An analysis of forest biomass sampling strategies across scales

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Abstract. Tropical forests play an important role in the global carbon cycle, as they store a large amount of biomass. To estimate the biomass of a forested landscape, sample plots are often used, assuming that the biomass of these plots represents

10 the biomass of the surrounding forest.

In this study, we investigated the conditions under which a limited number of sample plots conform to this assumption. Therefore, minimum sample sizes for predicting the mean biomass of tropical forest landscapes were determined by combining statistical methods with simulations of sampling strategies. We examined forest biomass maps of Barro Colorado Island (50 ha), Panama (50,000 km^2), and South America, Africa and Southeast Asia (7 million – 15 million km^2). The

15 results showed that 100-200 plots (1-25 ha each) are necessary for continental biomass estimations if the sampled plots are spatially randomly distributed.

The locations of the current inventory plots in the tropics and the data obtained from remote sensing often do not meet this requirement. Considering the typical aggregation of these plots considerably increase the minimum sample size required. In the case of South America, it can increase to 70,000 plots.

20 To establish more reliable biomass predictions across South American tropical forests, we recommend more spatially randomly distributed inventory plots. If samples are generated by remote sensing, distances of more than 5 km between the measurements increase the reliability of the overall estimate, as they cover a larger area with minimum effort. The use of a combination of remote sensing data and field inventory measurements seems to be a promising strategy for overcoming sampling limitations at larger scales.

25 **1 Introduction**

For a better understanding of the global carbon cycle, reliable estimations of carbon stocks in vegetation have become increasingly important(Broich et al., 2009; Malhi et al., 2006; Marvin et al., 2014), especially for tropical forests, as they store more carbon than any other terrestrial ecosystem (Pan et al., 2011). Current mapping approaches are based on forest field inventory plots (Chave et al., 2003; Lewis et al., 2004; Lopez-Gonzalez et al., 2014; Malhi et al., 2002; Mitchard et al.,

30 2014) or remote sensing measurements (Asner et al., 2013; Baccini et al., 2012; Saatchi et al., 2011) and involve statistical

approaches (e.g., Malhi *et al.* (2006)) or vegetation modeling (e.g., Rödig *et al.* (2017)). Remote sensing-derived maps have a typical spatial resolution of 100 - 1000 m and capture the biomass of large landscapes or even entire continents (Asner et al., 2013; Baccini et al., 2012; Saatchi et al., 2011). In contrast, biomass maps based on field inventories have a higher resolution so that the biomass distribution of local regions can be described in detail. To combine the advantages of the two

35   methods, we may transfer insights from field plots to high-resolution large-scale biomass maps.

However, the extrapolation of field inventory plots (typically between 0.25 and 1 ha) to larger areas poses several challenges, in the tropics, where field inventory campaigns of species-rich, densely grown forests are costly and labor intensive, resulting in a much smaller number of available plots than in temperate and boreal regions (Schimel et al., 2015). In South America, for example, some studies created biomass maps of the whole Amazonian forest area (more than 1 billion

40   ha) based on a very small percentage of investigated forest area (400 ha) (Lopez-Gonzalez et al., 2014; Mitchard et al., 2014). Moreover, the locations of forest plots are often influenced by accessibility because some regions are excluded for topographic, logistic or political reasons (Houghton et al., 2009; Mitchard et al., 2014). Even if plots are representative of the landscapes they are located in (Anderson et al., 2009), extrapolations from clustered plot networks to larger scales can be biased (Fisher et al., 2008). Consequently, related estimates include large uncertainties; e.g., estimates of the total biomass of

45   the Amazon forest vary by more than 100 %, from 38.9 to 93 PgC t/ha (Houghton et al., 2001).

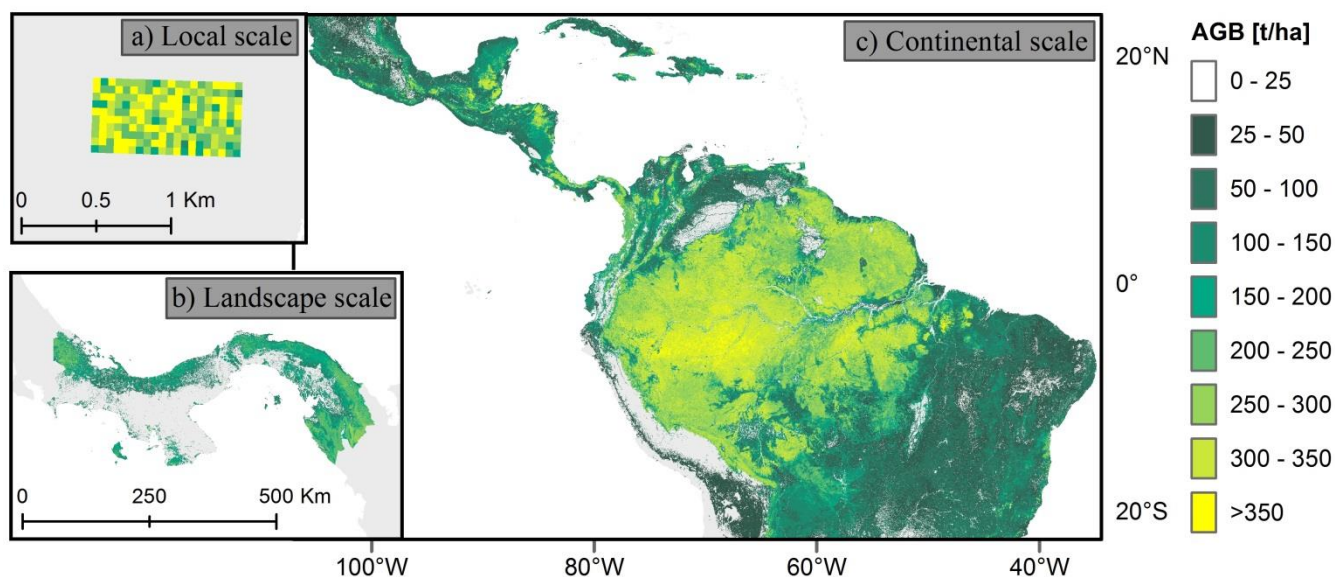
A first step to ensure reliable extrapolations of forest biomass from field plots to large scales is to determine how many plots would be necessary to accurately estimate mean biomass on a landscape scale. Previous studies suggested that for regions of about 1,000 ha, 10 - 100 sampled one-hectare plots would be necessary (Marvin et al., 2014). However, most investigations assume that plots are distributed randomly in space (Chave et al., 2004; Fisher et al., 2008; Keller et al., 2001; Marvin et al.,

50   2014) and therefore do not consider a possible bias due to the choice of sampling strategy. The selected sampling design can significantly influence uncertainty and, consequently, the number of sample plots required (Clark and Kellner, 2012). For example, in a study of different sampling designs, about 20 stratified sample plots of 0.5 ha were recommended for a region in Costa Rica (study site of 600 ha, Clark and Clark, 2000). A deeper understanding of how the choice of sampling design affects the number of plots required and the influence of the size of the plots is still missing.

55   In this study, we present a novel simulation approach for determining the number of plots necessary across scales and answering the following questions: (I) How many sample plots are necessary for forest biomass estimations in South America and what is the role of the sampling strategy? (II) What is the influence of scale on the sampling design?

More specifically, we analyze different sampling strategies for biomass in tropical forests at different scales: 50 ha (Barro Colorado Island), 50,000 km^2 (Panama, (Asner et al., 2013)) and 15 million km^2 (South America, (Baccini et al., 2012)).

60   Following the scenario of a "virtual ecologist" (Zurell et al., 2010), we investigate through Monte Carlo simulations and analytical investigations the plot size and sample size that are necessary for accurate biomass estimations. Furthermore, we simulate nonrandom sampling strategies that imitate measurements via remote sensing and real-world forest inventories.

2 Methods

65 **Figure 1** Forest aboveground biomass (AGB) maps used for the study. **(a)** Biomass map of a forest plot on Barro Colorado Island (50 ha, 50 m resolution (Condit et al., 2012)). **(b)** Biomass map for Panama (~50,000 km^2, 100 m resolution (Asner et al., 2013)). **(c)** Biomass map for South America (~15 million km^2, 500 m resolution (Baccini et al., 2012)).

2.1 Biomass maps at different scales

We focus on three forest biomass datasets for the South American tropical region covering different scales (Fig. 1). For an
70 analysis at the local scale, a biomass map of the Barro Colorado Island forest in Panama was applied (BCI, 50 ha) with resolutions between 10 m and 100 m. The map was based on the forest inventory of 2010 (Condit et al., 2012), which included measurements of all trees with a stem diameter greater than 1 cm (Condit, 1998). The aboveground biomass (AGB) per plot was determined using allometric relationships (Knapp, Fischer and Huth (2018)).

Landscape-scale analysis was carried out using a carbon density map of Panama that was derived from Airborne Light
75 Detection and Ranging (LiDAR) measurements from 2012, in combination with field measurements and satellite measurements (Asner et al., 2013). The AGB values for this study were calculated by multiplying the carbon values by a factor of two. We aggregated the AGB map from a 100 m resolution to resolutions of 200 m, 300 m, 400 m and 500 m. For this purpose, between 4 and 25 plots from the original map were averaged. If these plots covered both forest and nonforest areas, we assumed the nonforest areas to have a biomass of zero. If the plots only covered nonforest areas, the aggregated
80 plot was still considered as a nonforest area.

At the continental scale, a biomass map with a resolution of 500 m for South America was investigated (~15 Mio km^2, (Baccini et al., 2012)), which was mainly derived from space-based LiDAR (observations from years between 2008 and 2010) and covered regions of the American continent between 23.4378° north latitude and 23.4378° south latitude. Based on

this map, we constructed a biomass map of South America with a 100 m resolution. For downscaling in this case, we used

85 relationships derived from the Panama maps at 100 m and 500 m resolutions (for details, see S3). In addition, we examined

AGB maps for Africa (~12 Mio km^2) and Asia (~7 Mio km^2) derived from Baccini *et al.* (2012) with a 500 m resolution

(Table S1). All maps were simplified by excluding nonforest plots and plots with biomass values of less than 25 t/ha.

2.2 Simulated sampling strategies

We investigated three different sampling strategies: (a) random sampling (b) remote sensing sampling and (c) clustered

90 sampling (Fig. 2), with different sample sizes. For example, for analysis of the BCI forest, we divided the 50 ha biomass map

into 200 plots with a size of 50 m x 50 m. Then, we ran simulations with sample sets containing one sample (0.25 ha), two

samples (0.50 ha), and so forth until we reached a sample size of 100 samples (25 ha, half of the study area). For large-scale

investigations, we analyzed sample sizes of up to 5,000 plots for Panama and 200,000 plots for South America.

a) Random sampling   **b) Remote sensing sampling**   **c) Clustered sampling**

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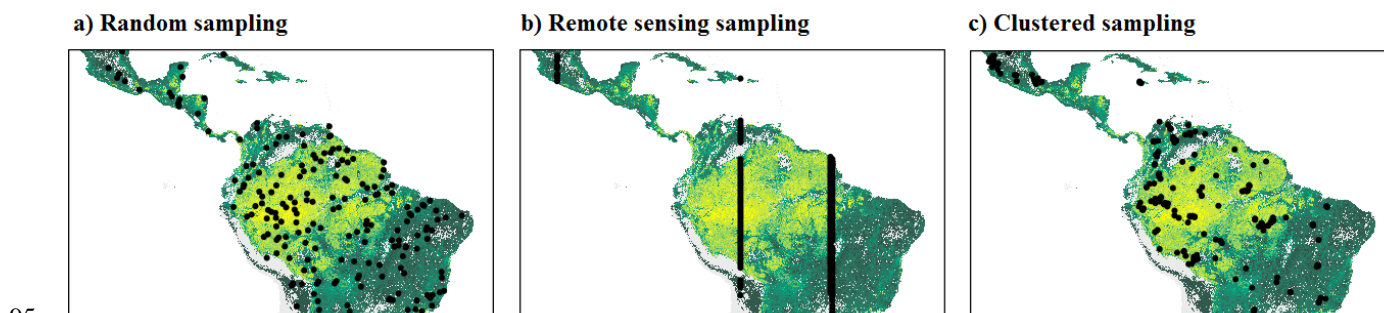


Figure 2 Examples of different simulated sampling strategies. Aboveground biomass samples based on the map of South America (AGB values are indicated by different colors; for the legend, please see Fig. 1). Each black dot represents the location of one selected plot (25 ha). **(a)** Randomly distributed plots. **(b)** Remote sensing samples (strips with distances of 50 km between the plots). **(c)** Clustered samples (reconstructions of PP4).

100 ### 2.2.1 Random sampling

Analysis of random sampling was performed using Monte Carlo simulations. For every map, we selected sampling plots at

randomly selected positions (without replications) until the sample set reached the desired sample size. Associated results

were additionally determined analytically using the central limit theorem (Supplement S1).

2.2.2 Remote sensing sampling

105 For the remote sensing sampling strategies, we tried to mimic typical features of airborne or satellite measurements, e.g.,

assuming that a satellite is flying over a direct north-south track. Starting at a randomly selected position of the map, we

selected plots with a fixed distance in a north-south direction (while nonforest plots were excluded). In this study, we

focused on distances between 500 m and 5 km. When the plot selection reaches the southern end of the map, the algorithm

starts again at the northern border on a new randomly selected north-south track. The analysis of Panama was conducted by
110 selecting plots of 1 ha (map with 100 m resolution). For South America, we selected plots of 25 ha (map with 500 m resolution). To test whether the results were influenced by the direction of the remote sensing flight tracks, we also tested west-east instead of north-south tracks. With this strategy, we tried to explore how the north-south climatic gradient influences the results. However, the sampling performance remained similar (i.e., the probability of estimating the mean biomass accurately did not change significantly compared to north-east tracks).

115 **2.2.3 Clustered sampling**

The clustered sampling approach mimics the spatial clustering of real-world field inventory networks. To this end, we reconstructed the spatial pattern of the plot networks of four studies that estimated forest biomass, including Houghton *et al.* (2001), PP1; Poorter *et al.* (2015), PP2; Malhi *et al.* (2006), PP3; and Mitchard *et al.* (2014), PP4 and analyzed them separately regarding the South American map with a resolution of 500 m (25 ha plot size). After removing duplicate
120 locations within the 500 m grid, the number of plots per network ranged between 25 and 189. To generate 1,000 plot networks with similar spatial configurations as the original ones, we applied the method of pattern reconstruction (Wiegand, He and Hubbell (2013); software "Pattern-Reconstruction"). This annealing method produces stochastic reconstructions of an observed point pattern that shows the same spatial characteristics as the observed pattern, as quantified by several point pattern summary functions (for details see S2).

125 **2.3 Determining the minimum sample size**

For each map and each sample size n, we calculated the sampling probability P_n, which quantifies how often the mean of a sample equals the mean of the underlying "true" biomass distribution (under a given accuracy) as the relative frequency out of 1,000 sample sets. For each sample set, the mean biomass ($\overline{X_{i,n}}$ in t/ha) was estimated, where i is the sample set number, and n is the sample size. $\overline{X_{i,n}}$ was then compared with the "true" mean biomass, μ [t/ha], of the underlying biomass map. A
130 sample set was assumed to be acceptable if $\overline{X_{i,n}}$ was within $\mu \pm 10 \%$. The sampling performance can be assessed as follows:

$$P_n \cong \frac{1}{1000} \sum_{i=1}^{1000} w_i \text{ , with } w_i = \begin{cases} 1, if \ \dfrac{|\overline{X_{i,n}} - \mu|}{\mu} \leq 0.1 \\ 0, if \ \dfrac{|\overline{X_{i,n}} - \mu|}{\mu} > 0.1 \end{cases}$$

P_n typically increases with the sample size from 0 (no sample could represent the mean biomass) to 1 (all samples could represent the biomass). We defined n_{min} as the minimum sample size n, at which P_n reaches 90 %. The minimum sampling area, a_{min}, is calculated by multiplying the number of plots, n_{min}, by the plot size.

Results

3.1 Random sampling

3.1.1 Local scale (Barro Colorado Island)

(a)

(b)

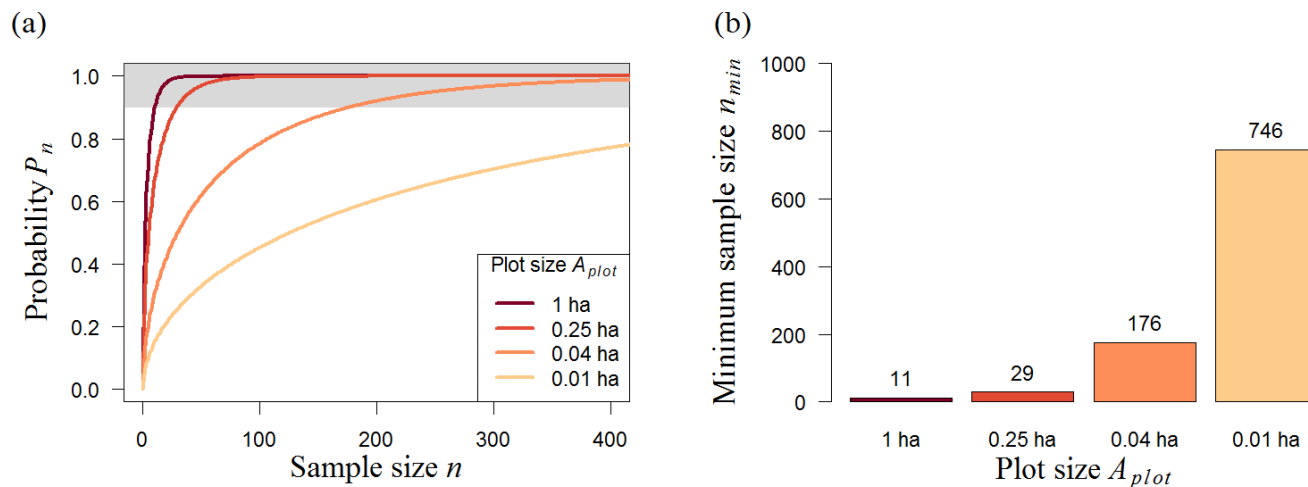



Figure 3 Analysis of different random sampling strategies for the Barro Colorado Island forest (BCI, 50 ha). **(a)** Analytical results showing the number of plots and probability P_n that the mean biomass of those plots reflects the mean biomass of the forest (for details, see Methods). We consider strategies using 0.01-1 ha plots (plot size, represented by line colors). The upper boundary (gray) indicates sample sizes with accurate biomass estimations ($P_n \geq 90$ %, see Methods for details). **(b)** Necessary number of plots, n_{min}, to estimate the biomass accurately (plot sizes are displayed below the bars).

The results for a 50 ha biomass map (BCI) showed that samples with larger plot sizes produce more accurate biomass estimates (Fig. 3a). A randomly chosen 0.01-ha plot has a probability (P_n) of 5 % of representing the mean biomass of the whole BCI forest, but if the plot has an area of 1 ha, P_n reaches 40 %. The size of the plots also affects the minimum number of plots required (n_{min}). For small plots (plot size ≤ 0.04 ha), n_{min} decreases significantly (Fig. 3b). While only 11 one-hectare plots are needed to measure the biomass correctly, the number of plots increases to 176 if the plot size is 0.04 ha (20 m x 20 m). However, the minimum total area of the samples (a_{min}) remains similar (Table 1, BCI); i.e., it makes no difference in sample performance whether the samples are taken from 29 plots of 0.25 ha each or 746 plots of 0.01 ha each, as an area of about 7 ha is sampled in both scenarios. Therefore, the most efficient sampling strategy for the 50 ha scale would involve 0.25 ha plots, as greater plot sizes would result in a greater total sampling area (a_{min}), and smaller plot sizes would simply increase the number of plots.

3.1.2 Large scale (Panama and South America)

In the last section, random sampling of a small homogeneous forest area was evaluated. In the next step, we analyzed the sampling results in large heterogeneous landscapes and whole continents. We analyzed the biomass map of Panama (50,000 km²) using plot sizes between 1 ha and 25 ha (Table 1, Panama). In contrast to the BCI analysis, plot size has no significant

influence on the minimum sample size in this case, since the results range between 70 and 74 plots. Larger plots lead to a slight increase in the number of plots needed. However, the total sampling area (a_{min}) increases from 70 ha to 1850 ha for different plot sizes. The most efficient sampling strategy at the landscape scale is therefore to sample 70 plots of 1 ha each.

160 For the biomass map of South America (15 million km^2), 102 plots of 25 ha are necessary to estimate the mean biomass with sufficient accuracy (Table 1, South America; for Africa and Southeast Asia, see Table S1). This corresponds to a total sampling area (a_{min}) of about 26 km^2. For plot sizes of 1 ha each, the minimum number of plots decreases slightly to 92 plots (necessary sample area of 92 ha).

165 **Table 1** Analyzed forest biomass maps and the corresponding minimum sample size. The forest biomass maps for South America (15,000,000 km^2, (Baccini et al., 2012)), Panama (50,000 km^2, (Asner et al., 2013)) and Barro Colorado Island (50 ha, (Condit et al., 2012)) and their random sampling performance are shown. Different resolutions of the maps led to different results. The minimum sample size refers to the necessary number of plots to accurately estimate the observed mean biomass of the forest (the mean of the samples does not deviate more than 10 % from the observed mean biomass with a probability of at least 90 %). The last column shows the necessary

170 sampling area $a_{min} = A_{plot} \cdot n_{min}$.

Map (Resolution)	Plot size A_{plot} [ha]	Coefficient of variation CV [%]	Minimum sample size n_{min} [plots]	Minimum total area of samples a_{min} [ha]
South America (500 m)	25	61.34	102	2550
South America (100 m)	1	58.16	92	92
Panama (500 m)	25	52.22	74	1850
Panama (400 m)	16	51.97	74	1184
Panama (300 m)	9	51.68	73	657
Panama (200 m)	4	51.27	72	288
Panama (100 m)	1	50.77	70	70
BCI (100 m)	1	19.32	11	11
BCI (50 m)	0.25	32.57	29	7.25
BCI (20 m)	0.04	80.55	176	7.04
BCI (10 m)	0.01	165.95	746	7.46

3.2 Remote sensing sampling

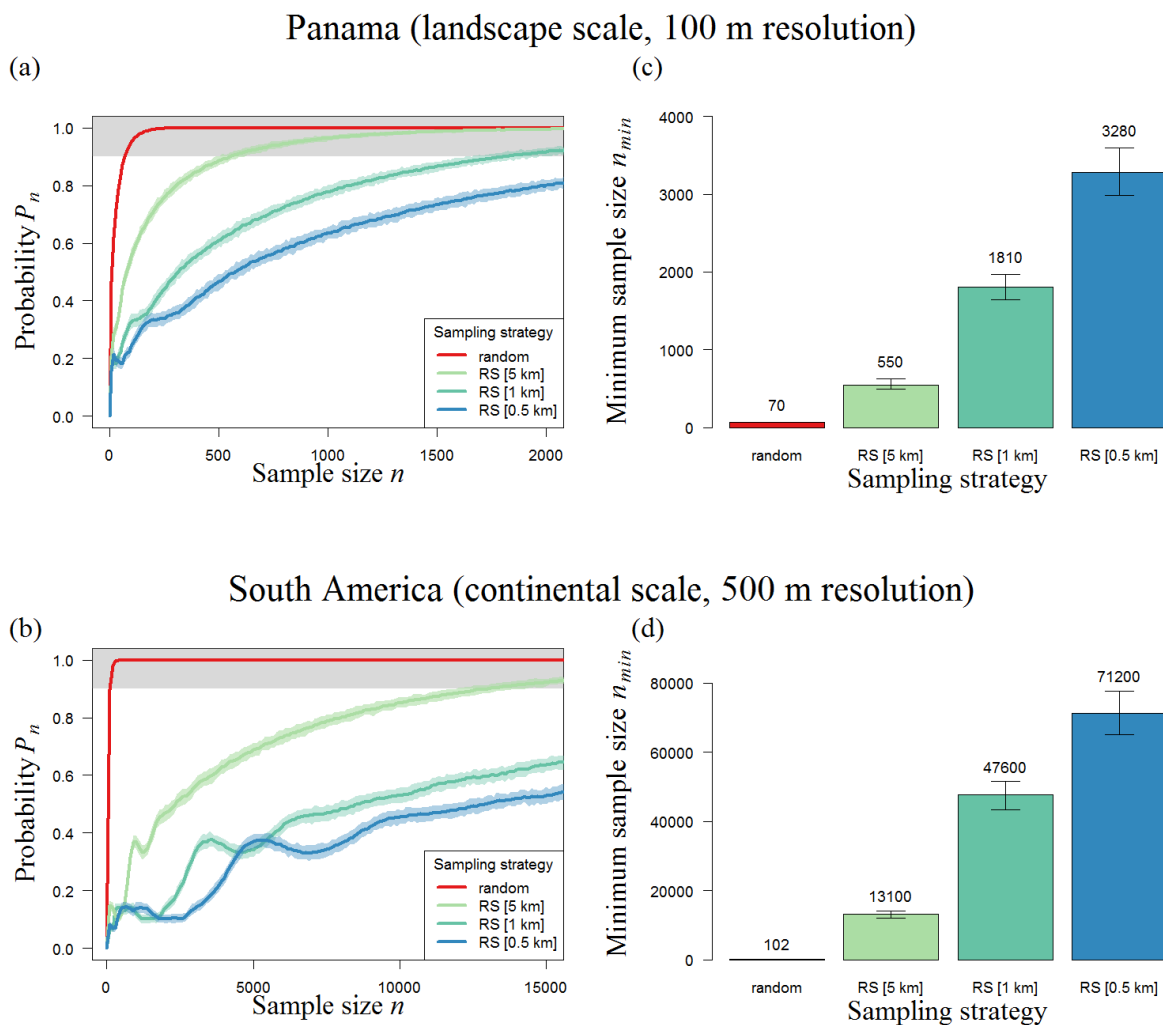



Figure 4 Results of remote sensing (RS) sampling for (a-b) Panama and (c-d) South America. Left: Simulation results showing the number
of plots and probability (P_n) that the mean biomass of those plots reflects the mean biomass of the forest (for details, see Methods). We
focus on three RS strategies using distances of 500 m, 1 km and 5 km between plots (shown in blue) and compare them to random
sampling (red). The area around each line indicates the 95 % confidence intervals of 100 repetitions (total of 1000*100 runs for each
sample size). The upper boundary (gray) indicates sample sizes with accurate biomass estimations ($P_n \geq 90$ %). Right: Necessary number
(n_{min}) of 1 ha plots for Panama and of 25 ha plots for South America (error bars show the 95 % confidence intervals of 100 repetitions).

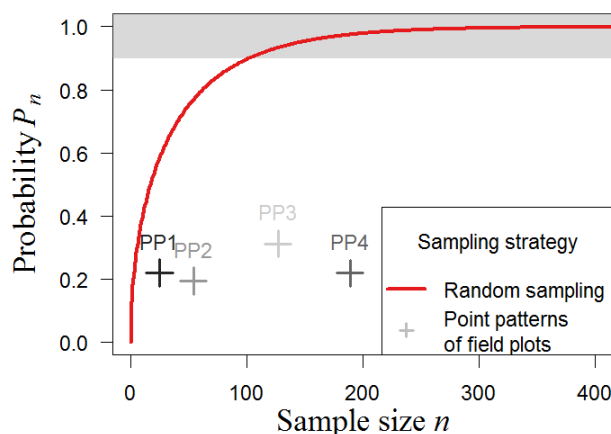
Sampling strategies with a specific spatial structure, such as those generated by aircraft or satellites, are tested by remote
sensing (RS) sampling. The performance of nonrandom strategies was related to the spatial characteristics of maps (S4, Fig.
S3). When the spatial clustering of the BCI forest biomass map is analyzed at the scale of 50 m, the obtained spatial biomass
distribution is comparable to a random configuration; thus, the design of the sampling strategy has no influence on the results
for this local forest area. For Panama and South America, the biomass is distributed in such a way that similar biomass

185 values are more likely to be close to each other, which leads to biased estimation of the mean biomass if the samples are close to each other (e.g., RS with distances of 0.5 km between the plots). This results in differences between random and remote sensing sampling: compared to random sampling, RS samples show a lower probability (P_n) of estimating the mean biomass of the forest accurately independent of the sample size (Fig. 4). For Panama, random samples based on 100 one ha plots exhibit a P_n = 95 %, while RS samples are less than 60 % reliable (Fig. 4a). For South America, RS samples based on

190 100 plots (25 ha plot size) show a P_n of less than 20 % (Fig. 4b).

The results show that if the distances between the plots increase from 0.5 km to 5 km, about 80 % fewer plots are necessary for accurate estimations. Larger distances between the remote sensing measurements make the strategy "more random", and it therefore performs better. In summary, even with large distances between plots, RS sampling leads to higher sampling efforts than random sampling. For Panama, an area of 550 ha (instead of 70 ha with random sampling) is necessary to

195 estimate the biomass of the 50,000 km^2 forest with a sufficient precision (Fig. 4c). For South America (15 million km^2), the minimum sampling size increases by a factor of 130 compared to random sampling (Fig. 4d), leading to a total sample area of about 3275 km^2.

3.3 Clustered sampling

200 **Figure 5** Clustered sampling of biomass in South America. We tested different clustered sampling strategies using reconstructed point patterns based on the locations of existing field plots in South America (PP1-PP4). The simulation was performed with the South America map with a resolution of 500 m (25 ha plot size). Results show the probability (P_n) of accurate sampling for the spatial clustering of each point pattern (gray crosses). The upper boundary (gray) indicates sample sizes with accurate biomass estimations ($P_n \geq 90$ %, see Methods for details). As a reference, the results for random sampling are shown (red line).

205 Samples based on forest inventory plots are often influenced by accessibility, which leads to nonrandom locations of the sample plots that are simulated under the clustered sampling approach. Here, we examine the biomass map of South America with reconstructed point patterns PP1-PP4 based on the locations of existing inventories in South America (25-189 plots, see

Methods). The results show that the probability (P_n) of estimating forest biomass accurately is considerably lower compared to the probability associated with random samples (Fig. 5). All samples present less than a 35 % chance of reflecting the real

210 mean biomass for South America. For clustered sampling, a greater number of samples per se does not lead to better biomass estimations. The positions of the plots therefore play a crucial role. Although PP4 combines many plots of PP1 and PP3, the stochastic sampling scheme based on the spatial aggregation of plots cannot capture the biomass distribution significantly better than those based on the single datasets alone. In summary, the simulation results demonstrate that nonrandom strategies such as remote sensing sampling and clustered sampling differ significantly from random sampling, leading to

215 increased sampling efforts and noticeably greater sampling uncertainties.

4 Discussion

Due to the large area of tropical forest, only a few parts of the forest can be investigated in detail. Therefore, effective sampling strategies for these forests are relevant (Broich et al., 2009; Chave et al., 2004; Malhi et al., 2006; Marvin et al., 2014). The question of how many forest plots are necessary to predict forest biomass has not yet been fully answered. Thus

220 far, sampling quality has often been determined on the basis of the assumption that samples are spatially randomly distributed (Chave et al., 2004; Fisher et al., 2008; Keller et al., 2001; Marvin et al., 2014). However, sampling at large scales in the tropics often does not fulfill this condition because in many cases, random locations are difficult to access (Wang et al., 2012). In this study, we compared different sampling strategies for tropical forests across various scales and plot sizes examining the probability to obtain the correct biomass estimate and the associated minimum sample size.

225 Therefore, we simulated random samples and compared them to samples that are specified by remote sensing flight routes or spatially clustered.

4.1 Random sampling

We showed that 11-92 randomly distributed plots (1 ha each, depending on the forest extent) are necessary to estimate the mean biomass for tropical forests in the South American region. This result is in line with a study by Marvin *et al.* (2014) in

230 which the minimum sample sizes for biomass maps of regions in Peru (1 -10 km^2) were investigated. The results demonstrated that the main factor influencing the minimum sample size is the variability in biomass values in the map, so homogeneous Amazonian landscapes require fewer plots than heterogeneous regions in the Andes (Marvin et al., 2014).

By testing plot sizes between 0.01 ha and 1 ha, we demonstrated that sample plots should not be smaller than 0.25 ha because sampling effort increases with smaller plot sizes. To estimate the minimum sample size of a particular forest region,

235 it might be useful to assess variability, for example, by using forest models (Zurell et al., 2010), forest type maps (Marvin et al., 2014) or topography (Réjou-Méchain et al., 2014).

For large areas (tropical forests in South America, Africa, Southeast Asia), we obtained minimum sample sizes of about 100-200 plots (randomly distributed, 25 ha each) on each continent. We also tested larger plot sizes with a biomass map from

Saatchi *et al.* (2011), but the results were similar (100-230 plots, 100 ha each). Furthermore, our tests included smaller plot

240 sizes obtained by downscaling the South American biomass map using relationships derived from the Panama forest biomass map (50,000 km^2 forest area). The results indicated that 100 plots of 1 ha that are randomly distributed in space are sufficient for biomass estimations in South America at large scales (Table 1). Please note that we tested a simple downscaling procedure, so caution must be applied to these initial findings.

Although the coefficient of variation (CV) of the biomass distribution decreases with increasing plot size for local forests

245 (Réjou-Méchain et al., 2014; Wagner et al., 2010), there seem to be only small effects for larger landscapes. For Panama, we even found a slight increase in CV when the plot size was changed from 1 ha to 25 ha, since the mean biomass value for the region was reduced due to averaging forest with non-forest plots.

4.2 Nonrandom sampling

Our analysis showed that sampling efforts change significantly if samples are not random in space. For South America,

250 nonrandom samples of forests are less reliable and require significantly more plots to achieve accurate biomass estimations. This means that the necessary plots for nonrandom sampling strategies (as can be found in real-world inventories and RS measurements) cannot be assessed by Monte Carlo simulations that implicitly assume that samples are random (as in related studies of (Chave et al., 2004; Fisher et al., 2008; Keller et al., 2001; Marvin et al., 2014). Instead simulation procedures need to incorporate more advanced methods that include aggregated plot placement.

255 We demonstrated that a spatial autocorrelation has an effect on the sampling strategy if plots close to each other are more similar than plots located farther apart (positive autocorrelation). Larger regions were shown to be more spatially clustered in terms of biomass (e.g., large biomass stocks occur more frequently within the Amazon basin than in the surrounding landscape) because biomass varies due to environmental gradients and geographical reasons (Houghton et al., 2009). Therefore, large-scale analyses are more affected by the sampling design than regional estimations.

260 The methods presented above can also be applied to other forest attributes (e.g., species richness and carbon fluxes) and can be adapted to other ecosystems, such as grasslands or farmlands. Please note that in this study, we did not consider additional error sources, e.g., due to tree size measurements or allometric models, even though they are also known to influence estimates (Chave et al., 2004).

5 Conclusions

265 In summary, our study shows that the accuracy of the biomass estimates derived from samples depends considerably on the sampling strategy. Inventories are highly relevant for studying forest structure and dynamics. For South America, we have shown that more spatially randomly distributed plots are beneficial for continental-wide biomass estimations. Plot size should not fall below 0.25 ha, as the variability of biomass values will strongly increase (Chave et al., 2003; Clark et al., 2001; Keller et al., 2001; Réjou-Méchain et al., 2014), and tree-level measurement errors can dominate (Chave et al., 2004).

270 Since remote sensing can sample forest regions in a short time (Houghton et al., 2009; Schimel et al., 2015), a combination of remote sensing data and field inventory data seems to be a promising approach to overcome current limitations.

Code and Data availability

Biomass data (BCI, Panama, tropics) is available in the corresponding reference. The R code for sampling simulations is available upon request from the corresponding author.

275 **Author contribution**

JH, RF, and AH conceptualized the research; JH prepared the data and ran analyses. TW supported point pattern analysis. HJD contributed to analytical solutions. JH, RF and AH prepared the first draft of the manuscript and all the co-authors contributed substantially to subsequent versions, including the final draft.

Competing interests

280 The authors declare no competing interests.

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References

285 Anderson, L. O., Malhi, Y., Ladle, R. J., Aragão, L. E. O. C., Shimabukuro, Y., Phillips, O. L., Baker, T., Costa, A. C. L., Espejo, J. S., Higuchi, N., Laurance, W. F., López-González, G., Monteagudo, A., Núñez-Vargas, P., Peacock, J., Quesada, C. A. and Almeida, S.: Influence of landscape heterogeneity on spatial patterns of wood productivity, wood specific density and above ground biomass in Amazonia, Biogeosciences, 6(9), 1883–1902, doi:10.5194/bg-6-1883-2009, 2009.

Asner, G. P., Mascaro, J., Anderson, C., Knapp, D. E., Martin, R. E., Kennedy-Bowdoin, T., van Breugel, M., Davies, S.,
290 Hall, J. S., Muller-Landau, H. C., Potvin, C., Sousa, W., Wright, J. and Bermingham, E.: High-fidelity national carbon mapping for resource management and REDD+, Carbon Balance Manag., 8(1), 1, doi:10.1186/1750-0680-8-7, 2013.

Baccini, A., Goetz, S. J., Walker, W. S., Laporte, N. T., Sun, M., Sulla-Menashe, D., Hackler, J., Beck, P. S. A., Dubayah, R., Friedl, M. A., Samanta, S. and Houghton, R. A.: Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps, Nat. Clim. Chang., 2(3), 182–185 [online] Available from:
295 http://dx.doi.org/10.1038/nclimate1354, 2012.

Broich, M., Stehman, S. V., Hansen, M. C., Potapov, P. and Shimabukuro, Y. E.: A comparison of sampling designs for estimating deforestation from Landsat imagery: A case study of the Brazilian Legal Amazon, Remote Sens. Environ.,

113(11), 2448–2454, doi:10.1016/j.rse.2009.07.011, 2009.

Chave, J., Condit, R., Lao, S., Caspersen, J. P., Foster, R. B. and Hubbell, S. P.: Spatial and temporal variation of biomass in
300   a tropical forest : results from a large census plot in Panama, , 240–252, 2003.

Chave, J., Condit, R., Aguilar, S., Hernandez, A., Lao, S. and Perez, R.: Error propagation and scaling for tropical forest
biomass estimates, Philos. Trans. R. Soc. B Biol. Sci., 359(1443), 409–420, doi:10.1098/rstb.2003.1425, 2004.

Clark, D. A., Brown, S., Kicklighter, D. W., Chambers, J. Q., Thomlinson, J. R., Ni, J. and Holland, E. A.: Net Primary
Productivity in Tropical Forests: An evaluation and Synthesis of Existing Field Data, Ecol. Appl., 11(2 (Apr., 2001)), 371–
305   384, doi:10.2307/3060895, 2001.

Clark, D. B. and Clark, D. A.: Landscape-scale variation in forest structure and biomass in a tropical rain forest, , 137, 2000.

Clark, D. B. and Kellner, J. R.: Tropical forest biomass estimation and the fallacy of misplaced concreteness, , 23, 1191–
1196, doi:10.1111/j.1654-1103.2012.01471.x, 2012.

Condit, R.: Tropical Forest Census Plots: Methods and Results from Barro Colorado Island, Panama and a Comparison with
310   Other Plots, Springer Berlin Heidelberg. [online] Available from: https://books.google.de/books?id=i59sdrERVwIC, 1998.

Condit, R., Lao, S., Pérez, R., Dolins, S. B., Foster, R. and Hubbell, S.: Barro Colorado Forest Census Plot Data, Version
2012, , doi:http://dx.doi.org/10.5479/data.bci.20130603, 2012.

Fisher, J. I., Hurtt, G. C., Thomas, R. Q. and Chambers, J. Q.: Clustered disturbances lead to bias in large-scale estimates
based on forest sample plots, Ecol. Lett., 11(6), 554–563, doi:10.1111/j.1461-0248.2008.01169.x, 2008.

315   Houghton, R. A., Hall, F. and Goetz, S. J.: Importance of biomass in the global carbon cycle, J. Geophys. Res.
Biogeosciences, 114(3), 1–13, doi:10.1029/2009JG000935, 2009.

Houghton, R. a, Lawrence, K. T., Hackler, J. L. and Brown, S.: The spatial distribution of forest biomass in the Brazilian
Amazon: a comparison of estimates, Glob. Chang. Biol., 7(7), 731–746, doi:DOI 10.1046/j.1365-2486.2001.00426.x, 2001.

Keller, M., Palace, M. and Hurtt, G.: Biomass estimation in the Tapajos National Forest, Brazil examination of sampling and
320   allometric uncertainties, For. Ecol. Manage., 154(3), 371–382, doi:10.1016/S0378-1127(01)00509-6, 2001.

Knapp, N., Fischer, R. and Huth, A.: Linking lidar and forest modeling to assess biomass estimation across scales and
disturbance states, Remote Sens. Environ., 205(November 2017), 199–209, doi:10.1016/j.rse.2017.11.018, 2018.

Lewis, S. L., Phillips, O. L., Baker, T. R., Lloyd, J., Malhi, Y., Almeida, S., Higuchi, N., Laurance, W. F., Neill, D. a, Silva,
J. N. M., Terborgh, J., Lezama, a T., Martinez, R. V, Brown, S., Chave, J., Kuebler, C., Vargas, P. N. and Vinceti, B. C. A.
325   C. D. C. N. P.: Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term
plots, Philosophical Transactions of the Royal Society of London B Biological Sciences, 359(1443), 421-436 ST-Concerted
changes in tropical forest, doi:10.1098/rstb.2003.1431, 2004.

Lopez-Gonzalez, G., Mitchard, E. T. A., Feldpausch, T. R., Brienen, R. J. W., Monteagudo, A., Baker, T. R., Lewis, S. L.,
Lloyd, J., Quesada, C. A., Gloor, E., ter Steege, H., Meir, P., Alvarez, E., Araujo-Murakami, A., Aragão, L. E. O. C.,
330   Arroyo, L., Aymard, G., Banki, O., Bonal, D., Brown, S., Brown, F. I., Cerón, C. E., Chama Moscoso, V., Chave, J.,
Comiskey, J. M., Cornejo, F., Corrales Medina, M., Da Costa, L., Costa, F. R. C., Di Fiore, A., Domingues, T., Erwin, T. L.,

Fredericksen, T., Higuchi, N., Honorio Coronado, E. N., Killeen, T. J., Laurance, W. F., Levis, C., Magnusson, W. E., Marimon, B. S., Marimon-Junior, B. H., Mendoza Polo, I., Mishra, P., Nascimento, M., Neill, D., Nunez Vargas, M. P., Palacios, W. A., Parada-Gutierrez, A., Pardo Molina, G., Peña-Claros, M., Pitman, N., Peres, C. A., Poorter, L., Prieto, A.,

335   Ramírez-Angulo, H., Restrepo Correa, Z., Roopsind, A., Roucoux, K. H., Rudas, A., Salomao, R. P., Schietti, J., Silveira, M., De Souza, P. F., Steiniger, M., Stropp, J., Terborgh, J., Thomas, R. P., Toledo, M., Torres-Lezama, A., Van Andel, T. R., van der Heijden, G. M. F., Vieira, I. C. G., Vieira, S., Vilanova-Torre, E., Vos, V. A., Wang, O., Zartman, C. E., de Oliveira, E. A., Morandi, P. S., Malhi, Y. and Phillips, O. L.: Amazon forest biomass measured in inventory plots. Plot Data from "Markedly divergent estimates of Amazon forest carbon density from ground plots and satellites.," [online] Available from:

340   https://doi.org/10.5521/FORESTPLOTS.NET/2014_1, 2014.

Malhi, Y., Phillips, O. L., Lloyd, J., Baker, T., Wright, J., Almeida, S., Arroyo, L., Frederiksen, T., Grace, J., Higuchi, N., Killeen, T., Laurance, W. F., Leano, C., Lewis, S., Meir, P., Monteagudo, A., Neill, D., Nunez Vargas, P., Panfil, S. N., Patino, S., Pitman, N., Quesada, C. a., Rudas-Ll, A., Salomao, R., Saleska, S., Silva, N., Silveira, M., Sombroek, W. G., Valencia, R., Vasquez Martinez, R., Vieira, I. C. G. and Vinceti, B.: An international network to monitor the structure,

345   composition and dynamics of Amazonian forests (RAINFOR), J. Veg. Sci., 13, 439–450, doi:10.1111/j.1654-1103.2002.tb02068.x, 2002.

Malhi, Y., Wood, D., Baker, T. R., Wright, J., Phillips, O. L., Cochrane, T., Meir, P., Chave, J., Almeida, S., Arroyo, L., Higuchi, N., Killeen, T. J., Laurance, S. G., Laurance, W. F., Lewis, S. L., Monteagudo, A., Neill, D. A., Vargas, P. N., Pitman, N. C. A., Quesada, C. A., Salomão, R., Silva, J. N. M., Lezama, A. T., Terborgh, J., Martínez, R. V. and Vinceti, B.:

350   The regional variation of aboveground live biomass in old-growth Amazonian forests, Glob. Chang. Biol., 12(7), 1107–1138, doi:10.1111/j.1365-2486.2006.01120.x, 2006.

Marvin, D. C., Asner, G. P., Knapp, D. E., Anderson, C. B., Martin, R. E., Sinca, F. and Tupayachi, R.: Amazonian landscapes and the bias in field studies of forest structure and biomass, , doi:10.1073/pnas.1412999111, 2014.

Mitchard, E. T. A., Feldpausch, T. R., Brienen, R. J. W., Lopez- Gonzalez, G., Monteagudo, A., Baker, T. R., Lewis, S. L.,

355   Lloyd, J., Quesada, C. A., Gloor, M., Steege, H., Meir, P., Alvarez, E., Araujo- Murakami, A., Aragão, L. E. O. C., Arroyo, L., Aymard, G., Banki, O., Bonal, D., Brown, S., Brown, F. I., Cerón, C. E., Moscoso, V. C., Chave, J., Comiskey, J. A., Cornejo, F., Medina, M. C., Costa, L. Da, Costa, F. R. C., Fiore, A. Di, Domingues, T. F., Erwin, T. L., Frederickson, T., Higuchi, N., Coronado, E. N. H., Killeen, T. J., Laurance, W. F., Levis, C., Magnusson, W. E., Marimon, B. S., Junior, B. H. M., Polo, I. M., Mishra, P., Nascimento, M. T., Neill, D., Vargas, M. P. N., Palacios, W. A., Parada, A., Molina, G. P.,

360   Peña- Claros, M., Pitman, N., Peres, C. A., Poorter, L., Prieto, A., Ramirez- Angulo, H., Correa, Z. R., Roopsind, A., Roucoux, K. H., Rudas, A., Salomão, R. P., Schietti, J., Silveira, M., Souza, P. F., Steininger, M. K., Stropp, J., Terborgh, J., Thomas, R., Toledo, M., Torres- Lezama, A., Andel, T. R., Heijden, G. M. F., Vieira, I. C. G., Vieira, S., Vilanova- Torre, E., Vos, V. A., Wang, O., Zartman, C. E., Malhi, Y. and Phillips, O. L.: Markedly divergent estimates of Amazon forest carbon density from ground plots and satellites, Glob. Ecol. Biogeogr., 23(8), 935–946, doi:10.1111/geb.12168, 2014.

365   Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L., Shvidenko, A., Lewis, S. L.,

Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S. W., McGuire, A. D., Piao, S., Rautiainen, A., Sitch, S. and Hayes, D.: A Large and Persistent Carbon Sink in the World's Forests, Science (80-.)., 333(6045), 988–993 [online] Available from: http://science.sciencemag.org/content/333/6045/988.abstract, 2011.

Poorter, L., van der Sande, M. T., Thompson, J., Arets, E. J. M. M., Alarcón, A., Álvarez-Sánchez, J., Ascarrunz, N.,
370 Balvanera, P., Barajas-Guzmán, G., Boit, A., Bongers, F., Carvalho, F. A., Casanoves, F., Cornejo-Tenorio, G., Costa, F. R. C., de Castilho, C. V., Duivenvoorden, J. F., Dutrieux, L. P., Enquist, B. J., Fernández-Méndez, F., Finegan, B., Gormley, L. H. L., Healey, J. R., Hoosbeek, M. R., Ibarra-Manríquez, G., Junqueira, A. B., Levis, C., Licona, J. C., Lisboa, L. S., Magnusson, W. E., Martínez-Ramos, M., Martínez-Yrizar, A., Martorano, L. G., Maskell, L. C., Mazzei, L., Meave, J. A., Mora, F., Muñoz, R., Nytch, C., Pansonato, M. P., Parr, T. W., Paz, H., Pérez-García, E. A., Rentería, L. Y., Rodríguez-
375 Velazquez, J., Rozendaal, D. M. A., Ruschel, A. R., Sakschewski, B., Salgado-Negret, B., Schietti, J., Simões, M., Sinclair, F. L., Souza, P. F., Souza, F. C., Stropp, J., ter Steege, H., Swenson, N. G., Thonicke, K., Toledo, M., Uriarte, M., van der Hout, P., Walker, P., Zamora, N. and Peña-Claros, M.: Diversity enhances carbon storage in tropical forests, Glob. Ecol. Biogeogr., 24(11), 1314–1328, doi:10.1111/geb.12364, 2015.

Réjou-Méchain, M., Muller-Landau, H. C., Detto, M., Thomas, S. C., Le Toan, T., Saatchi, S. S., Barreto-Silva, J. S., Bourg,
380 N. A., Bunyavejchewin, S., Butt, N., Brockelman, W. Y., Cao, M., Cárdenas, D., Chiang, J. M., Chuyong, G. B., Clay, K., Condit, R., Dattaraja, H. S., Davies, S. J., Duque, A., Esufali, S., Ewango, C., Fernando, R. H. S., Fletcher, C. D., N. Gunatilleke, I. A. U., Hao, Z., Harms, K. E., Hart, T. B., Hérault, B., Howe, R. W., Hubbell, S. P., Johnson, D. J., Kenfack, D., Larson, A. J., Lin, L., Lin, Y., Lutz, J. A., Makana, J. R., Malhi, Y., Marthews, T. R., Mcewan, R. W., Mcmahon, S. M., Mcshea, W. J., Muscarella, R., Nathalang, A., Noor, N. S. M., Nytch, C. J., Oliveira, A. A., Phillips, R. P.,
385 Pongpattananurak, N., Punchi-Manage, R., Salim, R., Schurman, J., Sukumar, R., Suresh, H. S., Suwanvecho, U., Thomas, D. W., Thompson, J., Uríarte, M., Valencia, R., Vicentini, A., Wolf, A. T., Yap, S., Yuan, Z., Zartman, C. E., Zimmerman, J. K. and Chave, J.: Local spatial structure of forest biomass and its consequences for remote sensing of carbon stocks, , 6827–6840, doi:10.5194/bg-11-6827-2014, 2014.

Rödig, E., Cuntz, M., Heinke, J., Rammig, A. and Huth, A.: Spatial heterogeneity of biomass and forest structure of the
390 Amazon rain forest: Linking remote sensing, forest modelling and field inventory, Glob. Ecol. Biogeogr., 26(11), 1292–1302, doi:10.1111/geb.12639, 2017.

Saatchi, S. S., Harris, N. L., Brown, S., Lefsky, M., Mitchard, E. T. A. and Salas, W.: Benchmark map of forest carbon stocks in tropical regions across three continents, , 108(24), doi:10.1073/pnas.1019576108, 2011.

Schimel, D., Pavlick, R., Fisher, J. B., Asner, G. P., Saatchi, S., Townsend, P., Miller, C., Frankenberg, C., Hibbard, K. and
395 Cox, P.: Observing terrestrial ecosystems and the carbon cycle from space, Glob. Chang. Biol., 21(5), 1762–1776, doi:10.1111/gcb.12822, 2015.

Wagner, F., Rutishauser, E., Blanc, L. and Herault, B.: Effects of Plot Size and Census Interval on Descriptors of Forest Structure and Dynamics, , 1–8, doi:10.1111/j.1744-7429.2010.00644.x, 2010.

Wang, J. F., Stein, A., Gao, B. B. and Ge, Y.: A review of spatial sampling, Spat. Stat., 2(1), 1–14,

400 doi:10.1016/j.spasta.2012.08.001, 2012.

Wiegand, T., He, F. and Hubbell, S. P.: A systematic comparison of summary characteristics for quantifying point patterns in ecology, Ecography (Cop.)., 36(1), 092–103, doi:10.1111/j.1600-0587.2012.07361.x, 2013.

Zurell, D., Berger, U., Cabral, J. S., Jeltsch, F., Meynard, C. N., Münkemüller, T., Nehrbass, N., Pagel, J., Reineking, B., Schröder, B. and Grimm, V.: The virtual ecologist approach: Simulating data and observers, Oikos, 119(4), 622–635,

405 doi:10.1111/j.1600-0706.2009.18284.x, 2010.