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1 **Title**

2 Pan-tropical prediction of forest structure from the largest trees

3 **Authors**

4 Jean-François Bastin<sup>1,2,3,4</sup>, Ervan Rutishauser<sup>4,5</sup>, James R. Kellner<sup>6,7</sup>, Sassan Saatchi<sup>8</sup>,  
5 Raphael Pélissier<sup>9</sup>, Bruno Hérault<sup>10,11</sup>, Ferry Slik<sup>12</sup>, Jan Bogaert<sup>13</sup>, Charles De Cannière<sup>2</sup>,  
6 Andrew R. Marshall<sup>14,15,16</sup>, John Poulsen<sup>17</sup>, Patricia Alvarez-Loyayza<sup>18</sup>, Ana Andrade<sup>19</sup>,  
7 Albert Angbonga-Basia<sup>20</sup>, Alejandro Araujo-Murakami<sup>21</sup>, Luzmila Arroyo<sup>22</sup>, Narayanan  
8 Ayyappan<sup>23,24</sup>, Celso Paulo de Azevedo<sup>25</sup>, Olaf Banki<sup>26</sup>, Nicolas Barbier<sup>9</sup>, Jorcely G.  
9 Barroso<sup>26</sup>, Hans Beeckman<sup>27</sup>, Robert Bitariho<sup>28</sup>, Pascal Boeckx<sup>29</sup>, Katrin Boehning-  
10 Gaese<sup>30,31</sup>, Hilandia Brandão<sup>32</sup>, Francis Q. Brearley<sup>33</sup>, Mireille Breuer Ndoundou Hockemba<sup>34</sup>,  
11 Roel Brienen<sup>35</sup>, Jose Luis C. Camargo<sup>19</sup>, Sto<sup>36</sup>, Benoit Cassart<sup>37,38</sup>, Jérôme Chave<sup>39</sup>, Robin  
12 Chazdon<sup>40</sup>, Georges Chuyong<sup>41</sup>, David B. Clark<sup>42</sup>, Connie J. Clark<sup>17</sup>, Richard Condit<sup>43</sup>,  
13 Euridice N. Honorio Coronado<sup>44</sup>, Priya Davidar<sup>22</sup>, Thalès de Haulleville<sup>13,27</sup>, Laurent  
14 Descroix<sup>45</sup>, Jean-Louis Doucet<sup>13</sup>, Aurelie Dourdain<sup>46</sup>, Vincent Droissart<sup>9</sup>, Thomas Duncan<sup>47</sup>,  
15 Javier Silva Espejo<sup>48</sup>, Santiago Espinosa<sup>49</sup>, Nina Farwig<sup>50</sup>, Adeline Fayolle<sup>13</sup>, Ted R.  
16 Feldpausch<sup>51</sup>, Antonio Ferraz<sup>8</sup>, Christine Fletcher<sup>36</sup>, Krisna Gajapersad<sup>52</sup>, Jean-François  
17 Gillet<sup>13</sup>, Iêda Leão do Amaral<sup>32</sup>, Christelle Gonmadje<sup>53</sup>, James Grogan<sup>54</sup>, David  
18 Harris<sup>55</sup>, Sebastian K. Herzog<sup>56</sup>, Jürgen Homeier<sup>57</sup>, Wannes Hubau<sup>27</sup>, Stephen P. Hubbell<sup>58,59</sup>,  
19 Koen Hufkens<sup>29</sup>, Johanna Hurtado<sup>60</sup>, Narcisse G. Kamdem<sup>61</sup>, Elizabeth Kearsley<sup>62</sup>, David  
20 Kenfack<sup>63</sup>, Michael Kessler<sup>64</sup>, Nicolas Labrière<sup>10,65</sup>, Yves Laumonier<sup>10,66</sup>, Susan Laurance<sup>67</sup>,  
21 William F. Laurance<sup>68</sup>, Simon L. Lewis<sup>35</sup>, Moses B. Libalah<sup>61</sup>, Gauthier Ligot<sup>13</sup>, Jon Lloyd<sup>67,68</sup>,  
22 Thomas E. Lovejoy<sup>69</sup>, Yadvinder Malhi<sup>70</sup>, Beatriz S. Marimon<sup>71</sup>, Ben Hur Marimon Junior<sup>71</sup>,  
23 Emmanuel H. Martin<sup>72</sup>, Paulus Matius<sup>73</sup>, Victoria Meyer<sup>8</sup>, Casimero Mendoza Bautista<sup>74</sup>, Abel  
24 Monteagudo-Mendoza<sup>75</sup>, Arafat Mtui<sup>76</sup>, David Neill<sup>77</sup>, Germaine Alexander Parada  
25 Gutierrez<sup>78</sup>, Guido Pardo<sup>79</sup>, Marc Parren<sup>80</sup>, N. Parthasarathy<sup>23</sup>, Oliver L. Phillips<sup>35</sup>, Nigel C.A.  
26 Pitman<sup>80</sup>, Pierre Ploton<sup>9</sup>, Quentin Ponette<sup>37</sup>, B.R. Ramesh<sup>23</sup>, Jean-Claude  
27 Razafimahaimodison<sup>81</sup>, Maxime Réjou-Méchain<sup>9</sup>, Samir Gonçalves Rolim<sup>82</sup>, Hugo Romero  
28 Saltos<sup>83</sup>, Luiz Marcelo Brum Rossi<sup>82</sup>, Wilson Roberto Spironello<sup>32</sup>, Francesco Rovero<sup>76</sup>,

29 Philippe Saner<sup>84</sup>, Denise Sasaki<sup>85</sup>, Mark Schulze<sup>86</sup>, Marcos Silveira<sup>87</sup>, James Singh<sup>88</sup>, Plinio  
30 Sist<sup>10,89</sup>, Bonaventure Sonke<sup>61</sup>, J.Daniel Soto<sup>90</sup>, Cintia Rodrigues de Souza<sup>24</sup>, Juliana  
31 Stropp<sup>91</sup>, Martin J.P. Sullivan<sup>35</sup>, Ben Swanepoel<sup>34</sup>, Hans ter Steege<sup>25,92</sup>, John  
32 Terborgh<sup>93,94</sup>, Nicolas Texier<sup>95</sup>, T.Toma<sup>96</sup>, Renato Valencia<sup>97</sup>, Luis Valenzuela<sup>75</sup>, Leandro  
33 Valle Ferreira<sup>98</sup>, Fernando Cornejo Valverde<sup>99</sup>, Tinde R Van Andel<sup>25</sup>, Rodolfo Vasque<sup>77</sup>, Hans  
34 Verbeeck<sup>62</sup>, Pandi Vivek<sup>22</sup>, Jason Vleminckx<sup>100</sup>, Vincent A.Vos<sup>79,101</sup>, Fabien H.Wagner<sup>102</sup>,  
35 Warsudi<sup>103</sup>, Verginia Wortel<sup>104</sup>, Roderick J. Zagt<sup>105</sup>, Donatien Zebaze<sup>61</sup>

36 1. Institute of Integrative Biology, Department of Environmental Systems Science, ETH  
37 Zürich, 8092 Zürich, Switzerland

38 2. Landscape Ecology and Plant Production System, Université libre de Bruxelles.  
39 CP264-2, B-1050 Bruxelles, Belgium

40 3. Affiliated during analysis and writing at NASA, Jet Propulsion Laboratory, California  
41 Institute of Technology, 4800 Oak Grove Drive, Pasadena, CA 91109, USA

42 4. Carboforexpert (carboforexpert.ch), 1248 Hermance, Switzerland

43 5. Smithsonian Tropical Research Institute, Box 0843-03092, Balboa, Ancon, Panama

44 6. Department of Ecology and Evolutionary Biology, Brown University, Providence, RI  
45 02912, USA

46 7. Institute at Brown for Environment and Society, Brown University, Providence, RI  
47 02912, USA

48 8. NASA, Jet Propulsion Laboratory, California Institute of Technology, 4800 Oak Grove  
49 Drive, Pasadena, CA 91109, USA

50 9. AMAP Lab, IRD, CIRAD, CNRS, INRA, Univ. Montpellier, Montpellier, France

51 10. Cirad, UR Forest & Societies, 34398 Montpellier Cedex 5, France

- 52 11. INPHB (Institut National Polytechnique Félix Houphouet Boigny), Yamoussoukro,  
53 Ivory Coast
- 54 12. Faculty of Science, Universiti Brunei Darussalam, Gadong, Brunei Darussalam
- 55 13. Gembloux Agro-Bio Tech, Université de Liège, B-5030 Gembloux, Belgium
- 56 14. CIRCLE, Environment Department, Wentworth Way, University of York, Heslington,  
57 York, YO10 5NG, UK
- 58 15. Tropical Forests and People Research Centre, University of the Sunshine Coast, QLD  
59 4556, Australia
- 60 16. Flamingo Land Ltd., Kirby Misperton, YO17 6UX, UK
- 61 17. Nicholas School of the Environment, Duke University, PO Box 90328, Durham, NC  
62 27708, USA
- 63 18. Field Museum of Natural History, Chicago, USA.
- 64 19. Biological Dynamics of Forest Fragment Project (BDFFP - INPA/STRI), Manaus -  
65 Amazonas, Brazil
- 66 20. Institut Facultaire des Sciences Agronomiques de Yangambi. DRC
- 67 21. Museo de Historia Natural Noel Kempff Mercado, Santa Cruz, Bolivia
- 68 22. Department of Ecology and Environmental Sciences, Pondicherry University, Kalapet,  
69 Pondicherry 605014, India
- 70 23. French Institute of Pondicherry (IFP), 11 Saint Louis Street, Pondicherry 605 001,  
71 India
- 72 24. Embrapa Amazônia Ocidental, Brazil
- 73 25. Naturalis Biodiversity Centre, PO Box 9517, 2300 RA Leiden, The Netherlands
- 74 26. Universidade Federal do Acre, Campus Floresta, Cruzeiro do Sul, Acre, Brazil

- 75 27. Service of Wood Biology, Royal Museum for Central Africa, Tervuren, Belgium
- 76 28. Institute of Tropical Forest Conservation, Mbarara University of Science and  
77 Technology, Uganda.
- 78 29. Isotope Bioscience Laboratory – ISOFYS, Ghent University, Belgium
- 79 30. Senckenberg Biodiversity and Climate Research Centre (BiK-F), Frankfurt am Main,  
80 Germany
- 81 31. Dept of Biological Sciences, Goethe Universität, Frankfurt am Main, Germany
- 82 32. National Institute for Amazonian Research (INPA), Manaus, Amazonas, Brazil
- 83 33. School of Science and the Environment, Manchester Metropolitan University, Chester  
84 Street, Manchester, M1 5GD, UK
- 85 34. Wildlife Conservation Society, New York, USA
- 86 35. School of Geography, University of Leeds, Leeds, UK
- 87 36. Malaysia Campus, Jalan Broga, Semenyih 43500, Selangor, Malaysia
- 88 37. UCL-ELI, Earth and Life Institute, Université catholique de Louvain, Louvain-la-Neuve  
89 BE-1348, Belgium
- 90 38. Ecole Régionale Post-universitaire d'Aménagement et de Gestion Intégrés des Forêts  
91 et Territoires Tropicaux, Kinshasa, DRC
- 92 39. Laboratoire Evolution et Diversité biologique, CNRS & Université Paul Sabatier,  
93 Toulouse 31062, France
- 94 40. Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs,  
95 Connecticut 06268-3043, USA
- 96 41. Department of Botany and Plant Physiology, University of Buea, Cameroon
- 97 42. Department of Biology, University of Missouri-St Louis, Missouri, USA

- 98 43. Field Museum of Natural History and Morton Arboretum, Illinois, USA
- 99 44. Coronado, Inst. de Investigaciones de la Amazonia Peruana, Iquitos, Peru
- 100 45. ONF pôle R&D, Cayenne, France
- 101 46. Cirad, UMR EcoFoG (AgroParisTech, CNRS, Inra, Universite des Antilles, Universite  
102 de la Guyane), Kourou, French Guiana
- 103 47. Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR  
104 97331, USA
- 105 48. Departamento de Biología, Universidad de La Serena, Casilla 554 La Serena, Chile
- 106 49. Universidad Autónoma de San Luis Potosí, San Luis Potosí, México
- 107 50. Department of Conservation Ecology, Philipps-Universität Marburg, Karl-von-Frisch-  
108 Straße 8, 35032 Marburg, Germany
- 109 51. Geography, College of Life and Environmental Sciences, University of Exeter, Exeter,  
110 EX4 4RJ, UK
- 111 52. Conservation International Suriname, Paramaribo, Suriname
- 112 53. Department of Plant Biology, Faculty of science, University of Yaounde I, BP 812  
113 Yaoundé, Cameroon
- 114 54. Mount Holyoke College Botanic Garden, South Hadley, MA 01075, USA
- 115 55. Royal Botanic Garden Edinburgh, Edinburgh EH3 5LR, UK
- 116 56. Museo de Historia Natural Alcide d'Orbigny, Cochabamba, Bolivia
- 117 57. Plant Ecology, University of Goettingen, Untere Karspuele 2, 37073 Goettingen,  
118 Germany
- 119 58. Department of Ecology and Evolutionary Biology, University of California, Los  
120 Angeles, California 90095, USA

- 121 59. Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Republic of  
122 Panama
- 123 60. Organization for Tropical Studies, Costa Rica
- 124 61. Plant Systematic and Ecology Laboratory, Higher Teacher's Training College,  
125 University of Yaoundé I, P.O. Box 047, Yaoundé, Cameroon.
- 126 62. CAVElab – Computational and Applied Vegetation Ecology, Ghent University,  
127 Belgium
- 128 63. CTFS-ForestGEO, Smithsonian Tropical Research Institute, MRC 166, NMNH, P.O.  
129 Box 37012, Washington, DC 20013-7012, USA
- 130 64. Department of Systematic and Evolutionary Botany, University of Zurich,  
131 Zollikerstrasse 107, Zurich 8008, Switzerland
- 132 65. AgroParisTech, Doctoral School ABIES, 19 Avenue du Maine, 75732 Paris Cedex 15,  
133 France
- 134 66. Center for International Forestry Research, Jl. CIFOR, Situ Gede, Bogor Barat 16115,  
135 Indonesia
- 136 67. Centre for Tropical Environmental and Sustainability Science, College of Science and  
137 Engineering, James Cook University, Cairns, Queensland 4870, Australia.
- 138 68. Department of Life Sciences, Imperial College London, SL5 7PY, Ascot, UK
- 139 69. Department of Environmental Science and Policy, George Mason University, Fairfax,  
140 VA, USA
- 141 70. Environmental Change Institute, School of Geography and the Environment,  
142 University of Oxford, Oxford, UK
- 143 71. Universidade do Estado de Mato Grosso, Campus de Nova Xavantina, Nova  
144 Xavantina, MT, Brazil

- 145 72. Udzungwa Ecological Monitoring Centre, Udzungwa Mountains National Park,  
146 Tanzania, Sokoine University of Agriculture, Morogoro, Tanzania
- 147 73. Escuela de Ciencias Forestales, Unidad Académica del Trópico, Universidad Mayor  
148 de San Simón, Sacta, Bolivia
- 149 74. Faculty of Forestry, Mulawarman University, Indonesia
- 150 75. Jardín Botánico de Missouri, Oxapampa, Pasco, Peru.
- 151 76. MUSE - Museo delle Scienze, Trento, Italy
- 152 77. Universidad Estatal Amazónica, Puyo, Pastaza, Ecuador
- 153 78. Museo de Historia Natural Noel Kempff Mercado, Santa Cruz, Bolivia
- 154 79. Universidad Autónoma del Beni, Riberalta, Bolivia
- 155 80. Science and Education, The Field Museum, 1400 South Lake Shore Drive, Chicago,  
156 Illinois 60605–2496, USA
- 157 81. Centre ValBio, Ranomafana, Madagascar
- 158 82. Embrapa Florestas, Colombo/PR, Brazil
- 159 83. Yachay Tech University, School of Biological Sciences and Engineering. Urcuquí,  
160 Ecuador
- 161 84. Department of Evolutionary Biology and Environmental Studies, University of Zurich,  
162 CH-8057 Zurich, Switzerland
- 163 85. Fundação Ecológica Cristalino Alta Floresta, Brazil
- 164 86. HJ Andrews Experimental Forest, PO Box 300, Blue River, OR 97413, USA
- 165 87. Museu Universitário, Universidade Federal do Acre, Rio Branco 69910-900, Brazil
- 166 88. Guyana Forestry Commission, Georgetown, Guiana



- 167 89. Forests and Societies, Univ. Montpellier, CIRAD, Montpellier, France
- 168 90. Museo de Historia Natural Noel Kempff Mercado, Santa Cruz, Bolivia
- 169 91. Institute of Biological and Health Sciences, Federal University of Alagoas, Maceió,  
170 Brazil
- 171 92. Systems Ecology, Free University, De Boelelaan 1087, Amsterdam, 1081 HV,  
172 Netherlands.
- 173 93. Florida Museum of Natural History and Department of Biology, University of Florida -  
174 Gainesville, Gainesville, FL 32611, USA
- 175 94. Department of Biology, James Cook University, Cairns, Australia
- 176 95. Laboratoire d'Evolution Biologique et Ecologie, Faculté des Sciences, Université libre  
177 de Bruxelles, CP160/12, 1050 Bruxelles, Belgium
- 178 96. Forestry and Forest Products Research Institute, Matsunosato 1, Tsukuba 305-8687,  
179 Japan
- 180 97. Escuela de Ciencias Biológicas, Pontificia Universidad Católica del Ecuador, Quito,  
181 Ecuador
- 182 98. Coordenação de Botânica, Museu Paraense Emilio Goeldi, Belém, Brazil
- 183 99. Andes to Amazon Biodiversity Program, Madre de Dios, Peru
- 184 100. Department of Integrative Biology, University of California, Berkeley, 1005 Valley Life  
185 Sciences Building 3140, Berkeley, CA 94720-3140, USA
- 186 101. Centro de Investigación y Promoción del Campesinado - Norte Amazónico, Riberalta,  
187 Bolivia
- 188 102. Remote Sensing Division, National Institute for Space Research - INPE, São José  
189 dos Campos 12227-010, SP, Brazil

- 190 103. The Center for Reforestation Studies in the Tropical Rain Forest (PUSREHUT),  
191 Mulawarman University, Jln. Kihajar Dewantara Kampus Gunung Kelua, Samarinda 75123,  
192 East Kalimantan, Indonesia
- 193 104. Center for Agricultural Research in Suriname (CELOS), Suriname
- 194 105. Tropenbos International, PO Box 232, Wageningen 6700 AE, The Netherlands

195 **Abstract**

196 **Aim.** Large tropical trees form the interface between ground and airborne observations,  
197 offering a unique opportunity to capture forest properties remotely. However, despite rapid  
198 development of metrics to characterize the forest canopy from remotely sensed data, a gap  
199 remains between aerial and field inventories. To close this gap, we propose a new pan-tropical  
200 model to predict plot-level forest structure properties and biomass from just the largest trees,  
201 as a proxy for the whole plot inventory.

202 **Location.** Pan-tropical

203 **Method.** Using a dataset of 867 plots distributed among 118 sites across the tropics, we tested  
204 the ability to predict quadratic mean diameter, basal area, Lorey's height and community wood  
205 density from the  $i^{\text{th}}$  largest trees, i.e. testing the cumulative information gathered from these  $i$   
206 trees ranked by decreasing diameter. These tests served as a basis to select the optimal  
207 number of the largest trees and further predict plot-level biomass from a single model.

208 **Result.** Focusing on readily available information captured by airborne remote sensing, we  
209 show that measuring the largest trees in tropical forests enables unbiased predictions of plot  
210 and site-level forest structure. The 20 largest trees per hectare predicted quadratic mean  
211 diameter, basal area, Lorey's height and community wood density with 12%, 16%, 4% and 4%  
212 of relative error. Building on this result, we developed a new model to predict plot-level AGB  
213 from measurements of the 20 largest trees. This model allows an independent and unbiased  
214 prediction of biomass with 17.7% of error compared to ground estimates. Most of the remaining  
215 error is driven by differences in the proportion of total biomass held in medium size trees (50-  
216 70 cm), which shows some continental dependency with American tropical forests presenting  
217 the highest levels of total biomass share in these intermediate diameter classes.

218 **Conclusion.** Our approach provide new information on tropical forest structure and can be  
219 employed to generate accurately field estimates of tropical forest carbon stocks to support the  
220 calibration and validation of current and forthcoming space missions. It will reduce the cost of  
221 programs to monitor, report, and verify forest resources, and will contribute to scientific  
222 understanding of tropical forest ecosystems and response to climate change.

## 223 **Introduction**

224 The fundamental ecological function of large trees is well established for tropical forests. They  
225 offer shelter to a multiple organisms (Remm & Löhmus, 2011; Lindenmayer *et al.*, 2012),  
226 regulate forest dynamics, regeneration (Harms *et al.*, 2000; Rutishauser *et al.*, 2010) and total  
227 biomass (Stegen *et al.*, 2011), and are important contributor to the global carbon cycle  
228 (Meakem *et al.*, 2017). Being major components of the canopy, the largest trees also suffer  
229 more than sub-canopy and understory trees from climate change, as they are directly exposed  
230 to variations in solar radiation, wind strength, temperature seasonality and relative air humidity  
231 (Laurance *et al.*, 2000; Nepstad *et al.*, 2007; Lindenmayer *et al.*, 2012; Thomas *et al.*, 2013;  
232 Bennett *et al.*, 2015; Meakem *et al.*, 2017). Because they are visible from the sky, large trees  
233 are ideal for monitoring forest responses to climate change via remote sensing (Bennett *et al.*,  
234 2015; Asner *et al.*, 2017).

235 Large trees encompass a disproportionate fraction of total above-ground biomass (AGB) in  
236 tropical forests (Chave *et al.*, 2001), with some variations in their relative contribution to the  
237 total AGB among the tropical regions (Feldpausch *et al.*, 2012). In Central Africa, the largest  
238 5% of trees, i.e. the 5% of trees with the largest diameter at 130 cm per area, store 50% of  
239 forest aboveground biomass on average (Bastin *et al.*, 2015). Consequently, the density of  
240 large trees largely explains variation in AGB at local (Clark & Clark, 1996), regional (Malhi *et*  
241 *al.*, 2006; Saatchi *et al.*, 2007), and continental scales (Stegen *et al.*, 2011; Slik *et al.*, 2013).

242 Detailing the contribution of each single tree to the diameter structure, we showed previously  
243 that plot-level AGB can be predicted from a few large trees (Bastin *et al.*, 2015), with the  
244 measurement of the 20 largest trees per hectare being sufficient to estimate plot-level biomass  
245 with less than 15% errors in reference to ground estimates. These findings opened the  
246 possibility of measuring the largest trees to cost-effectively monitor forest biomass in Central  
247 Africa, rather than conducting full inventories of all size classes. Similarly, they suggested that  
248 remote sensing (RS) approaches should focus on the measurement of the largest trees,  
249 instead of properties of the entire forest.

250 Several efforts are underway to close the gap between remote sensing and field surveys (e.g.  
251 Jucker et al. 2016a, Coomes et al. 2017). However, field inventories still rely on exhaustive  
252 data collection, while remote sensing surveys provide a limited alternative for the following  
253 reasons. Existing RS approaches that provide predictions of biomass with less than 20% error  
254 for 1 ha plot size are either specific to the relationship between forest type and image/scene  
255 properties (Barbier *et al.*, 2011; Asner *et al.*, 2012; Barbier & Coutron, 2015), or require  
256 ground measurement of all trees above or equal to 10 cm of  $D$  for calibration (Asner *et al.*,  
257 2012; Asner & Mascaro, 2014). Using mean canopy height extracted from active sensors  
258 (Mascaro *et al.*, 2011; Ho Tong Minh *et al.*, 2016), or canopy grain derived from optical images  
259 (Proisy *et al.*, 2007; Ploton *et al.*, 2012, 2017; Bastin *et al.*, 2014), the biomass is predicted  
260 from remote sensing with a typical error of only 10-20% compared to ground-based estimates,  
261 but is limited to the extent of the scene used. An interesting development to alleviate this spatial  
262 restriction lies in the ‘universal approach’, proposed by Asner et al. (2012) and further adapted  
263 in Asner and Mascaro (2014), in which plot-level biomass is predicted by a linear combination  
264 of ground-based and remotely-sensed metrics. The ‘universal approach’ relies upon canopy  
265 height metrics derived from radar or LiDAR (top of canopy height, TCH), and basal area (BA,  
266 i.e. the cross-sectional stem area) and community wood density (i.e. weighted by basal area,  
267  $WD_{BA}$ ) derived from full field inventories. AGB is then predicted as follows (Asner *et al.*, 2012):  
268  $AGB = aTCH^{b1}BA^{b2}WD_{BA}^{b3}(1)$   
269 While generally performing better than approaches based solely on remote sensing of tree  
270 height (Coomes *et al.*, 2017), this model largely relies on exhaustive ground measurements  
271 (i.e. wood density and basal area of all trees above 10 cm of diameter at 130 cm, neither of  
272 which is measured using any existing remotely sensed data).

273 Recent advances in remote sensing allow the identification of single trees in the canopy (Ferraz  
274 *et al.*, 2016), estimation of adult mortality rates for canopy tree species (Kellner & Hubbell,  
275 2017), description of the forest diameter structure (Stark *et al.*, 2015), depiction of crown and  
276 gap shapes (Coomes *et al.*, 2017), and even identification of some functional traits of canopy  
277 species (Asner *et al.*, 2017). Building upon this work, we test the capacity of metrics from the

278 largest trees that can be potentially derived using remote sensing to predict plot-level biomass  
279 (i.e. the summed AGB of all live trees  $D \geq 10$  cm in a plot). To this end, we tested the following  
280 model:

$$281 \text{ AGB} = a(D_{\text{LT}}^2 H_{\text{LT}} W_{\text{LT}})^{b1} \quad (2)$$

282 Where for the  $i^{\text{th}}$  largest trees,  $D_{\text{LT}}$  is the quadratic mean diameter,  $H_{\text{LT}}$  the mean height, and  
283  $W_{\text{LT}}$  the mean wood density averaged among the  $i^{\text{th}}$  largest trees.

284 Using a large database of forest inventories gathered across the Tropics (Figure 1), including  
285 secondary and old growth forest plots, we test the ability of the largest trees to provide  
286 information on various metrics estimated at 1-ha plot level, such as the mean quadratic  
287 diameter, the basal area (BA), the Lorey's height (i.e. plot-average height weighted by BA), the  
288 community wood density (i.e. plot-average wood density weighted by BA) and mean above-  
289 ground live biomass (AGB) (supplementary figure 1). While previous work focused on  
290 estimating biomass in Central African forests (Bastin *et al.*, 2015), the present study aims at  
291 generalizing the potential of large trees in predicting these different plot metrics at continental  
292 and pan-tropical scales. Taking advantage of a unique dataset gathered across the tropics (XX  
293 ha, YYY plots), we also investigate major differences in forest structure across the three main  
294 tropical regions, South America, Africa and South East Asia. We further discuss how this  
295 approach can be used to guide innovative RS techniques and increase the frequency and  
296 representativeness of ground data to support global calibration and validation of current and  
297 planned space missions. These include the NASA Global Ecosystem Dynamics Investigation  
298 (GEDI), NASA-ISRO Synthetic Aperture Radar (NISAR), and ESA P-band radar (BIOMASS).  
299 This study is a step forward in bringing together remote sensing and field sampling techniques  
300 for quantification of terrestrial C stocks in tropical forests.

## 301 **Material & Methods**

### 302 **Database**

303 For this study, we compiled standard forest inventories conducted in 867 1-hectare plots from  
304 118 sites across the three tropical regions (Figure 1), including mature and secondary forests.  
305 Each site comprises all the plots in a given geographical location, i.e. within a 10 km radius  
306 and collected by a PI and its team. These consisted of 389 plots in America (69 sites), 302  
307 plots in Africa (35 sites) and 176 plots in Asia (14 sites). Data were provided by Principal  
308 Investigators (see supplementary Table 1), and through datasets available at ForestPlots  
309 (<https://www.forestplots.net/>), TEAM (<http://www.teamnetwork.org/>) and CTFS  
310 (<http://www.forestgeo.si.edu/>) networks.

311 We selected plots located between 23°N and 23°S, including tropical islands, with an area of  
312 at least 1-ha to ensure stable intra-sample variance in basal area (Clark & Clark, 2000). Plots  
313 in which at least 90% of the stems were identified to species, and in which all stems with the  
314 diameter at 130 cm greater than or equal to 10 cm had been measured were included. Wood  
315 density, here recorded as the wood dry mass divided by its green volume, was assigned to  
316 each tree using the lowest available taxonomic level of botanical identifications (i.e. species or  
317 genus) and the corresponding average wood density recorded in the Global Wood Density  
318 Database (GWDD, Chave *et al.*, 2009; Zanne *et al.*, 2009). Botanical identification was  
319 harmonized through the Taxonomic Names Resolution Service  
320 (<http://tnrs.iplantcollaborative.org>), for both plot inventories and the GWDD. For trees not  
321 identified to species or genus (~5%), we used plot-average wood density. We estimated  
322 heights of all trees using Chave *et al.*'s (2014) pan-tropical diameter-height model which  
323 accounts for heterogeneity in the D-H relationship using an environmental proxy:

$$324 \ln(H) = 0.893 - E + 0.760 \ln(D) - 0.0340 \ln(D)^2 \quad (3)$$

325 Where  $D$  is the diameter at 130cm and  $E$  is a measure of environmental stress (Chave *et al.*,  
326 2014). For sites with tree height measurements (N=20), we developed local D-H models, using  
327 a Michaelis-Menten function (Molto *et al.*, 2014). We used these local models to validate the

328 predicted Lorey's height (i.e. plot average height weighted by BA) from the largest trees, of  
329 which height has been estimated with a generic H-D model (equation 3, Chave et al. 2014).

330 We estimated plot biomass as the sum of the biomass of live tree with diameter at 130 cm  
331 superior or equal to 10 cm, using the following pan-tropical allometric model (Réjou-Méchain  
332 *et al.*, 2017):

$$333 \text{ AGB} = \exp(-2.024 - 0.896E + 0.920 \ln(\text{WD}) + 2.795 \ln(D) - 0.0461 (\ln(D^2))) \quad (4)$$

#### 334 **Plot-level metric estimation from the largest trees**

335 The relationship between each plot metric, namely basal area (BA), the quadratic mean  
336 diameter (D<sub>g</sub>), Lorey's height (H<sub>BA</sub>; the mean height weighted by the basal area) and the  
337 community wood density (WD<sub>BA</sub>; the mean wood density weighted by the basal area), and  
338 those derived from largest trees was determined using an iterative procedure following Bastin  
339 et al. (2015). Trees were first ranked by decreasing diameter in each plot. An incremental  
340 procedure (i.e. including a new tree at each step) was used to sum or average information of  
341 the *i* largest trees for each plot metric. Specifically, each plot-level metric was predicted by the  
342 respective metric derived from the *i*<sup>th</sup> largest trees. For each increment, the ability (goodness  
343 of fit) of the *i* largest trees to predict a given plot-metric was tested through a linear regression.  
344 To avoid overfitting, a Leave-One-Out procedure was used to develop independent site-  
345 specific models (N=118). Specifically, the model to be tested at a site was developed with data  
346 from all other sites. Errors were then estimated as the relative root mean square error (rRMSE)  
347 computed between observed and predicted values (X):

$$348 \text{ rRMSE} = \bar{X} \sum \sqrt{\frac{(X_{\text{obs}} - X_{\text{pred}})^2}{n}} \quad (5)$$

349 The form of the regression model (i.e. linear, exponential) was selected to ensure a normal  
350 distribution of the residuals.

351 To estimate plot basal area, we used a simple power-law constrained on the origin, as linear  
352 model resulted in non-normal residuals. Plot-level basal area (BA) was related to the basal  
353 area for the *i* largest trees (BA<sub>*i*</sub>) using:

$$354 \text{ BA} = b_1 \sum \text{BA}_i^{Y_1} \quad (6)$$



355 To estimate the quadratic mean diameter, Lorey's height and the wood density of the  
356 community, we used simple linear models relating the plot-level metrics and the value of the  
357 metrics for the  $i$  largest trees:

$$358 \quad D_g = a_2 + b_2 D_{gi} \quad (7)$$

$$359 \quad H_{BA} = a_3 + b_3 \overline{H_i} \quad (8)$$

$$360 \quad WD_{BA} = a_4 + b_4 \overline{WD_i} \quad (9)$$

361 Both Lorey's height ( $H_{BA}$ ) and the average height ( $\overline{H_i}$ ) of the  $i^{\text{th}}$  largest trees depend on the  
362 same D-H allometry, which always contains uncertainty whether we use a local, a continental  
363 or a pan-tropical model. To test the dependence of the prediction of  $H_{BA}$  from  $\overline{H_i}$  on the  
364 allometric model, we used measurement from Malebo in the Democratic Republic of the  
365 Congo, where all heights were measured on the ground (see supplementary figure 2).

366 The quality of the predictions of plot-level metrics from the largest trees is quantified using the  
367 relative root mean square error (rRMSE) between measured and predicted values, and  
368 displayed along the cumulated number of largest trees (Figure 2). Model coefficients are  
369 estimated for each metric derived from the largest trees ( $N_{LT}$ ) and averaged across the 118  
370 models (see supplementary table 2).

371 Mean rRMSE is plotted as a continuous variable, while its variation is presented as a  
372 continuous area between 5<sup>th</sup> and the 95<sup>th</sup> percentiles of observed rRMSE (Figure 2).

### 373 **The optimal number of largest trees for plot-level biomass estimation**

374 The optimal number of largest trees  $N_{LT}$  was determined from the prediction of each plot-level  
375 metric considered above, i.e. keeping a small number of trees while ensuring a low level of  
376 error for each structural parameter. We then predicted plot-level biomass from the  $N_{LT}$  model  
377 (equation 2). The final error was calculated by propagating the entire set of errors related to  
378 equation 4 (Réjou-Méchain *et al.*, 2017) in the  $N_{LT}$  model (i.e. error associated to each allometric  
379 model used). The model was then cross-validated across all plots ( $N=867$ ).

### 380 **Investigating residuals: what the largest trees do not explain**

381 To understand the limits of predicting AGB through  $N_{LT}$ , we further investigated the relationship  
382 between AGB residuals and key structural and environmental variables using linear modelling.  
383 Forest structure was investigated through the total stem density (N), the quadratic mean  
384 diameter ( $D_g$ ), Lorey's height ( $H_{BA}$ ) and community wood density ( $WB_{BA}$ ). As environmental  
385 data, we used the mean annual rainfall and the mean temperature computed over the last 10  
386 years at each site using the Climate Research Unit data (New *et al.*, 1999, 2002), along with  
387 rough information on soil types (Carré. *et al.*, 2010). Major soil types were computed from the  
388 soil classification of the Harmonized World Soil Database into IPCC (intergovernmental panel  
389 on climate change) soil classes. In addition, considering observed differences in forest  
390 structure across tropical continents (Feldpausch *et al.*, 2011) and recent results on pan-tropical  
391 floristic affinities (Slik *et al.*, 2015), we tested for an effect of continent (America, Africa and  
392 Asia) on the AGB residuals.

393 The importance of each variable was evaluated by calculating the type II sum of squares that  
394 measures the decrease in residual sum of squares due to an added variable once all the other  
395 variables have been introduced into the model (Langsrud, 2003). Residuals were investigated  
396 at both plot and site levels, the latter analyzed to test for any influence of the diameter structure,  
397 which is usually unstable at the plot level due to the dominance of large trees on forest metrics  
398 at small scales (Clark & Clark, 2000). Here we use a principal component analysis (PCA) to  
399 summarize the information held in the diameter structure by ordinating the sites along the  
400 abundance of trees in each diameter class (from 10 to +100 cm by 10 cm bins).

401

## 402 **Results**

### 403 **Plot-level metrics**

404 Plot metrics averaged at the site level (867 plots, 118 sites) present important variations within  
405 and between continents. In our database, the quadratic mean diameter varies from 15 to 42  
406  $\text{cm}^2\text{ha}^{-1}$ , the basal area from 2 to 58  $\text{m}^2\text{ha}^{-1}$ , Lorey's height from 11 to 33 m and the wood  
407 density weighted by the basal area from 0.48 to 0.84  $\text{gcm}^{-3}$  (Supplementary figure 1). Such  
408 important differences between minimal and maximal values are observed because our  
409 database cover sites with various forest types, from young forest colonizing savannas to old  
410 growth forest. However, most of our sites are found in mature forests, as shown by relatively  
411 high average and median value of each plot metric (average aboveground biomass = 302  
412  $\text{Mgha}^{-1}$ ; supplementary figure 1). In general, highest values of aboveground biomass are found  
413 in Africa, driven by highest values of basal area and highest estimations of Lorey's height.  
414 Highest values of wood density weighted by basal area are found in America.

### 415 **Plot-level estimation from the *i* largest trees**

416 Overall, plot metrics at 1 ha scale were well predicted by the largest trees, with qualitative  
417 agreement among global and continental models (Figure 2).

418

419 When using the 20 largest trees to predict basal area (BA) and quadratic mean diameter (Dg),  
420 the mean rRMSE was < 16% and 12%, respectively (Figs 3a and 3b). Lorey's height ( $H_{\text{BA}}$ ) and  
421 wood density weighted by basal area ( $WD_{\text{BA}}$ ) were even better predicted (Figs 3c and 3d), with  
422 mean rRMSE of 4% for the 20 largest trees. The prediction of Lorey's height from the largest  
423 trees using local diameter-height model (supplementary Figure 2a) yielded results similar to  
424 those obtained using equation 3 of Chave et al. (2014). More importantly, it also yielded similar  
425 results to prediction of Lorey's height from the largest trees using plots where all the trees were  
426 measured on the ground (supplementary figure 2b). This suggests that our conclusions are  
427 robust to the uncertainty introduced by height-diameter allometric models.

### 428 **AGB prediction from the largest trees**

429 We selected “20” as the number of largest trees to predict plot metrics. The resulting model  
430 predicting AGB (Mg ha<sup>-1</sup>) based on the 20 largest trees is:

$$431 \text{ AGB} = 0.0735 \times (\text{Dg}_{20}\text{H}_{20}\text{WD}_{20})^{1.1332} \text{ (rRMSE=0.179; R}^2\text{=0.85; AIC= -260.18) (10)}$$

432 Because the exponent was close to 1, we also developed an alternative and more operationa  
433 l model with the exponent constrained to 1, given by:

$$434 \text{ AGB} = 0.195 \times (\text{Dg}_{20}\text{H}_{20}\text{WD}_{20}) \text{ (rRMSE=0.177; R}^2\text{=0.85; AIC=-195) (11)}$$

435 Ground measurements of plot AGB were predicted by our N<sub>LT</sub> model with the exponent  
436 constrained to 1, with a total error of 17.9% (Figure 4), a value which encompass the error of  
437 the N<sub>LT</sub> model and the error related to the allometric model chosen. The Leave-One-Out cross-  
438 validation procedure yielded similar results (rRMSE=0.19; R<sup>2</sup>=0.81), validating the use of the  
439 model on independent sites.

#### 440 **Determining the cause of residual variations**

441 The explanatory variables all together explain about 37% of the variance in AGB both at plot  
442 and site levels when omitting the diameter structure, and about 63% at site level when included  
443 (Fig. 5). In general, forest structure and particularly the stem density explained most of the  
444 residuals (table 1; weights: 79% and 54% at plot- and site-level respectively). The stem density  
445 was followed by a continental effect (weights: 18%, 28% and 1%, respectively for Africa, South  
446 America and Asia) and by the effect of H<sub>BA</sub> and WD<sub>BA</sub> (respective weights: 1% and 0% at the  
447 plot level, 0% and 11% at the site level, and 23% and 0% when accounting for the diameter  
448 structure at the site level). Inclusion of the diameter structure provided the best explanation of  
449 residuals, with 63% of variance explained, and a weight of 69% for the first axis of the PCA  
450 (supplementary figure 3). This first axis of the PCA was related to the general abundance of  
451 trees at a site, and in particular medium-sized trees (40-60cm). Among environmental  
452 variables, only rainfall was significantly related to the residuals at the site level when the  
453 diameter structure was considered (2%).

## 454 **Discussion**

### 455 **The largest trees, convergences and divergences between continents**

456 Sampling a few largest trees per hectare generally allows an unbiased prediction of four key  
457 descriptors of forest structures across the Tropics. There is generally no improvement in  
458 predicting basal area, quadratic mean diameter, Lorey's height ( $H_{BA}$ ) or community wood  
459 density beyond the first 10-to-20 largest trees (Figure 2, Figure 3a). In some cases, e.g. when  
460 a forest plot presents an abundant number of large trees (Figure 5d), increasing the number  
461 of trees sampled improves the model's accuracy. This is the case for BA for which rRMSE  
462 continues to decrease up to 100 largest trees (Figure 2a). In contrast, Lorey's height  
463 predictions are altered when a large number of trees are included (Figure 2c), i.e. when  
464 smaller, often suppressed, trees draw the average down (Farrion *et al.*, 2016). This might  
465 explain why the prediction of AGB does not mirror that of basal area (Figure 2b, Figure 3a),  
466 and suggest that the number of largest trees shall be set independently to each predictor  
467 considered. Interestingly, the evolution of relative error in AGB prediction as a function of the  
468 number of largest trees considered does not follow the same path between continents. For  
469 instance, the error of prediction saturates more quickly in Africa and Asia than Asia, where  
470 high variations of residuals are observed. Investigation of residuals showed that the diameter  
471 structure (Figure 5c, supplementary Figure 3b), and in particular the number of medium size  
472 trees (Figure 5d), drives variability in AGB predictions. It is therefore not surprising to see that  
473 in our dataset the site with higher levels of underestimations is the one with the highest number  
474 of medium size trees, which is found in Asia in the Western Ghats of India.

475 The good performance of models based on the 20 largest trees in predicting Lorey's height  
476 and community wood density at site level was not surprising. Both metrics were indeed  
477 weighted by basal area, driven *de facto* by the largest trees. Their consistency across sites  
478 and continents was not expected though. This suggests that the relationship between the 20  
479 largest trees and descriptors of forest structures is stable across the tropics, and prove the  
480 generality of our approach. Slight differences are however noticeable when comparing the  
481 distribution of the pan-tropical model residuals across continents (Figure 6, supplementary

482 figure 4). In America, our pan-tropical model tend to slightly underestimate basal area (mean:  
483 -5%) and overestimate Lorey's height (mean: +3%) (supplementary figure 4), suggesting  
484 peculiar forest structures (i.e. higher tree height for a given diameter, and lower fractions of  
485 large trees, supplementary figure 2). In Asia, and in particular in Africa, large (i.e. DBH > 50  
486 cm) trees are more abundant and encompass a large fraction of plot biomass. The basal area  
487 tends to be slightly overestimated in Africa, resulting in average to a 3% overestimation of AGB  
488 (Figure 6a).

489 Interestingly, while a recent global phylogenetic classification of tropical forest groups  
490 American with African forests vs. Asian forests (Slik *et al.*, 2018), our results tend more to  
491 single out American forests. Although this deserves further investigations, it might reveal a lack  
492 of close relationship between forest structure properties and phylogenic similarity, which  
493 echoes recent results on the absence of relationship between tropical forest diversity and  
494 biomass (Sullivan *et al.*, 2017).

#### 495 **Largest trees, a gateway to global monitoring of tropical forests**

496 Revealing the predictive capacity held by the largest trees, our results constitute a major step  
497 forward to monitor forest structures and biomass stocks. The largest trees in tropical forests  
498 can therefore be used to accurately predict and efficiently infer various ground-measured  
499 properties (i.e. the quadratic mean diameter, the basal area, Lorey's height and community  
500 wood density), while previous work has predicted only biomass "estimates" (e.g. Slik *et al.*,  
501 2013; Bastin *et al.*, 2015). This approach allows us to (i) describe forest structure independently  
502 of any biomass allometric model (ii) and cover local variations in D-H relationship, known to  
503 vary locally (Feldpausch *et al.*, 2011; Kearsley *et al.*, 2013;). It is also (iii) relatively insensitive  
504 to differences in floristic composition and community wood density (Poorter *et al.*, 2015).

505 Furthermore, the "largest trees" models were developed for each plot-level metric and for any  
506 number of largest trees. Thus, they do not rely on any arbitrary threshold of tree diameter. Note  
507 that the optimal number of largest trees to be measured (i.e. 20) was set for demonstration  
508 and can vary depending on the needs and capacities of each country or project (see  
509 supplementary table 2). In the same way, local models could integrate locally-developed

510 biomass models, when available. Consequently our approach (i) can be used in young or  
511 regenerating un-managed forests with a low “largest tree” diameter threshold and (ii) is  
512 compatible with recent remote sensing approaches able to single out canopy trees and  
513 describe their crown and height metrics (Ferraz *et al.*, 2016; Coomes *et al.*, 2017).

#### 514 **Aboveground biomass model from the largest trees, a multiple opportunity**

515 Globally, the  $N_{LT}$  model for the 20 largest trees allows plot biomass to be predicted with 17.9%  
516 error. This result is a pan-tropical validation of results obtained in Central Africa (Bastin *et al.*,  
517 2015). It opens new perspectives towards cost-effective methods to monitor forest structures  
518 and carbon stocks through largest trees metrics, i.e. metrics of objects directly intercepted by  
519 remote-sensing products.

520 Developing countries willing to implement a Reduction of Emissions from Deforestation and  
521 Forest Degradation (REDD+), shall also report on their carbon emissions (CE) and develop a  
522 national CE reference level (IPCC, 2006; Maniatis & Mollicone, 2010). However, most tropical  
523 countries lack capacities to assume multiple, exhaustive and costly forest carbon assessment  
524 ( Romijn *et al.*, 2012). By measuring only a few large trees per hectare, our results show that  
525 it is possible to obtain unbiased estimates of aboveground C stocks in a time and cost-efficient  
526 manner. Assuming that 400 to 600 trees  $D > 10$  cm are measured in a typical 1-ha sample  
527 plot, monitoring only 20 trees is a significant improvement. Although finding the 20 largest trees  
528 in a plot of several hundred individuals requires evaluating more than 20 trees, in practice, a  
529 conservative diameter threshold could be defined to ensure that the 20 largest trees are  
530 sampled. An alternative approach could also be found in the development of relascope-based  
531 approach adapted to detection of the largest trees in tropical forests. Using such approach  
532 would facilitate rapid field sampling in extensive areas to produce large scale AGB estimates.  
533 Those could fulfil the needs in calibration and validation of current and forthcoming space  
534 missions focused on aboveground biomass.

535 Our findings also points towards the potential effectiveness of using remote sensing  
536 techniques to characterize canopy trees. Here, remote sensing data could be used for direct  
537 measurement (e.g. tree level metrics such as height, crown width, crown height) of the largest

538 trees instead of indirect development of complex metrics (e.g. mean canopy height, texture)  
539 used to extrapolate forest properties. While some further refinements are needed, most of the  
540 tools required to develop “largest trees” models are readily available. In particular, Ferraz et  
541 al. (2016) developed an automated procedure to locate canopy trees based on airborne LiDAR  
542 data, to measure their height and crown area. Crown area could further be linked to basal area,  
543 as the logarithm of crown area is consistently correlated with a slope of 1.2-1.3 to the logarithm  
544 of tree diameter across the tropics (Blanchard *et al.*, 2016). Regarding wood density,  
545 hyperspectral signature offers a promising way to assess functional traits remotely (e.g. Asner  
546 *et al.*, 2017) which could potentially be tested to detect variability in wood properties.  
547 Alternative approaches could focus on the development of plot-level AGB prediction by  
548 replacing the basal area of the largest trees with their crown metrics. While the measurement  
549 of crown areas have yet to be generalized when inventorying plots, several biomass allometric  
550 models already partition trunk and crown mass (Jucker *et al.*, 2016; Ploton *et al.*, 2016;  
551 Coomes *et al.*, 2017).

552 The main limitation of our approach lies in the understory and sub-canopy trees. We show that  
553 most of the remaining variance is explained by variations in diameter structures, and in  
554 particular among the total stem density. Interestingly, stem density was generally identified as  
555 a poor predictor of plot biomass in tropical forests (Slik *et al.*, 2010; Lewis *et al.*, 2013).  
556 However, our results show that stem density explains most of the remaining variance (Table  
557 S1). This suggests that, in addition to trying to understand large-scale variations in large trees  
558 and other plot metrics, which can be directly quantified from remote sensing, we should also  
559 put more effort into understanding variation in smaller trees, which mainly drives total stem  
560 density and the total floristic diversity. Smaller trees are also essential to characterize forest  
561 dynamics and understand changes in carbon stocks. Several options are nonetheless possible  
562 from remote sensing, considering the variation in lidar point density below the canopy layer  
563 (D’Oliveira *et al.*, 2012), the distribution of leaf area density (Stark *et al.*, 2012, 2015; Tang &  
564 Dubayah, 2017) or the use of multitemporal lidar data to get information on forest gap



565 generation dynamics and consequently on forest diameter structure (Kellner *et al.*, 2009;  
566 Farrior *et al.*, 2016).

### 567 **Large trees in degraded forests**

568 If large trees are a key feature of unmanaged forests, they are conspicuously absent from  
569 managed or degraded forests. Indeed, large trees are targeted by selective or illegal logging,  
570 and are the first to disappear or to suffer from incidental damages when tropical forests are  
571 exploited for timber (Sist *et al.*, 2014). The loss of largest trees drastically changes forest  
572 structures and diameter distributions, and their loss is likely to counteract the consistency in  
573 forest structures observed through this study. Understanding how, or whether, managed  
574 forests deviate from our model predictions could help characterize forest degradation, which  
575 accounts for a large fraction of carbon loss worldwide (Baccini *et al.*, 2017), acknowledging  
576 that rapid post-disturbance biomass recovery (Rutishauser *et al.*, 2015) will remain hard to  
577 capture.

### 578 **Conclusion – towards improved estimates of tropical forest biomass**

579 The acquisition, accessibility and processing capabilities of very high spatial, spectral and  
580 temporal resolution remote sensing data has increases exponentially in recent years (Bastin  
581 *et al.*, 2017). However, to develop accurate global maps, we will have to obtain a greater  
582 number of field plots and develop new ways to use remote sensing data. Our results provide  
583 a step forward for both by (i) decreasing drastically the number of individual tree measurements  
584 required to get an accurate, yet less precise, estimate of plot biomass and (ii) opening the door  
585 to direct measurement of plot metrics measured from remote sensing to estimate plot biomass.  
586 As highlighted by Clark and Kellner (2012), new biomass allometric models relating plot-level  
587 biomass measured from destructive sampling and plot-level metric measured from remote-  
588 sensing products should be developed, as an alternative to current tree-level allometric  
589 models. Such an effort will lead largely to lower operational costs and uncertainties surrounding  
590 terrestrial C estimates, and consequently, will help developing countries in the development of  
591 national forest inventories and aid the scientific community in better understanding the effect  
592 of climate change on forest ecosystems.

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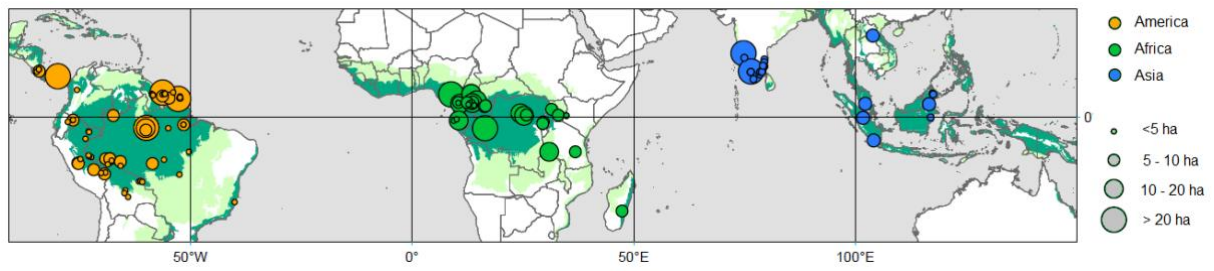
608 **Contributions**

609 J.F.Bastin and E.Rutishauser conceptualized the study, gathered the data, performed the  
610 analysis and wrote the manuscript. All the co-authors contributed by sharing data and  
611 reviewing the main text. A.R.Marshall, J.Poulsen and J.Kellner revised the English.

612 **Conflict of interest**

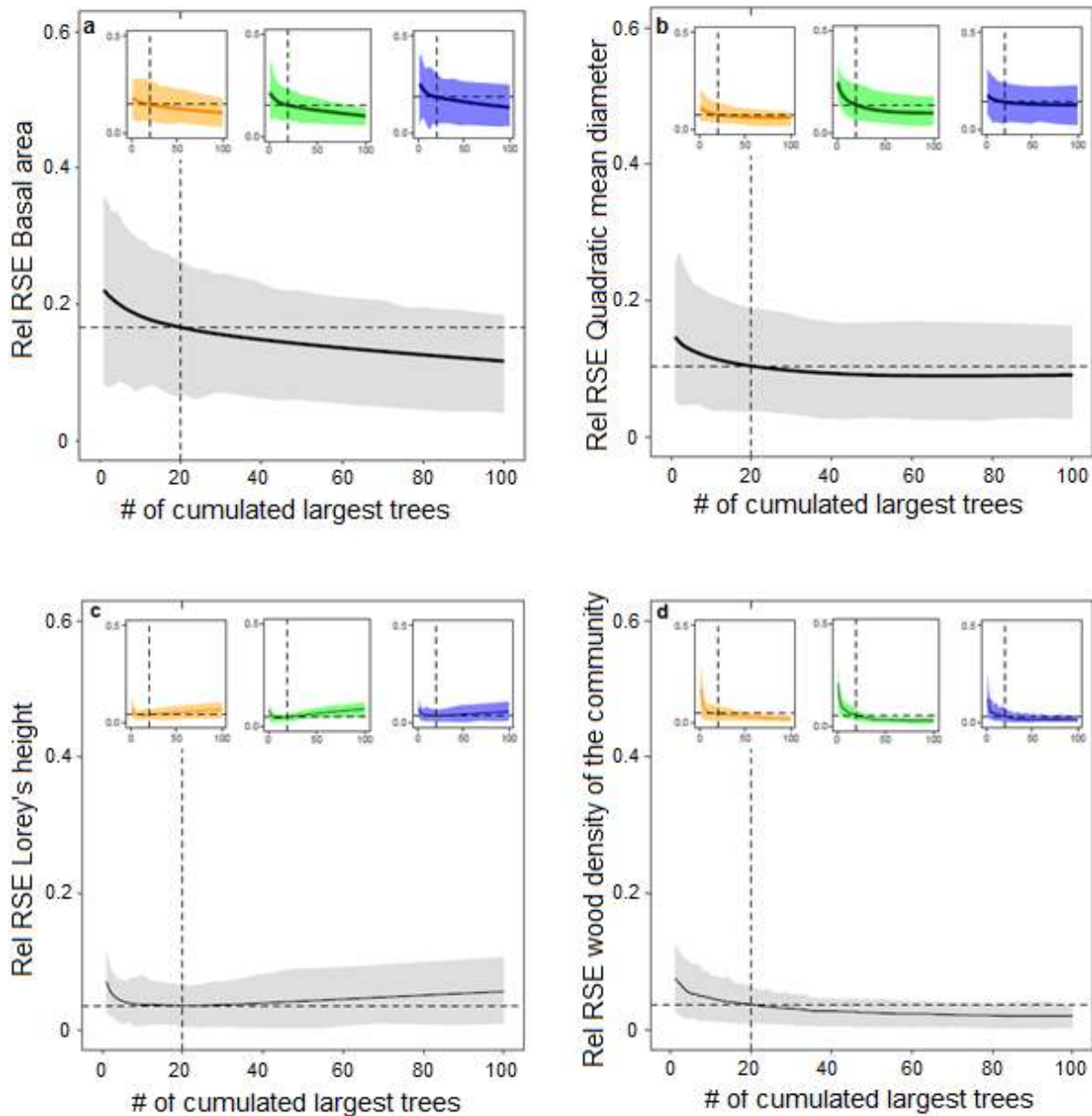
613 The authors declare there is no conflict of interest associated to this study.

614 **Figures**



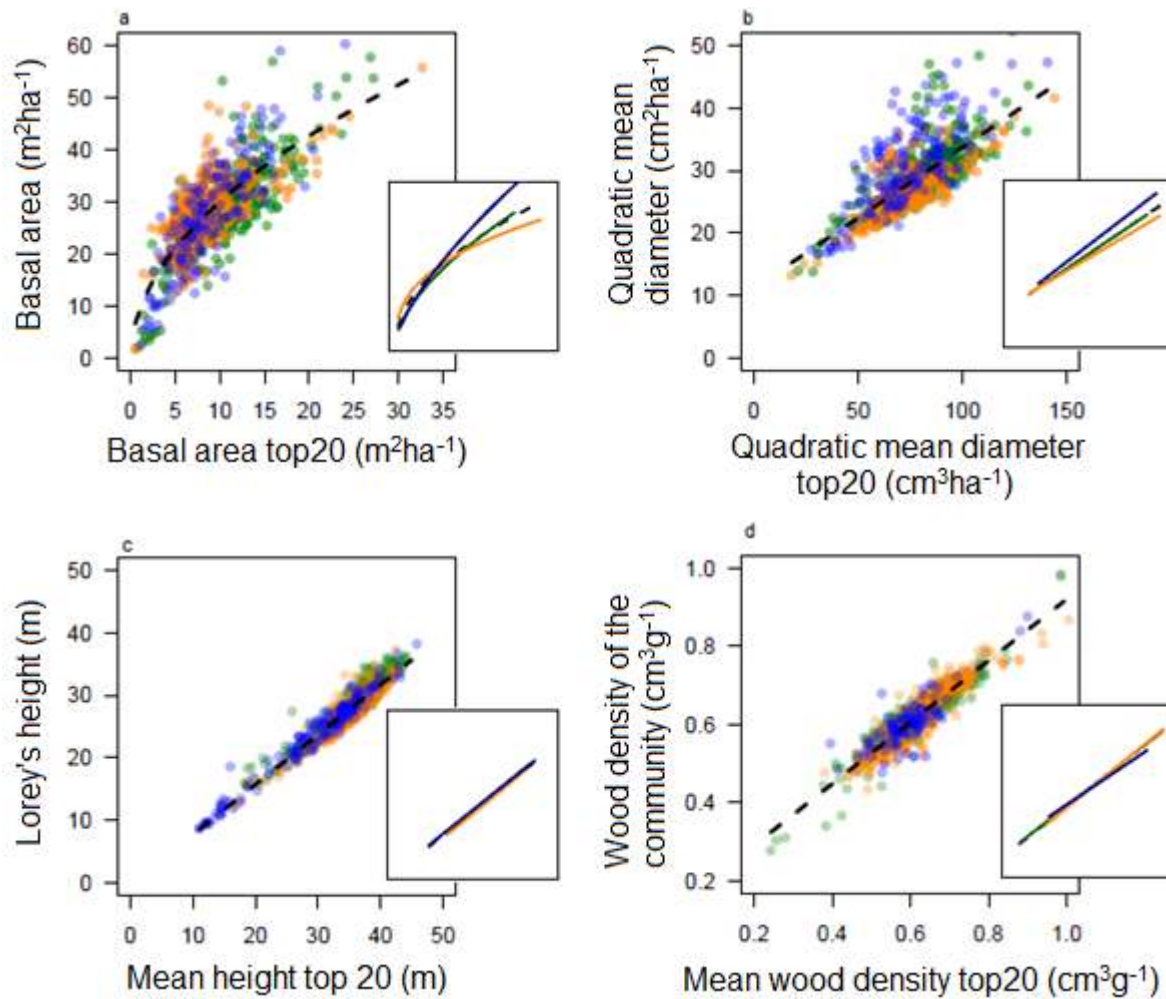
615

616 **Figure 1. Geographic distribution of the plot database.** We used 867 plots of 1 hectare  
617 from 118 sites. Dots are colored according to floristic affinities (Slik et al. 2015), with America,  
618 Africa and Asia respectively in orange, green and blue. They are also sized according the total  
619 area surveyed in each site.



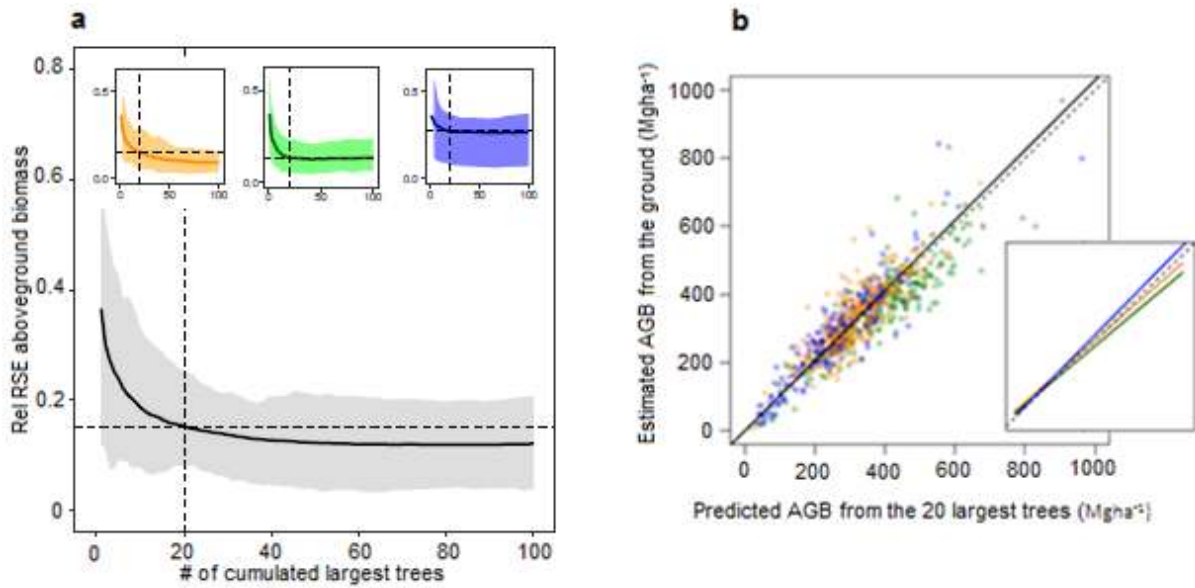
620

621 **Figure 2. Quality of the prediction of plot metrics from largest trees.** Variation of the  
 622 relative Root Mean Square Error (rRMSE) of the prediction of plot metric from  $i$  largest trees  
 623 versus the cumulative number of largest trees for (a) basal area, (b) quadratic mean diameter,  
 624 (c) Lorey's height and (d) wood density weighted by the basal area. Results are displayed at  
 625 the pan-tropical level (main plot in grey) and at the continental level (subplots; orange =  
 626 America; green = Africa; blue = Asia). The solid line and shading shows the mean rRMSE and  
 627 the 5<sup>th</sup> and the 95<sup>th</sup> percentiles. Dashed lines represent the mean rRMSE observed for each  
 628 model, when considering the 20 largest trees.



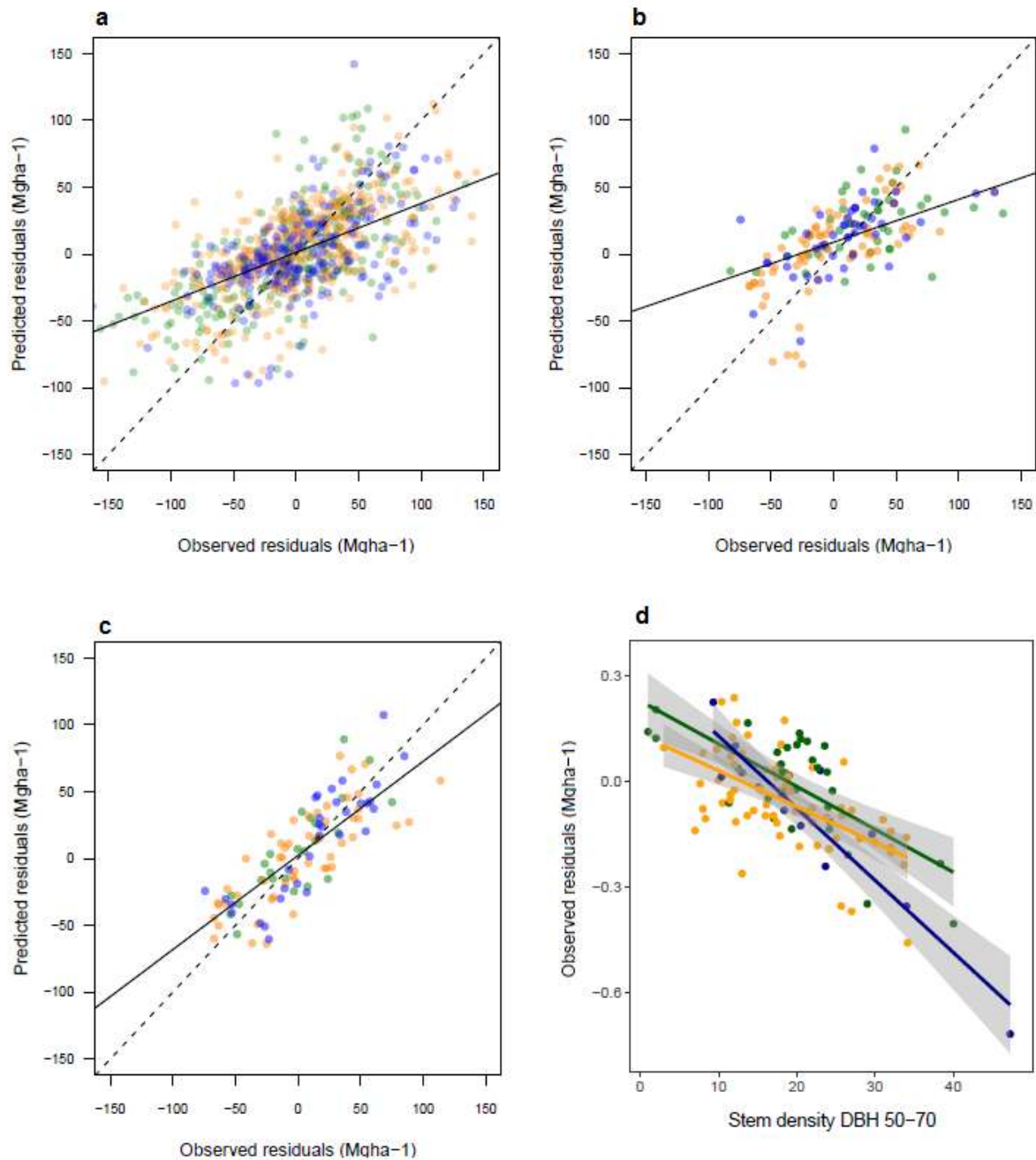
629

630 **Figure 3. Prediction of plot metrics (y-axis) from the 20 largest trees (x-axis).** Results are  
 631 shown for (a) basal area, (b) quadratic mean diameter, (c) Lorey's Height and (d) wood density  
 632 weighted by the basal area. Each dot corresponds to a single plot, colored in orange, green  
 633 and blue for America, Africa and Asia respectively. Both pan-tropical (black dashed lines) and  
 634 continental (coloured lines) regression models are displayed. These results show that  
 635 substantial part of remaining variance, i.e. not explained by largest trees, is found when  
 636 predicting the basal area and the quadratic mean diameter, with slight but significant  
 637 differences between continents.



638

639 **Figure 4. Prediction of AGB from plot metrics of the 20 largest trees.** Results are shown  
 640 for the 867 plots, among the three continents colored orange, green and blue for America,  
 641 Africa and Asia respectively. The regression line of the model is shown as a continuous black  
 642 line while the dashed black line shows a 1:1 relationship. The figure shows an unbiased  
 643 prediction of AGB across the 867 plots, with slight but significant differences between the 3  
 644 continents.



645

646 **Figure 5. Predicted vs. observed residuals of above ground biomass predicted from the**

647 **20 largest trees.** Residuals are explored at three different levels: (a) plot, (b) site [without

648 considering the diameter structure as an explanatory variable], (c) site [considering the

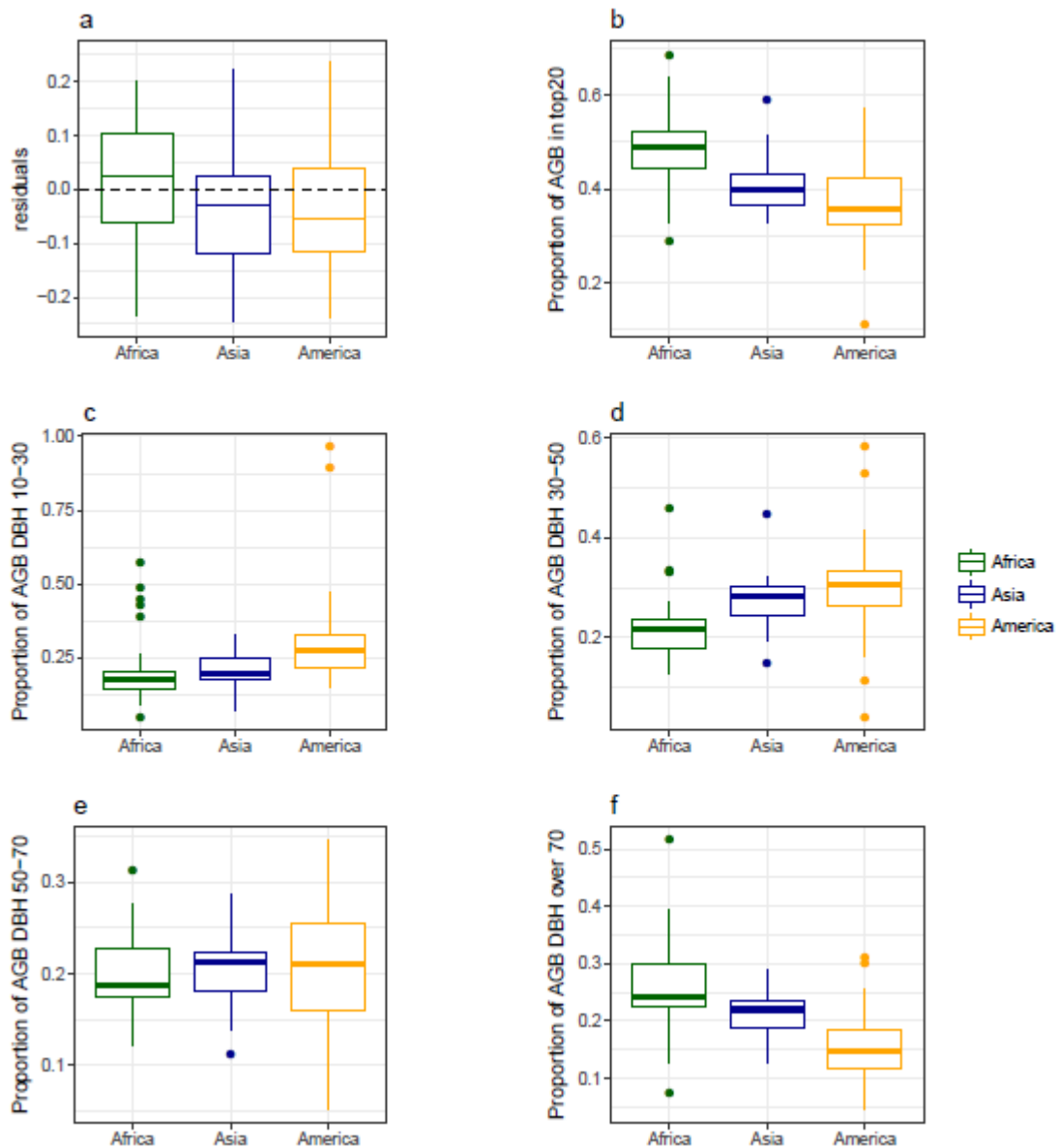
649 diameter structure] and (d) along the stem density of medium size trees. America, Africa and

650 Asia are colored in orange, green and blue respectively. The figures show a good prediction

651 of residuals in (a) and (b), driven by stem density, and a less biased prediction in (c), driven by

652 the diameter structure. Variance of observed residuals are also well explained by the stem  
653 density of medium size trees (d), which mainly drive the first axis of the PCA.





654

655 Figure 6. Comparison across continents of aboveground biomass prediction per site and their  
 656 contribution to different share of the diameter structure. Africa, Asia and America, are colored  
 657 in green, blue and orange, respectively. The distribution of the residuals of pan-tropical  
 658 aboveground biomass prediction from the 20 largest trees (a) shows predictions are slightly  
 659 overestimated in Africa (+2%), and slightly underestimated in Asia (-2%) and America (-6%).  
 660 The proportion of aboveground biomass in the 20 largest trees (b) is highest in Africa (48%),  
 661 followed by Asia (40%) and America (35%). The decomposition across four diameter classes  
 662 (c-f, i.e. from 10 to 30, 30 to 50, 50 to 70 and beyond 70 cm) of their relative share of the total  
 663 biomass shows that most of the biomass is found in the large trees in Africa, and in the small

664 to medium trees in America. Asia presenting a more balanced distribution of biomass across  
665 the diameter structure.

666 **Tables**

667 **Table 1. Weight of each variable retained for the explanation of AGB residuals.** Weights  
 668 are calculated as a type II sum of squares, which measures the decreased residual sum of  
 669 squares due to an added variable once all the other variables have been introduced into the  
 670 model. Results are shown for the exploration of residuals at the plot and at the site level, with  
 671 and without consideration of the diameter structure. Weights are dominated by structural  
 672 variables, and in particular the stem density and the diameter structure. Height, wood density  
 673 and continent have also a non-negligible influence on residuals.

<b>Level of residual</b>	<b>Parameter</b>	<b>Weight</b>	674
<b>Plot</b>	Stem density*	79	
	Continent*	18	
	Lorey's height*	1	
	Major soil types	1	
	Temperature	1	
	Wood density weighted by the basal area	0	
	Rainfall	0	
<b>Site without diametric structure</b>	Stem density*	54	
	Continent*	28	
	Wood density weighted by the basal area*	11	
	Rainfall	3	
	Major soil types	3	
	Temperature	2	
	Lorey's height	0	
<b>Site with diametric structure</b>	PCA axis 1*	69	
	Lorey's height*	23	
	Rainfall*	3	
	Major soil types	3	
	Continent	1	
	Temperature	1	
	Wood density weighted by the basal area	0	
	PCA axis 2	0	

675 **References**

- 676 Asner, G.G.P., Mascaro, J., Muller-Landau, H.H.C., Vieilledent, G., Vaudry, R., Rasamoelina,  
677 M., Hall, J.S. & van Breugel, M. (2012) A universal airborne LiDAR approach for tropical  
678 forest carbon mapping. *Oecologia*, **168**, 1147–1160.
- 679 Asner, G.P., Martin, R.E., Knapp, D.E., Tupayachi, R., Anderson, C.B., Sinca, F., Vaughn,  
680 N.R. & Llactayo, W. (2017) Airborne laser-guided imaging spectroscopy to map forest  
681 trait diversity and guide conservation. *Science*, **355**.
- 682 Asner, G.P. & Mascaro, J. (2014) Mapping tropical forest carbon: Calibrating plot estimates  
683 to a simple LiDAR metric. *Remote Sensing of Environment*, **140**, 614–624.
- 684 Baccini, A., Walker, W., Carvalho, L., Farina, M., Sulla-Menashe, D. & Houghton, R.A. (2017)  
685 Tropical forests are a net carbon source based on aboveground measurements of gain  
686 and loss. *Science (New York, N.Y.)*, **358**, 230–234.
- 687 Barbier, N. & Coutron, P. (2015) Attenuating the bidirectional texture variation of satellite  
688 images of tropical forest canopies. *Remote Sensing of Environment*, **171**, 245–260.
- 689 Barbier, N., Proisy, C., Véga, C., Sabatier, D. & Coutron, P. (2011) Bidirectional texture  
690 function of high resolution optical images of tropical forest: An approach using LiDAR  
691 hillshade simulations. *Remote Sensing of Environment*, **115**, 167–179.
- 692 Bastin, J.-F., Barbier, N., Coutron, P., Adams, B., Shapiro, A., Bogaert, J., De Cannière, C.,  
693 De Cannière, C. & De Cannière, C. (2014) Aboveground biomass mapping of African  
694 forest mosaics using canopy texture analysis: toward a regional approach. *Ecological*  
695 *Applications*, **24**, 1984–2001.
- 696 Bastin, J.-F., Barbier, N., Réjou-Méchain, M., Fayolle, A., Gourlet-Fleury, S., Maniatis, D., De  
697 Haulleville, T., Baya, F., Beeckman, H., Beina, D., Coutron, P., Chuyong, G., Dauby,  
698 G., Doucet, J.-L., Droissart, V., Dufrêne, M., Ewango, C., Gillet, J.F., Gonmadje, C.H.,  
699 Hart, T., Kavali, T., Kenfack, D., Libalah, M., Malhi, Y., Makana, J.-R., Pélissier, R.,  
700 Ploton, P., Serckx, A., Sonké, B., Stevart, T., Thomas, D.W., De Cannière, C. &  
701 Bogaert, J. (2015) Seeing Central African forests through their largest trees. *Scientific*  
702 *Reports*, **5**.

703 Bastin, J.-F., Berrahmouni, N., Grainger, A., Maniatis, D., Mollicone, D., Moore, R., Patriarca,  
704 C., Picard, N., Sparrow, B., Abraham, E.M., Aloui, K., Atesoglu, A., Attore, F., Bassüllü,  
705 Ç., Bey, A., Garzuglia, M., García-Montero, L.G., Groot, N., Guerin, G., Laestadius, L.,  
706 Lowe, A.J., Mamane, B., Marchi, G., Patterson, P., Rezende, M., Ricci, S., Salcedo, I.,  
707 Diaz, A.S.-P., Stolle, F., Surappaeva, V. & Castro, R. (2017) The extent of forest in  
708 dryland biomes. *Science*, **356**, 635–638.

709 Bennett, A.C., McDowell, N.G., Allen, C.D. & Anderson-Teixeira, K.J. (2015) Larger trees  
710 suffer most during drought in forests worldwide. *Nature Plants*.

711 Blanchard, E., Birnbaum, P., Ibanez, T., Boutreux, T., Antin, C., Ploton, P., Vincent, G.,  
712 Pouteau, R., Vandrot, H., Hequet, V., Barbier, N., Droissart, V., Sonké, B., Texier, N.,  
713 Kamdem, N.G., Zebaze, D., Libalah, M. & Couteron, P. (2016) Contrasted allometries  
714 between stem diameter, crown area, and tree height in five tropical biogeographic  
715 areas. *Trees*, **30**, 1953–1968.

716 Carré, F., Hiederer, R., Blujdea, V. & Koeble, R. (2010) *Background Guide for the*  
717 *Calculation of Land Carbon Stocks in the Biofuels Sustainability Scheme Drawing on*  
718 *the 2006 IPCC Guidelines for National Greenhouse Gas Inventories. EUR 24573 EN.*,  
719 Luxembourg.

720 Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009)  
721 Towards a worldwide wood economics spectrum. *Ecology letters*, **12**, 351–66.

722 Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C.,  
723 Duque, A., Eid, T., Fearnside, P.M., Goodman, R.C., Henry, M., Martínez-Yrizar, A.,  
724 Mugasha, W.A., Muller-Landau, H.C., Mencuccini, M., Nelson, B.W., Ngomanda, A.,  
725 Nogueira, E.M., Ortiz-Malavassi, E., Péllissier, R., Ploton, P., Ryan, C.M., Saldarriaga,  
726 J.G. & Vieilledent, G. (2014) Improved allometric models to estimate the aboveground  
727 biomass of tropical trees. *Global change biology*, **20**, 3177–3190.

728 Chave, J., Riera, B., Dubois, M.-A. & Riéra, B. (2001) Estimation of biomass in a neotropical  
729 forest of French Guiana : spatial and temporal variability. *Journal of Tropical Ecology*,  
730 **17**, 79–96.

731 Clark, D.B. & Clark, D.A. (1996) Abundance, growth and mortality of very large trees in  
732 neotropical lowland rain forest. *Forest Ecology and Management*, **80**, 235–244.

733 Clark, D.B. & Clark, D.A. (2000) Landscape-scale variation in forest structure and biomass in  
734 a tropical rain forest. *Forest Ecology and Management*, **137**, 185–198.

735 Clark, D.B. & Kellner, J.R. (2012) Tropical forest biomass estimation and the fallacy of  
736 misplaced concreteness. *Journal of Vegetation Science*, **23**, 1191–1196.

737 Coomes, D.A., Dalponte, M., Jucker, T., Asner, G.P., Banin, L.F., Burslem, D.F.R.P., Lewis,  
738 S.L., Nilus, R., Phillips, O.L., Phua, M.-H. & Qie, L. (2017) Area-based vs tree-centric  
739 approaches to mapping forest carbon in Southeast Asian forests from airborne laser  
740 scanning data. *Remote Sensing of Environment*, **194**, 77–88.

741 D’Oliveira, M.V.N., Reutebuch, S.E., McGaughey, R.J. & Andersen, H.-E. (2012) Estimating  
742 forest biomass and identifying low-intensity logging areas using airborne scanning lidar  
743 in Antimary State Forest, Acre State, Western Brazilian Amazon. *Remote Sensing of  
744 Environment*, **124**, 479–491.

745 Farrior, C.E., Bohlman, S.A., Hubbell, S. & Pacala, S.W. (2016) Dominance of the  
746 suppressed: Power-law size structure in tropical forests. *Science*, **351**.

747 Fayolle, A., Loubota Panzou, G.J., Drouet, T., Swaine, M.D., Bauwens, S., Vleminckx, J.,  
748 Biwole, A., Lejeune, P. & Doucet, J.-L. (2016) Taller trees, denser stands and greater  
749 biomass in semi-deciduous than in evergreen lowland central African forests. *Forest  
750 Ecology and Management*, **374**, 42–50.

751 Feldpausch, T.R., Banin, L., Phillips, O.L., Baker, T.R., Lewis, S.L., Quesada, C. a., Affum-  
752 Baffoe, K., Arets, E.J.M.M., Berry, N.J., Bird, M., Brondizio, E.S., de Camargo, P.,  
753 Chave, J., Djangbletey, G., Domingues, T.F., Drescher, M., Fearnside, P.M., França,  
754 M.B., Fyllas, N.M., Lopez-Gonzalez, G., Hladik, a., Higuchi, N., Hunter, M.O., Iida, Y.,  
755 Salim, K. a., Kassim, a. R., Keller, M., Kemp, J., King, D. a., Lovett, J.C., Marimon,  
756 B.S., Marimon-Junior, B.H., Lenza, E., Marshall, a. R., Metcalfe, D.J., Mitchard, E.T. a.,  
757 Moran, E.F., Nelson, B.W., Nilus, R., Nogueira, E.M., Palace, M., Patiño, S., Peh, K.S.-  
758 H., Raventos, M.T., Reitsma, J.M., Saiz, G., Schrodte, F., Sonké, B., Taedoumg, H.E.,

759 Tan, S., White, L., Wöll, H. & Lloyd, J. (2011) Height-diameter allometry of tropical forest  
760 trees. *Biogeosciences*, **8**, 1081–1106.

761 Feldpausch, T.R., Lloyd, J., Lewis, S.L., Brienen, R.J.W., Gloor, E., Monteagudo Mendoza,  
762 a., Lopez-Gonzalez, G., Banin, L., Abu Salim, K., Affum-Baffoe, K., Alexiades, M.,  
763 Almeida, S., Amaral, I., Andrade, a., Aragão, L.E.O.C., Araujo Murakami, a., Arets,  
764 E.J.M.M., Arroyo, L., Baker, T.R., Bánki, O.S., Berry, N.J., Cardozo, N., Chave, J.,  
765 Comiskey, J. a., Dávila, E. a., de Oliveira, a., DiFiore, a., Djagbletey, G., Domingues,  
766 T.F., Erwin, T.L., Fearnside, P.M., França, M.B., Freitas, M. a., Higuchi, N., Iida, Y.,  
767 Jiménez, E., Kassim, a. R., Killeen, T.J., Laurance, W.F., Lovett, J.C., Malhi, Y.,  
768 Marimon, B.S., Marimon-Junior, B.H., Lenza, E., Marshall, a. R., Mendoza, C.,  
769 Metcalfe, D.J., Mitchard, E.T. a., Nelson, B.W., Nilus, R., Nogueira, E.M., Parada, a.,  
770 Peh, K.S.-H., Pena Cruz, a., Peñuela, M.C., Pitman, N.C. a., Prieto, a., Quesada, C.  
771 a., Ramírez, F., Ramírez-Angulo, H., Reitsma, J.M., Rudas, a., Saiz, G., Salomão,  
772 R.P., Schwarz, M., Silva, N., Silva-Espejo, J.E., Silveira, M., Sonké, B., Stropp, J.,  
773 Taedoumg, H.E., Tan, S., ter Steege, H., Terborgh, J., Torello-Raventos, M., van der  
774 Heijden, G.M.F., Vásquez, R., Vilanova, E., Vos, V., White, L., Wilcock, S., Woell, H. &  
775 Phillips, O.L. (2012) Tree height integrated into pan-tropical forest biomass estimates.  
776 *Biogeosciences Discussions*, **9**, 2567–2622.

777 Ferraz, A., Saatchi, S., Mallet, C. & Meyer, V. (2016) Lidar detection of individual tree size in  
778 tropical forests. *Remote Sensing of Environment*, **183**, 318–333.

779 Gibbs, H.K., Brown, S., Niles, J.O. & Foley, J. a (2007) Monitoring and estimating tropical  
780 forest carbon stocks: making REDD a reality. *Environmental Research Letters*, **2**, 1–13.

781 Harms, K.E., Wright, S.J., Calderón, O., Hernández, a & Herre, E. a (2000) Pervasive  
782 density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature*,  
783 **404**, 493–5.

784 Ho Tong Minh, D., Le Toan, T., Rocca, F., Tebaldini, S., Villard, L., Réjou-Méchain, M.,  
785 Phillips, O.L., Feldpausch, T.R., Dubois-Fernandez, P., Scipal, K. & Chave, J. (2016)  
786 SAR tomography for the retrieval of forest biomass and height: Cross-validation at two

787 tropical forest sites in French Guiana. *Remote Sensing of Environment*, **175**, 138–147.

788 IPCC (2006) *2006 IPCC Guidelines for National Greenhouse Gas Inventories, Prepared by*  
789 *the National Greenhouse Gas Inventories Programme*, IGES. (ed. by H.S. Eggleston),  
790 L. Buendia), K. Miwa), T. Ngara), and K. Tanabe) Japan, Japan.

791 Jucker, T., Caspersen, J., Chave, J., Antin, C., Barbier, N., Bongers, F., Dalponte, M., van  
792 Ewijk, K.Y., Forrester, D.I., Haeni, M., Higgins, S.I., Holdaway, R.J., Iida, Y., Lorimer, C.,  
793 Marshall, P.L., Momo, S., Moncrieff, G.R., Ploton, P., Poorter, L., Rahman, K.A.,  
794 Schlund, M., Sonké, B., Sterck, F.J., Trugman, A.T., Usoltsev, V.A., Vanderwel, M.C.,  
795 Waldner, P., Wedeux, B.M.M., Wirth, C., Wöll, H., Woods, M., Xiang, W., Zimmermann,  
796 N.E. & Coomes, D.A. (2016) Allometric equations for integrating remote sensing  
797 imagery into forest monitoring programmes. *Global Change Biology*, n/a-n/a.

798 Kearsley, E., de Haulleville, T., Hufkens, K., Kidimbu, A., Toirambe, B., Baert, G., Huygens,  
799 D., Kebede, Y., Defourny, P., Bogaert, J., Beeckman, H., Steppe, K., Boeckx, P. &  
800 Verbeeck, H. (2013) Conventional tree height-diameter relationships significantly  
801 overestimate aboveground carbon stocks in the Congo Basin. *Nature communications*.

802 Kellner, J.R., Clark, D.B. & Hubbell, S.P. (2009) Pervasive canopy dynamics produce short-  
803 term stability in a tropical rain forest landscape. *Ecology Letters*, **12**, 155–164.

804 Kellner, J.R. & Hubbell, S.P. (2017) Adult mortality in a low-density tree population using  
805 high-resolution remote sensing. *Ecology*, **98**, 1700–1709.

806 Langsrud, Ø. (2003) ANOVA for unbalanced data: Use Type II instead of Type III sums of  
807 squares. *Statistics and Computing*, **13**, 163–167.

808 Laurance, W.F., Delamônica, P., Laurance, S.G., Vasconcelos, H.L. & Lovejoy, T.E. (2000)  
809 Conservation: Rainforest fragmentation kills big trees. *Nature*, **404**, 836–836.

810 Lewis, S.L.L., Sonké, B., Sunderland, T., Begne, S.K.S.K., Lopez-Gonzalez, G., Heijden,  
811 G.M.F. Van Der, Phillips, O.L.O.L., Affum-Baffoe, K., Baker, T.R.T.R., Banin, L., Bastin,  
812 J.-F.J.-F., Beeckman, H., Boeckx, P., Bogaert, J., De Cannière, C., Chezeaux, V., Clark,  
813 C.J.C.J., Collins, M., Djagbletey, G., Droissart, V., Doucet, J.-L.J.-L., Ewango,  
814 C.E.N.C.E.N., Fauset, S., Feldpausch, T.R.R., Foli, E.G., Gillet, J.-F.J.-F., Hamilton,



815 A.C.A.C., Harris, D.J.D.J., Hart, T.B.T.B., de Haulleville, T., Hladik, A., Hufkens, K.,  
816 Huygens, D., Jeanmart, P., Jeffery, K.J., Kamdem, M.-N.D., Kearsley, E., Leal, M.E.E.,  
817 Lloyd, J., Lovett, J.C.J.C., Makana, J.-R.J.-R., Malhi, Y., Marshall, A.R.R., Ojo, L., Peh,  
818 K.S.-H.K.S.-H., Pickavance, G., Poulsen, J.R., Reitsma, M., Sheil, D., Simo, M., Steppe,  
819 K., Taedoumg, H.E.E., Talbot, J., Taplin, J.J.R.D., Taylor, D., Thomas, S.C.S.C.,  
820 Toirambe, B., Verbeeck, H., Vleminckx, J., White, L.J.T.J.T., Willcock, S., Woell, H.,  
821 Zemagho, L., van der Heijden, G.M.F., Phillips, O.L.O.L., Affum-Baffoe, K., Baker,  
822 T.R.T.R., Banin, L., Bastin, J.-F.J.-F., Beeckman, H., Boeckx, P., Bogaert, J., De  
823 Cannière, C., Chezeaux, E., Clark, C.J.C.J., Collins, M., Djangbletey, G., Djuikouo,  
824 M.N.K., Droissart, V., Doucet, J.-L.J.-L., Ewango, C.E.N.C.E.N., Fauset, S., Feldpausch,  
825 T.R.R., Foli, E.G., Gillet, J.-F.J.-F., Hamilton, A.C.A.C., Harris, D.J.D.J., Hart, T.B.T.B.,  
826 de Haulleville, T., Hladik, A., Hufkens, K., Huygens, D., Jeanmart, P., Jeffery, K.J.,  
827 Kearsley, E., Leal, M.E.E., Lloyd, J., Lovett, J.C.J.C., Makana, J.-R.J.-R., Malhi, Y.,  
828 Marshall, A.R.R., Ojo, L., Peh, K.S.-H.K.S.-H., Pickavance, G., Poulsen, J.R., Reitsma,  
829 J.M., Sheil, D., Simo, M., Steppe, K., Taedoumg, H.E.E., Talbot, J., Taplin, J.J.R.D.,  
830 Taylor, D., Thomas, S.C.S.C., Toirambe, B., Verbeeck, H., Vleminckx, J., White,  
831 L.J.T.J.T., Willcock, S., Woell, H. & Zemagho, L. (2013) Above-ground biomass and  
832 structure of 260 African tropical forests. *Philosophical transactions of the Royal Society*  
833 *of London. Series B, Biological sciences*, **368**.

834 Lindenmayer, D.B., Laurance, W.F. & Franklin, J.F. (2012) Global decline in large old trees.  
835 *Science*, **338**, 1305–1306.

836 Malhi, Y., Wood, D., Baker, T.R., Wright, J., Phillips, O.L., Cochrane, T., Meir, P., Chave, J.,  
837 Almeida, S., Arroyo, L., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F.,  
838 Lewis, S.L., Monteagudo, A., Neill, D. a., Vargas, P.N., Pitman, N.C. a., Quesada, C.A.,  
839 Salomao, R., Silva, J.N.M., Lezama, A.T., Terborgh, J., Martinez, R.V. & Vinceti, B.  
840 (2006) The regional variation of aboveground live biomass in old-growth Amazonian  
841 forests. *Global Change Biology*, **12**, 1107–1138.

842 Maniatis, D. & Mollicone, D. (2010) Options for sampling and stratification for national forest

843 inventories to implement REDD+ under the UNFCCC. *Carbon balance and*  
844 *management*, **5**, 9.

845 Mascaro, J., Detto, M., Asner, G.P. & Muller-Landau, H.C. (2011) Evaluating uncertainty in  
846 mapping forest carbon with airborne LiDAR. *Remote Sensing of Environment*, **115**,  
847 3770–3774.

848 Meakem, V., Tepley, A.J., Gonzalez-Akre, E.B., Herrmann, V., Muller-Landau, H.C., Wright,  
849 S.J., Hubbell, S.P., Condit, R. & Anderson-Teixeira, K.J. (2017) Role of tree size in  
850 moist tropical forest carbon cycling and water deficit responses. *New Phytologist*.

851 Molto, Q., Hérault, B., Boreux, J.-J., Daullet, M., Rousteau, A. & Rossi, V. (2014) Predicting  
852 tree heights for biomass estimates in tropical forests – a test from French Guiana.  
853 *Biogeosciences*, **11**, 3121–3130.

854 Nepstad, D.C., Tohver, I.M., Ray, D., Moutinho, P. & Cardinot, G. (2007) Mortality of large  
855 trees and lianas following experimental drought in an Amazon forest. *Ecology*, **88**,  
856 2259–69.

857 New, M., Hulme, M., Jones, P., New, M., Hulme, M. & Jones, P. (1999) Representing  
858 Twentieth-Century Space–Time Climate Variability. Part I: Development of a 1961–90  
859 Mean Monthly Terrestrial Climatology. *Journal of Climate*, **12**, 829–856.

860 New, M., Lister, D., Hulme, M. & Makin, I. (2002) A high-resolution data set of surface  
861 climate over global land areas. *Climate Research*, **21**, 1–25.

862 Ploton, P., Barbier, N., Coutron, P., Antin, C.M., Ayyappan, N., Balachandran, N., Barathan,  
863 N., Bastin, J.-F., Chuyong, G., Dauby, G., Droissart, V., Gastellu-Etchegorry, J.-P.,  
864 Kamdem, N.G., Kenfack, D., Libalah, M., Mofack, G., Momo, S.T., Pargal, S., Petronelli,  
865 P., Proisy, C., Réjou-Méchain, M., Sonké, B., Texier, N., Thomas, D., Verley, P.,  
866 Zebaze Dongmo, D., Berger, U. & Pélissier, R. (2017) Toward a general tropical forest  
867 biomass prediction model from very high resolution optical satellite images. *Remote*  
868 *Sensing of Environment*, **200**.

869 Ploton, P., Barbier, N., Takoudjou Momo, S., Réjou-Méchain, M., Boyemba Bosela, F.,  
870 Chuyong, G., Dauby, G., Droissart, V., Fayolle, A., Goodman, R.C., Henry, M.,

871 Kamdem, N.G., Mukirania, J.K., Kenfack, D., Libalah, M., Ngomanda, A., Rossi, V.,  
872 Sonké, B., Texier, N., Thomas, D., Zebaze, D., Couteron, P., Berger, U. & Pélissier, R.  
873 (2016) Closing a gap in tropical forest biomass estimation: taking crown mass variation  
874 into account in pantropical allometries. *Biogeosciences*, **13**, 1571–1585.

875 Ploton, P., Pélissier, R. & Proisy, C. (2012) Assessing aboveground tropical forest biomass  
876 using Google Earth canopy images. *Ecological Applications*, **22**, 993–1003.

877 Poorter, L., van der Sande, M.T., Thompson, J., Arets, E.J.M.M., Alarcón, A., Álvarez-  
878 Sánchez, J., Ascarrunz, N., Balvanera, P., Barajas-Guzmán, G., Boit, A., Bongers, F.,  
879 Carvalho, F.A., Casanoves, F., Cornejo-Tenorio, G., Costa, F.R.C., de Castilho, C. V.,  
880 Duivenvoorden, J.F., Dutrieux, L.P., Enquist, B.J., Fernández-Méndez, F., Finegan, B.,  
881 Gormley, L.H.L., Healey, J.R., Hoosbeek, M.R., Ibarra-Manríquez, G., Junqueira, A.B.,  
882 Levis, C., Licona, J.C., Lisboa, L.S., Magnusson, W.E., Martínez-Ramos, M., Martínez-  
883 Yrizar, A., Martorano, L.G., Maskell, L.C., Mazzei, L., Meave, J.A., Mora, F., Muñoz, R.,  
884 Nytch, C., Pansonato, M.P., Parr, T.W., Paz, H., Pérez-García, E.A., Rentería, L.Y.,  
885 Rodríguez-Velazquez, J., Rozendaal, D.M.A., Ruschel, A.R., Sakschewski, B., Salgado-  
886 Negret, B., Schiatti, J., Simões, M., Sinclair, F.L., Souza, P.F., Souza, F.C., Stropp, J.,  
887 ter Steege, H., Swenson, N.G., Thonicke, K., Toledo, M., Uriarte, M., van der Hout, P.,  
888 Walker, P., Zamora, N. & Peña-Claros, M. (2015) Diversity enhances carbon storage in  
889 tropical forests. *Global Ecology and Biogeography*, **24**, 1314–1328.

890 Proisy, C., Couteron, P. & Fromard, F. (2007) Predicting and mapping mangrove biomass  
891 from canopy grain analysis using Fourier-based textural ordination of IKONOS images.  
892 *Remote Sensing of Environment*, **109**, 379–392.

893 Réjou-Méchain, M., Tanguy, A., Piponiot, C., Chave, J. & Hérault, B. (2017) biomass : an r  
894 package for estimating above-ground biomass and its uncertainty in tropical forests.  
895 *Methods in Ecology and Evolution*, **8**, 1163–1167.

896 Remm, J. & Lõhmus, A. (2011) Tree cavities in forests – The broad distribution pattern of a  
897 keystone structure for biodiversity. *Forest Ecology and Management*, **262**, 579–585.

898 Romijn, E., Herold, M., Kooistra, L., Murdiyarso, D. & Verchot, L. (2012) Assessing

899 capacities of non-Annex I countries for national forest monitoring in the context of  
900 REDD+. *Environmental Science & Policy*, **19–20**, 33–48.

901 Rutishauser, E., Hérault, B., Baraloto, C., Blanc, L., Descroix, L., Sotta, E.D., Ferreira, J.,  
902 Kanashiro, M., Mazzei, L., d'Oliveira, M.V.N., de Oliveira, L.C., Peña-Claros, M., Putz,  
903 F.E., Ruschel, A.R., Rodney, K., Roopsind, A., Shenkin, A., da Silva, K.E., de Souza,  
904 C.R., Toledo, M., Vidal, E., West, T.A.P., Wortel, V. & Sist, P. (2015) Rapid tree carbon  
905 stock recovery in managed Amazonian forests. *Current biology : CB*, **25**, R787-8.

906 Rutishauser, E., Wagner, F., Hérault, B., Nicolini, E.-A. & Blanc, L. (2010) Contrasting above-  
907 ground biomass balance in a Neotropical rain forest. *Journal of Vegetation Science*,  
908 672–682.

909 Saatchi, S.S., Houghton, R. a., Dos Santos Alvalá, R.C., Soares, J. V. & Yu, Y. (2007)  
910 Distribution of aboveground live biomass in the Amazon basin. *Global Change Biology*,  
911 **13**, 816–837.

912 Sist, P., Mazzei, L., Blanc, L. & Rutishauser, E. (2014) Large trees as key elements of  
913 carbon storage and dynamics after selective logging in the Eastern Amazon. *Forest  
914 Ecology and Management*, **318**, 103–109.

915 Slik, J.W.F., Aiba, S.-I., Brearley, F.Q., Cannon, C.H., Forshed, O., Kitayama, K., Nagamasu,  
916 H., Nilus, R., Payne, J., Paoli, G., Poulsen, A.D., Raes, N., Sheil, D., Sidiyasa, K.,  
917 Suzuki, E. & Van Valkenburg, J.L.C.H. (2010) Environmental correlates of tree biomass,  
918 basal area, wood specific gravity and stem density gradients in Borneo's tropical forests.  
919 *Global Ecology and Biogeography*, **19**, 50–60.

920 Slik, J.W.F., Alvarez-loayza, P., Alves, L.F., Ashton, P., Balvanera, P., Bastian, M.L.,  
921 Bellingham, P.J., Berg, E. Van Den, Bernacci, L., Conceição, P., Blanc, L., Böhning-  
922 gaese, K., Boeckx, P., Boyle, B., Bradford, M., Brearley, F.Q., Hockemba, B.,  
923 Bunyavejchewin, S., Matos, C.L., Castillo-santiago, M., Eduardo, L.M., Chai, S., Chen,  
924 Y., Colwell, R.K., Robin, C.L., Clark, C., Clark, D.B., Deborah, A., Culmsee, H., Damas,  
925 K., Dattaraja, H.S., Dauby, G., Davidar, P., Dewalt, S.J., Doucet, J., Duque, A., Durigan,  
926 G., Eichhorn, K.A.O., Pedro, V., Eler, E., Ewango, C., Farwig, N., Feeley, K.J., Ferreira,

927 L., Field, R., Ary, T., Filho, D.O., Fletcher, C., Forshed, O., Fredriksson, G., Gillespie, T.,  
928 Amarnath, G., Griffith, D.M., Grogan, J., Gunatilleke, N., Harris, D., Harrison, R., Hector,  
929 A., Homeier, J., Imai, N., Itoh, A., Jansen, P.A., Joly, C.A., Jong, B.H.J. De,  
930 Kartawinata, K., Kearsley, E., Kelly, D.L., Kenfack, D., Kitayama, K., Kooyman, R.,  
931 Larney, E., Laurance, S., Laurance, W.F., Michael, J., Leao, I., Letcher, S.G., Lindsell,  
932 J., Lu, X., Mansor, A., Marjokorpi, A., Martin, E.H., Meilby, H., Melo, F.P.L., Metcalfe,  
933 D.J., Vincent, P., Metzger, J.P., Millet, J., Mohandass, D., Juan, C., Nagamasu, H.,  
934 Nilus, R., Ochoa-gaona, S., Paudel, E., Permana, A., Maria, T.F., Rovero, F., Rozak,  
935 A.H., Santos, B.A., Santos, F., Sarker, S.K., Satdichanh, M., Schmitt, C.B., Schöngart,  
936 J., Tabarelli, M., Tang, J., Targhetta, N., Theilade, I., Thomas, D.W., Tchouto, P.,  
937 Hurtado, J., Valkenburg, J.L.C.H. Van, Do, T. Van, Verbeeck, H., Adekunle, V., Vieira,  
938 S.A., Alvarez-loayza, P., Alves, L.F., Berg, E. Van Den & Bernacci, L. (2015) An  
939 estimate of the number of tropical tree species. *Proceedings of the National Academy of*  
940 *Sciences*, **112**, E4628–E4629.

941 Slik, J.W.F., Franklin, J., Arroyo-Rodríguez, V., Field, R., Aguilar, S., Aguirre, N., Ahumada,  
942 J., Aiba, S.-I., Alves, L.F., Anitha, K., Avella, A., Mora, F., Aymard, G.A.C., Báez, S.,  
943 Balvanera, P., Bastian, M.L., Bastin, J.-F., Bellingham, P.J., Van Den Berg, E., Da  
944 Conceição Bispo, P., Boeckx, P., Boehning-Gaese, K., Bongers, F., Boyle, B.,  
945 Brambach, F., Brearley, F.Q., Brown, S., Chai, S.-L., Chazdon, R.L., Chen, S., Chhang,  
946 P., Chuyong, G., Ewango, C., Coronado, I.M., Cristóbal-Azkarate, J., Culmsee, H.,  
947 Damas, K., Dattaraja, H.S., Davidar, P., DeWalt, S.J., Din, H., Drake, D.R., Duque, A.,  
948 Durigan, G., Eichhorn, K., Eler, E.S., Enoki, T., Ensslin, A., Fandohan, A.B., Farwig, N.,  
949 Feeley, K.J., Fischer, M., Forshed, O., Garcia, Q.S., Garkoti, S.C., Gillespie, T.W.,  
950 Gillet, J.-F., Gonmadje, C., Granzow-De La Cerda, I., Griffith, D.M., Grogan, J.,  
951 Hakeem, K.R., Harris, D.J., Harrison, R.D., Hector, A., Hemp, A., Homeier, J., Hussain,  
952 M.S., Ibarra-Manríquez, G., Hanum, I.F., Imai, N., Jansen, P.A., Joly, C.A., Joseph, S.,  
953 Kartawinata, K., Kearsley, E., Kelly, D.L., Kessler, M., Killeen, T.J., Kooyman, R.M.,  
954 Laumonier, Y., Laurance, S.G., Laurance, W.F., Lawes, M.J., Letcher, S.G., Lindsell, J.,

955 Lovett, J., Lozada, J., Lu, X., Lykke, A.M., Bin Mahmud, K., Mahayani, N.P.D., Mansor,  
956 A., Marshall, A.R., Martin, E.H., Matos, D.C.L., Meave, J.A., Melo, F.P.L., Mendoza,  
957 Z.H.A., Metali, F., Medjibe, V.P., Metzger, J.P., Metzker, T., Mohandass, D., Munguía-  
958 Rosas, M.A., Muñoz, R., Nurtjahy, E., De Oliveira, E.L., Onrizal, Parolin, P., Parren, M.,  
959 Parthasarathy, N., Paudel, E., Perez, R., Pérez-García, E.A., Pommer, U., Poorter, L.,  
960 Qi, L., Piedade, M.T.F., Pinto, J.R.R., Poulsen, A.D., Poulsen, J.R., Powers, J.S.,  
961 Prasad, R.C., Puyravaud, J.-P., Rangel, O., Reitsma, J., Rocha, D.S.B., Rolim, S.,  
962 Rovero, F., Rozak, A., Ruokolainen, K., Rutishauser, E., Rutten, G., Mohd Said, M.N.,  
963 Saiter, F.Z., Saner, P., Santos, B., Dos Santos, J.R., Sarker, S.K., Schmitt, C.B.,  
964 Schoengart, J., Schulze, M., Sheil, D., Sist, P., Souza, A.F., Spironello, W.R., Sposito,  
965 T., Steinmetz, R., Stevart, T., Suganuma, M.S., Sukri, R., Sultana, A., Sukumar, R.,  
966 Sunderland, T., Supriyadi, Suresh, H.S., Suzuki, E., Tabarelli, M., Tang, J., Tanner,  
967 E.V.J., Targhetta, N., Theilade, I., Thomas, D., Timberlake, J., De Morisson Valeriano,  
968 M., Van Valkenburg, J., Van Do, T., Van Sam, H., Vandermeer, J.H., Verbeeck, H.,  
969 Vetaas, O.R., Adekunle, V., Vieira, S.A., Webb, C.O., Webb, E.L., Whitfeld, T., Wich, S.,  
970 Williams, J., Wiser, S., Wittmann, F., Yang, X., Yao, C.Y.A., Yap, S.L., Zahawi, R.A.,  
971 Zakaria, R. & Zang, R. (2018) Phylogenetic classification of the world's tropical forests.  
972 *Proceedings of the National Academy of Sciences of the United States of America*, **115**.  
973 Slik, J.W.F., Paoli, G., McGuire, K., Amaral, I., Barroso, J., Bastian, M., Blanc, L., Bongers,  
974 F., Boundja, P., Clark, C., Collins, M., Dauby, G., Ding, Y., Doucet, J.-L., Eler, E.,  
975 Ferreira, L., Forshed, O., Fredriksson, G., Gillet, J.-F., Harris, D., Leal, M., Laumonier,  
976 Y., Malhi, Y., Mansor, A., Martin, E., Miyamoto, K., Araujo-Murakami, A., Nagamasu, H.,  
977 Nilus, R., Nurtjahya, E., Oliveira, Á., Onrizal, O., Parada-Gutierrez, A., Permana, A.,  
978 Poorter, L., Poulsen, J., Ramirez-Angulo, H., Reitsma, J., Rovero, F., Rozak, A., Sheil,  
979 D., Silva-Espejo, J., Silveira, M., Spironelo, W., ter Steege, H., Stevart, T., Navarro-  
980 Aguilar, G.E., Sunderland, T., Suzuki, E., Tang, J., Theilade, I., van der Heijden, G., van  
981 Valkenburg, J., Van Do, T., Vilanova, E., Vos, V., Wich, S., Wöll, H., Yoneda, T., Zang,  
982 R., Zhang, M.-G. & Zweifel, N. (2013) Large trees drive forest aboveground biomass

983 variation in moist lowland forests across the tropics. *Global Ecology and Biogeography*,  
984 **22**, 1261–1271.

985 Stark, S.C., Enquist, B.J., Saleska, S.R., Leitold, V., Schiatti, J., Longo, M., Alves, L.F.,  
986 Camargo, P.B. & Oliveira, R.C. (2015) Linking canopy leaf area and light environments  
987 with tree size distributions to explain Amazon forest demography. *Ecology Letters*, **18**,  
988 636–645.

989 Stark, S.C., Leitold, V., Wu, J.L., Hunter, M.O., de Castilho, C. V., Costa, F.R.C., McMahon,  
990 S.M., Parker, G.G., Shimabukuro, M.T., Lefsky, M.A., Keller, M., Alves, L.F., Schiatti, J.,  
991 Shimabukuro, Y.E., Brandt, D.O., Woodcock, T.K., Higuchi, N., de Camargo, P.B.,  
992 de Oliveira, R.C. & Saleska, S.R. (2012) Amazon forest carbon dynamics predicted by  
993 profiles of canopy leaf area and light environment. *Ecology Letters*, **15**, 1406–1414.

994 Stegen, J.C., Swenson, N.G., Enquist, B.J., White, E.P., Phillips, O.L., Jørgensen, P.M.,  
995 Weiser, M.D., Monteagudo Mendoza, A. & Núñez Vargas, P. (2011) Variation in above-  
996 ground forest biomass across broad climatic gradients. *Global Ecology and*  
997 *Biogeography*, **20**, 744–754.

998 Sullivan, M.J.P., Talbot, J., Lewis, S.L., Phillips, O.L., Qie, L., Begne, S.K., Chave, J., Cuni-  
999 Sanchez, A., Hubau, W., Lopez-Gonzalez, G., Miles, L., Monteagudo-Mendoza, A.,  
1000 Sonké, B., Sunderland, T., Ter Steege, H., White, L.J.T., Affum-Baffoe, K., Aiba, S.-I.,  
1001 De Almeida, E.C., De Oliveira, E.A., Alvarez-Loayza, P., Dávila, E.Á., Andrade, A.,  
1002 Aragão, L.E.O.C., Ashton, P., Aymard, G.A., Baker, T.R., Balinga, M., Banin, L.F.,  
1003 Baraloto, C., Bastin, J.-F., Berry, N., Bogaert, J., Bonal, D., Bongers, F., Brienen, R.,  
1004 Camargo, J.L.C., Cerón, C., Moscoso, V.C., Chezeaux, E., Clark, C.J., Pacheco, Á.C.,  
1005 Comiskey, J.A., Valverde, F.C., Coronado, E.N.H., Dargie, G., Davies, S.J., De  
1006 Caniere, C., Djuikouo, M.N., Doucet, J.-L., Erwin, T.L., Espejo, J.S., Ewango, C.E.N.,  
1007 Fauset, S., Feldpausch, T.R., Herrera, R., Gilpin, M., Gloor, E., Hall, J.S., Harris, D.J.,  
1008 Hart, T.B., Kartawinata, K., Kho, L.K., Kitayama, K., Laurance, S.G.W., Laurance, W.F.,  
1009 Leal, M.E., Lovejoy, T., Lovett, J.C., Lukasu, F.M., Makana, J.-R., Malhi, Y.,  
1010 Maracahipes, L., Marimon, B.S., Junior, B.H.M., Marshall, A.R., Morandi, P.S., Mukendi,

1011 J.T., Mukinzi, J., Nilus, R., Vargas, P.N., Camacho, N.C.P., Pardo, G., Peña-Claros, M.,  
1012 Pétronelli, P., Pickavance, G.C., Poulsen, A.D., Poulsen, J.R., Primack, R.B., Priyadi,  
1013 H., Quesada, C.A., Reitsma, J., Réjou-Méchain, M., Restrepo, Z., Rutishauser, E.,  
1014 Salim, K.A., Salomão, R.P., Samsedin, I., Sheil, D., Sierra, R., Silveira, M., Slik,  
1015 J.W.F., Steel, L., Taedoumg, H., Tan, S., Terborgh, J.W., Thomas, S.C., Toledo, M.,  
1016 Umunay, P.M., Gamarra, L.V., Vieira, I.C.G., Vos, V.A., Wang, O., Willcock, S. &  
1017 Zemagho, L. (2017) Diversity and carbon storage across the tropical forest biome.  
1018 *Scientific Reports*, **7**.

1019 Tang, H. & Dubayah, R. (2017) Light-driven growth in Amazon evergreen forests explained  
1020 by seasonal variations of vertical canopy structure. *Proceedings of the National*  
1021 *Academy of Sciences of the United States of America*, **114**, 2640–2644.

1022 Thomas, R.Q., Kellner, J.R., Clark, D.B. & Peart, D.R. (2013) Low mortality in tall tropical  
1023 trees. *Ecology*, **94**, 920–929.

1024 West, G.B., Enquist, B.J., Brown, J.H., West, G.B., Brown, J.H., Enquist, B.J. & Brown, J.H.  
1025 (2009) Extensions and evaluations of a general quantitative theory of forest structure  
1026 and dynamics. *Proceedings of the National Academy of Sciences of the United States*  
1027 *of America*, **106**, 7040–7045.

1028 Zanne, A.E., Lopez-Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., Miller, R.B.,  
1029 Swenson, N.G., Wiemann, M.C. & Chave, J. (2009) Global wood density database.  
1030 *Dryad*, **235**, 33.

1031

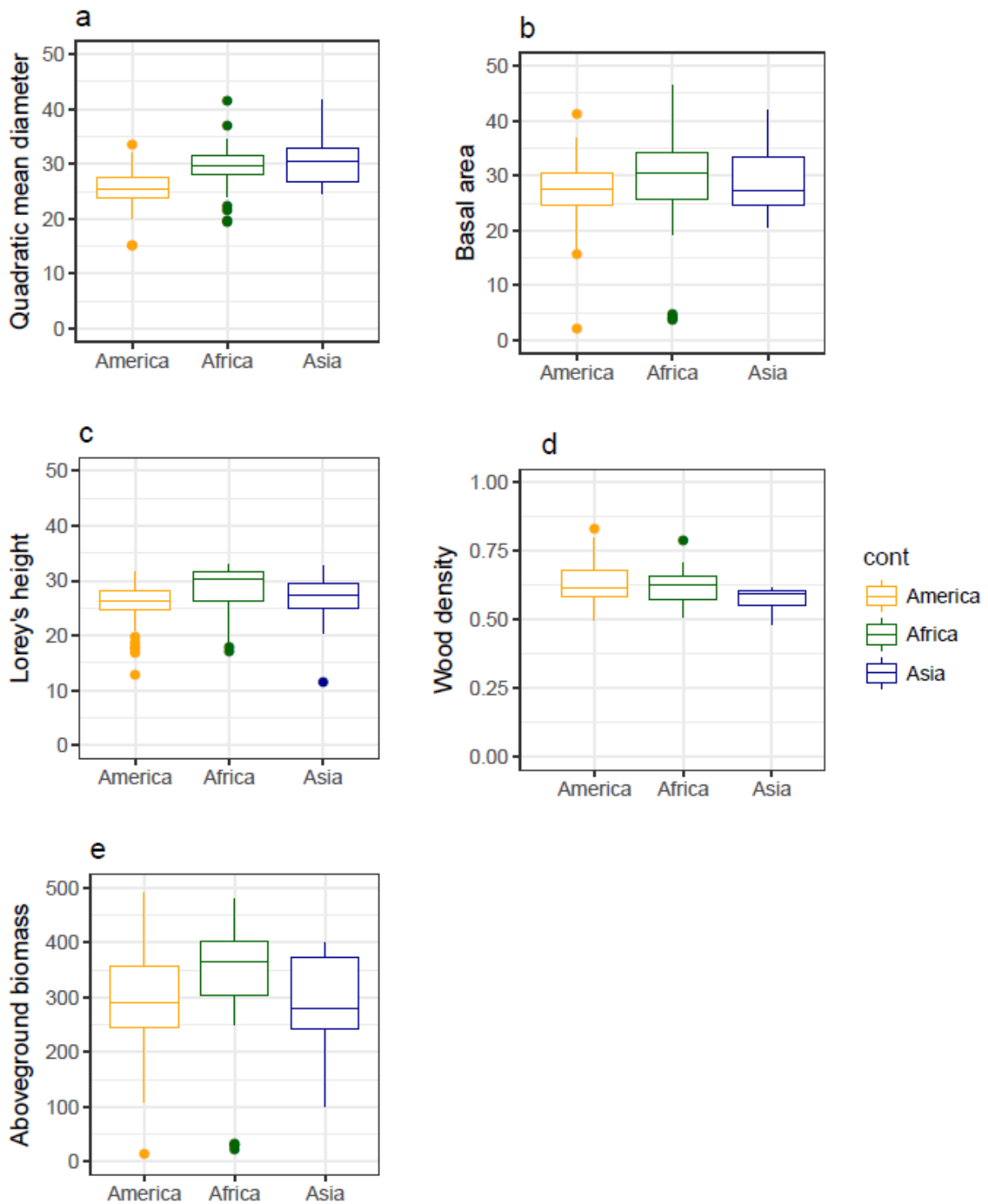


1032 **Supplementary information.**

1033 **Supplementary table 1. Plot, Site and Pls**

1034 **Supplementary table 2. Coefficients of plot level structure prediction from the *ith***

1035 **largest trees.**



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**Supplementary figure 1. Cross-continent comparison of plot-metrics distribution**

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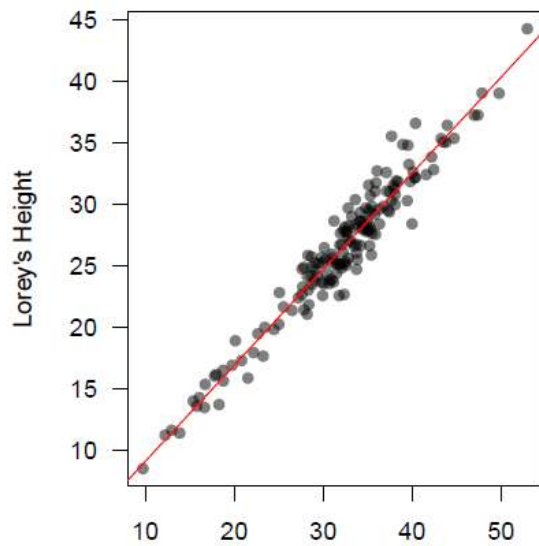
**averaged at the site level.** Figures illustrates respectively the distribution of the values for

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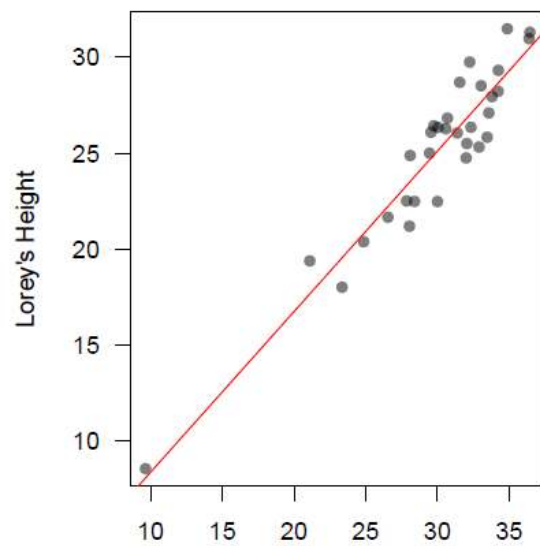
the quadratic mean diameter (a), basal area (b), Lorey's height (c), wood density (d) and

1040

aboveground biomass (e).



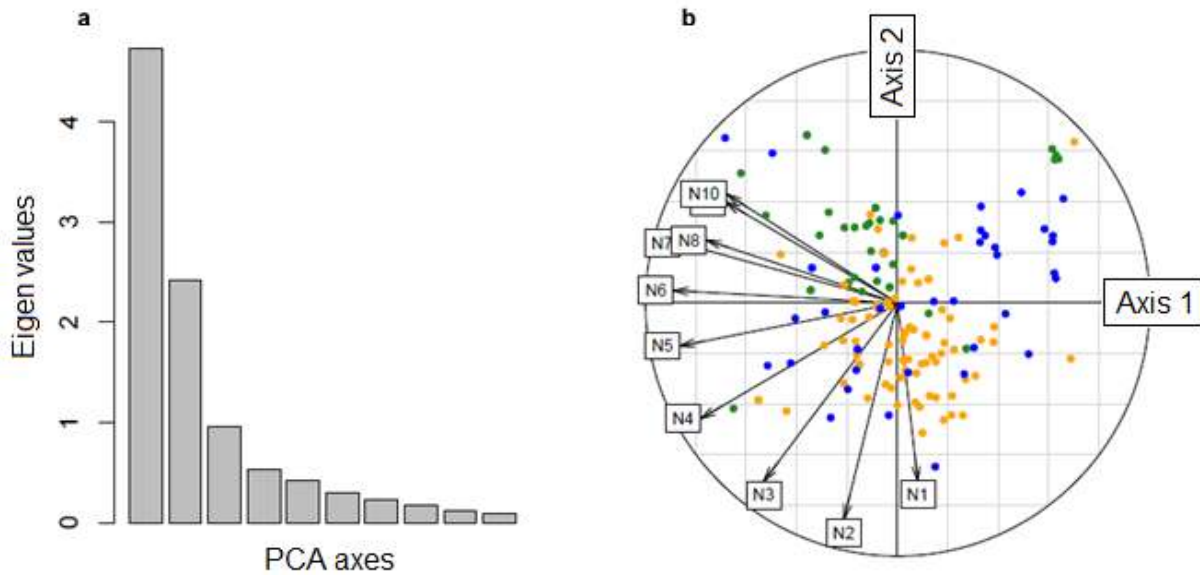
Mean Height - 20 largest trees (m) - local HD



Mean Height - 20 largest trees (m) - Observed H

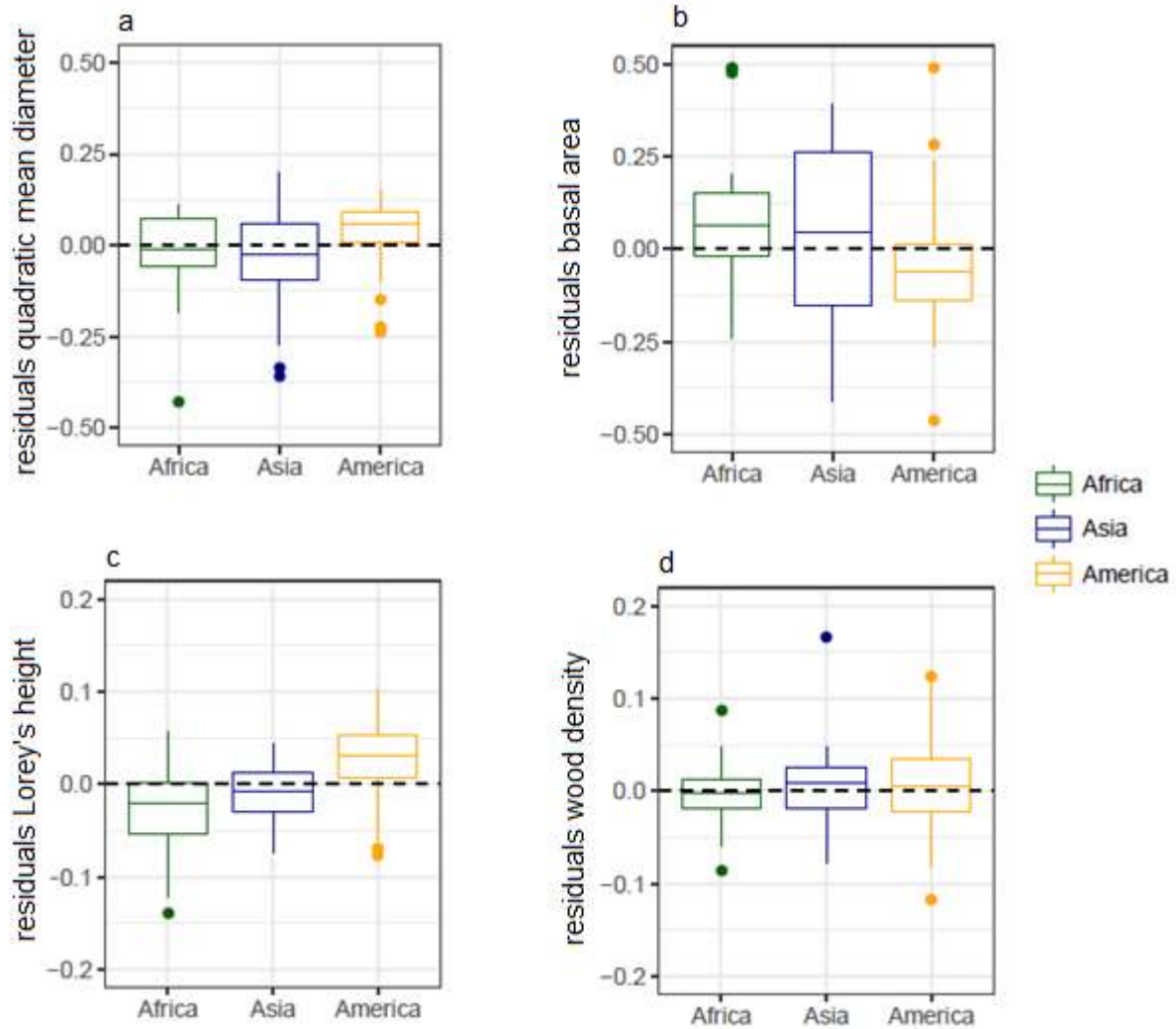
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1042 **Supplementary figure 2. Lorey's Height prediction from the 20 largest trees.** Figures  
 1043 show the results using (i) local D-H allometries for 20 sites (left subfigure) and (ii) using plots  
 1044 where height is measured on all trees in Malebo site in the Democratic Republic of the Congo  
 1045 (right subfigure).



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1047 **Supplementary figure 3. PCA on the diameter structure and corresponding mean**  
 1048 **distribution for high contributions of axis 1 and axis 2.** (A) Illustration of top and low  
 1049 percentile observed for each axis, with diameter distributions represented as the relative  
 1050 difference with the average observed distribution.(B) Biplot with contribution to the PCA of all  
 1051 the diameter classes, with the respective position of each site in the space defined by axis1  
 1052 and 2. Axis 1 is driven by differences in global abundance of trees and axis 2 is driven by a  
 1053 difference of balance between abundance of small vs. large trees. Colors represent continent,  
 1054 with Africa, America and Asia respectively in green, orange and blue.



1055  
 1056 **Supplementary figure 4. Cross-continent comparison of the relative residuals from the**  
 1057 **prediction of plot-metrics from the 20 largest trees.** The relative residuals are generally  
 1058 low (<10%). Systematic small differences can however be found in America, where the  
 1059 quadratic mean diameter and Lorey's height tend to be slightly overestimated and the basal  
 1060 area slightly underestimated.