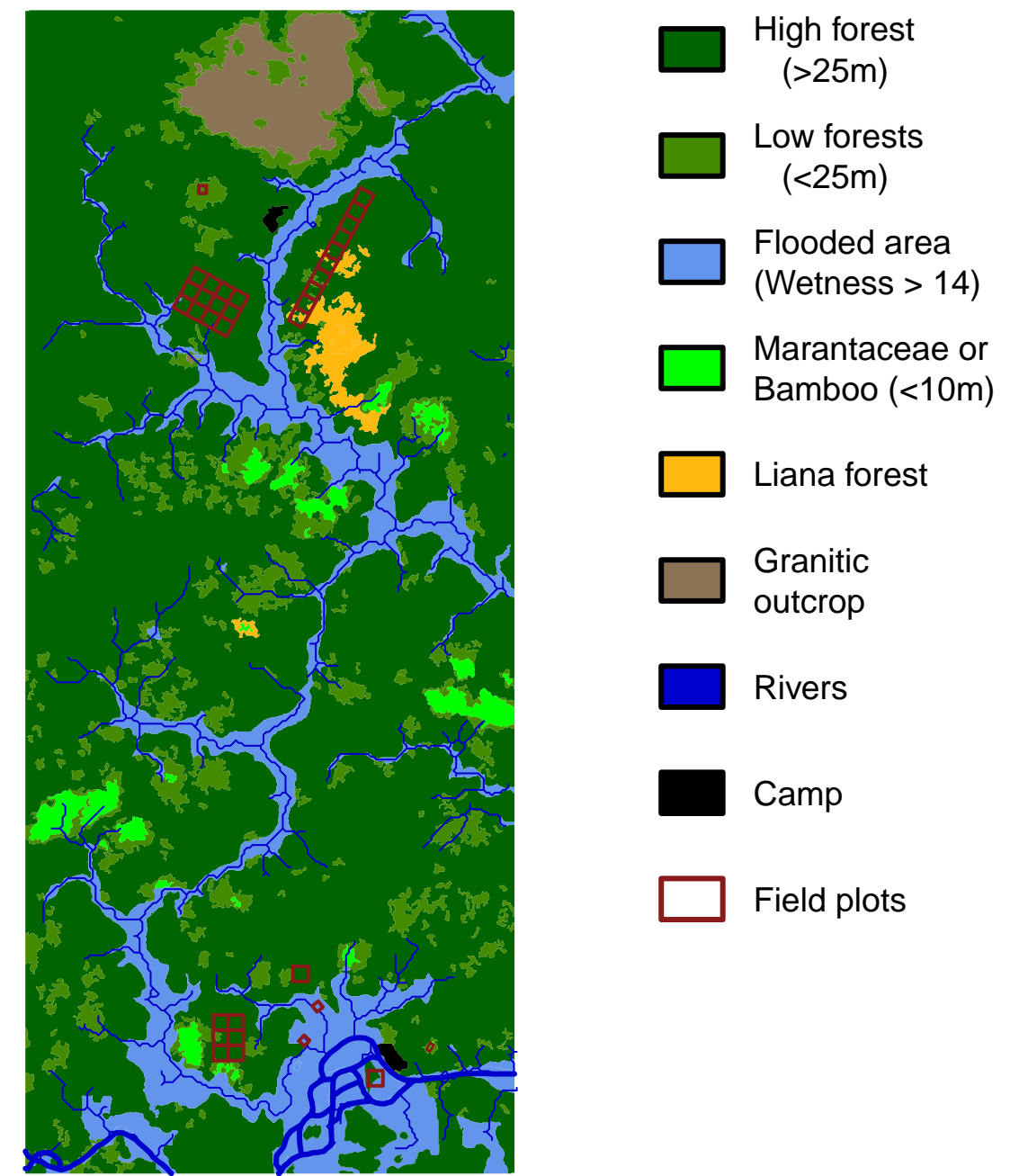
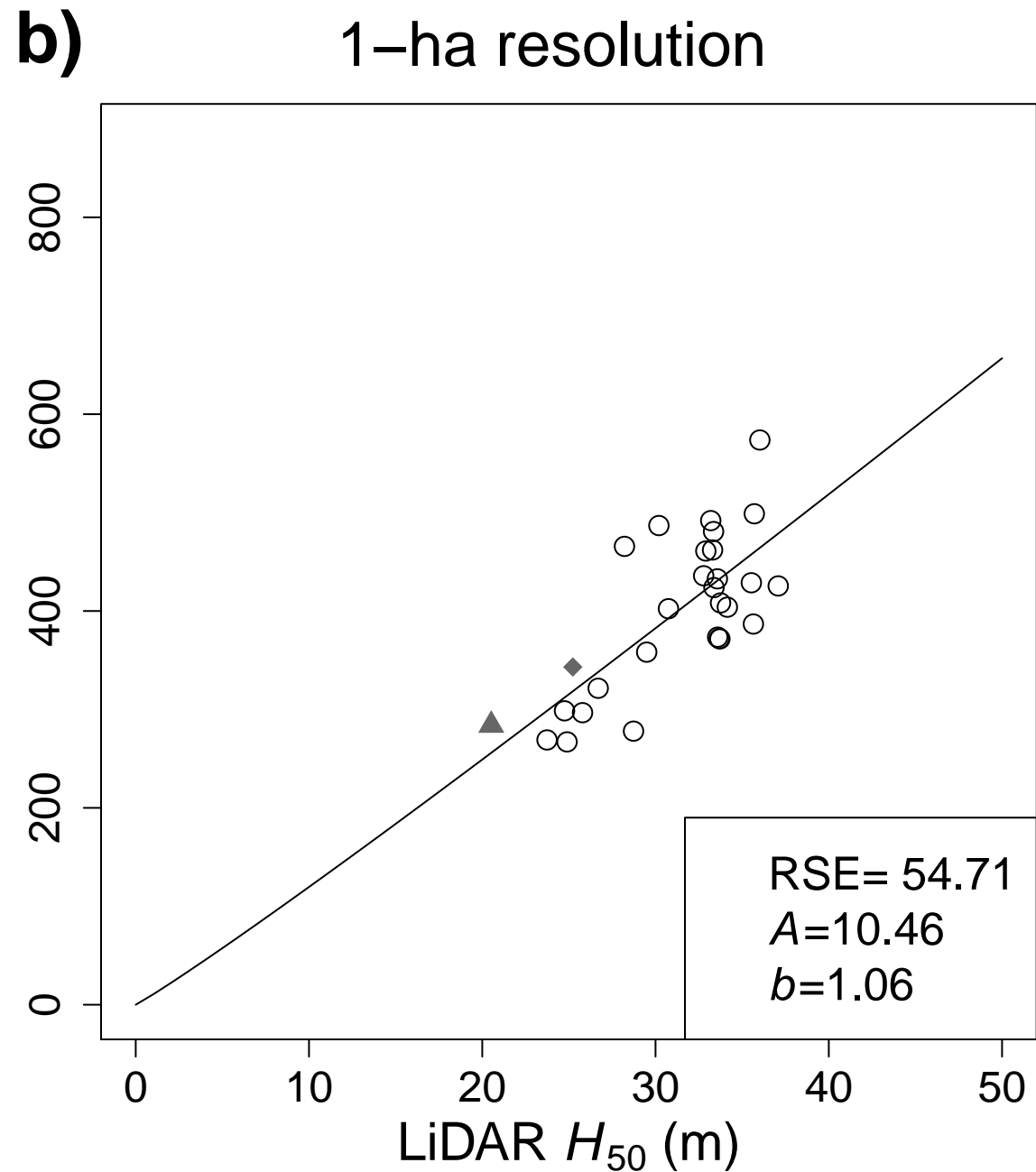
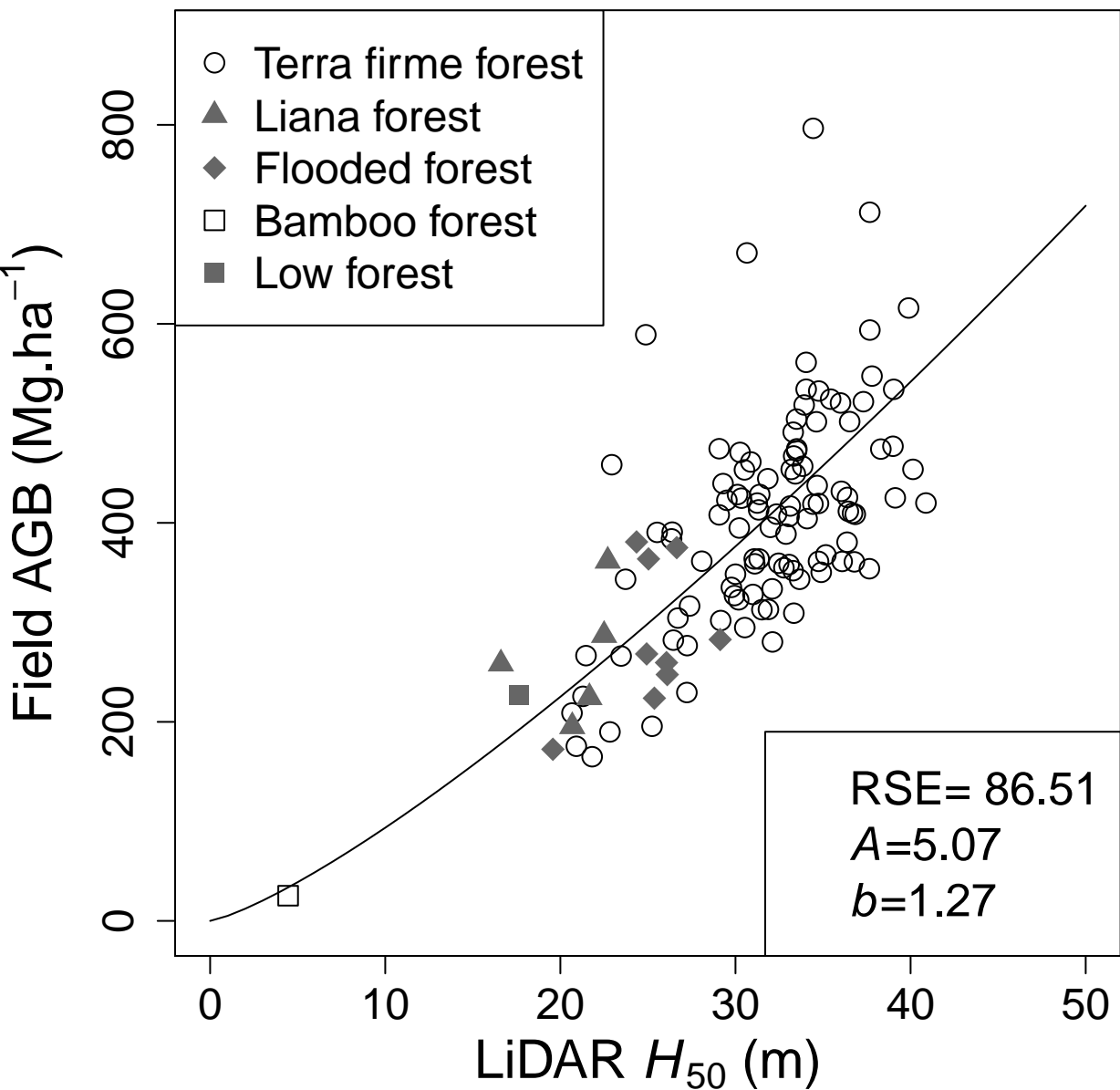
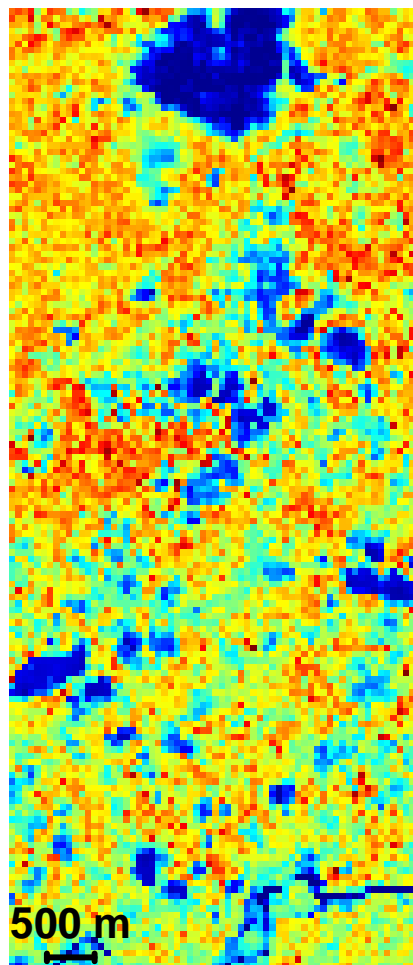


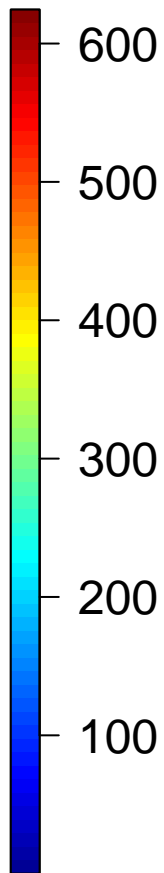
Figure 3
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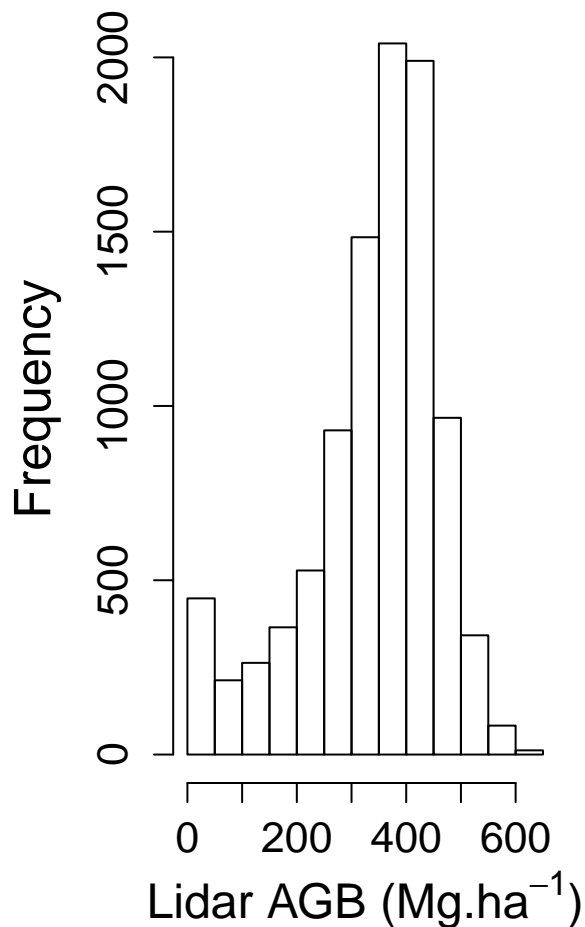
a) AGB map



AGB ($\text{Mg}\cdot\text{ha}^{-1}$)



b) Histogram of AGB



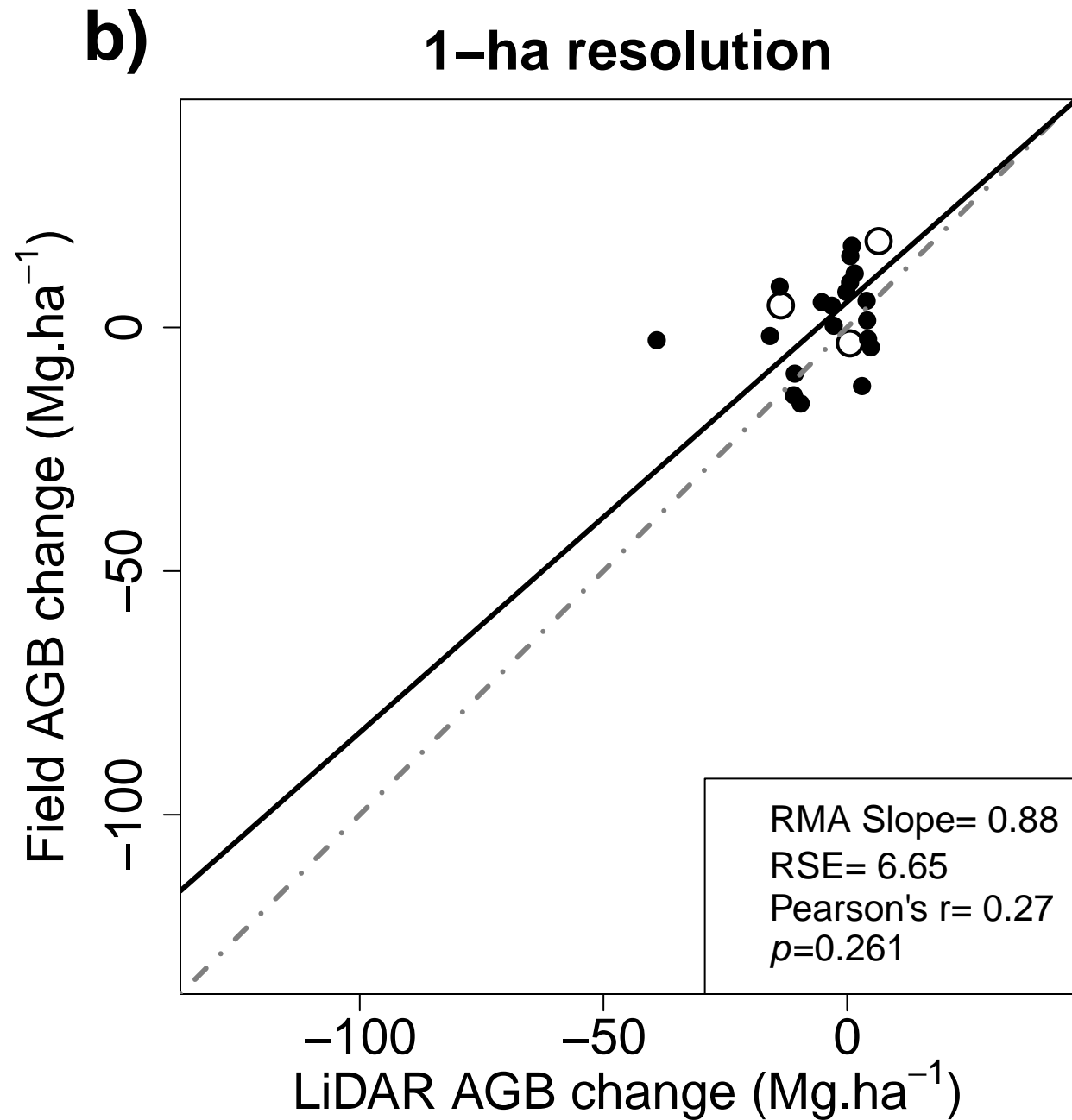
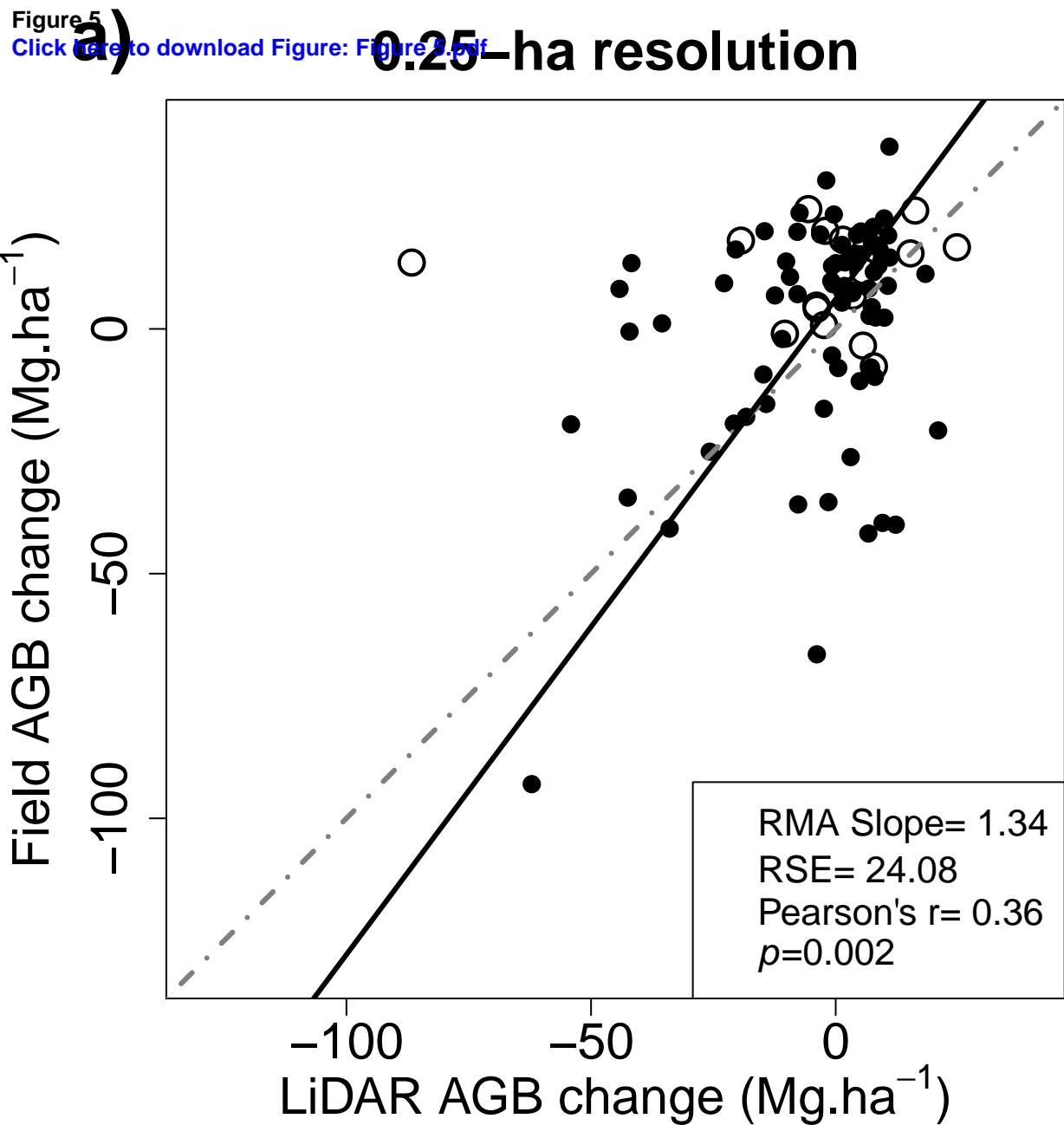
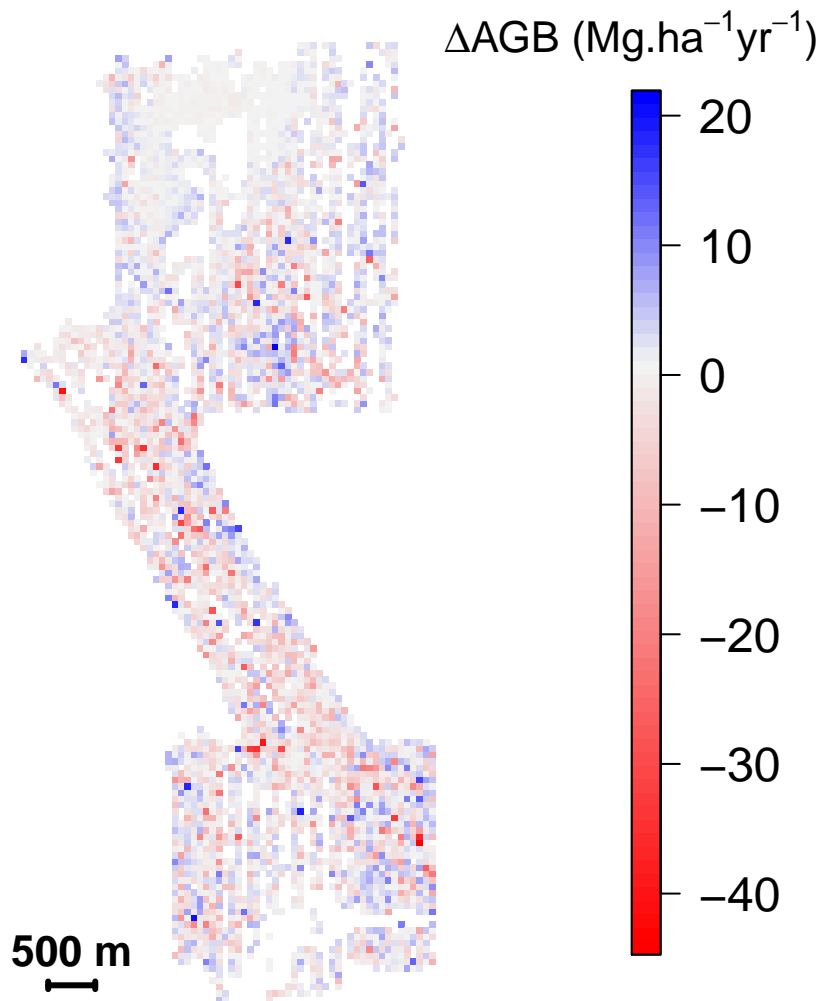


Figure 6

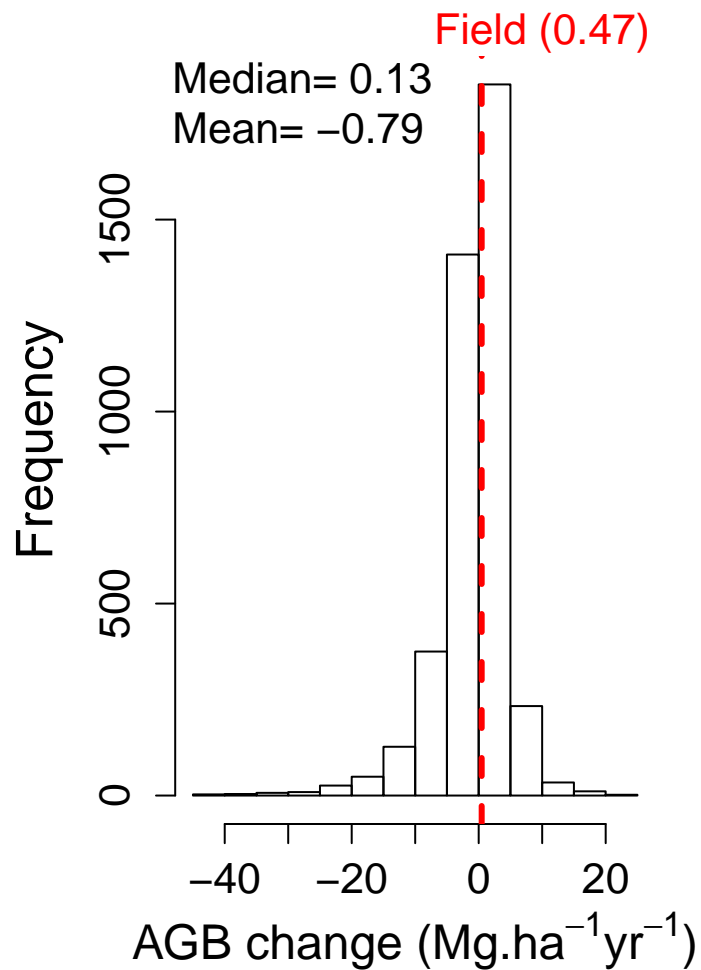
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a) AGB change map



b)

Histogram



Supplementary Data

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