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1 High above-ground carbon stock of African tropical montane forests

2
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23 24 Abstract

25 Tropical forests store 40-50% of terrestrial vegetation carbon¹. Spatial variations in aboveground live
26 tree biomass carbon (AGC) stocks remain poorly understood, in particular in tropical montane
27 forests². **Because of climatic and soil changes with increasing elevation³**, AGC stocks are lower in
28 tropical montane compared to lowland forests². Here we assemble and analyse a dataset of
29 structurally intact old-growth forests (AfriMont) spanning 44 montane sites in 12 African countries.
30 We find that montane sites in the AfriMont plot network have a mean AGC-stock of 149.4 Mg C ha⁻¹
31 (95% CI 137.1-164.2), comparable to lowland forests in the African Tropical Rainforest Observation
32 Network⁴ and about **70% and 32%** higher than averages from plot networks in montane^{2,5,6} and
33 lowland⁷ forests in the Neotropics, respectively. Notably, our results are two-thirds higher than the
34 IPCC default values for these forests in Africa⁸. We find that the low stem density and high
35 abundance of large trees of African lowland forests⁴ is mirrored in the montane forests sampled. This
36 carbon store is endangered: we estimate that 0.8 million ha of old-growth African montane forest
37 have been lost since 2000. We provide country-specific montane forest AGC **stock** estimates
38 modelled from our plot network to help guide forest conservation and reforestation interventions.
39 Our findings highlight the need for conserving these biodiverse^{9,10} and carbon-rich ecosystems.

40
41

42 **Main text**

43 Tropical forests cover less than 10% of the global land area yet store 40–50% of terrestrial
44 vegetation carbon¹ and contribute more than one third of primary productivity¹¹ so are a key
45 component of the global carbon cycle^{12,13}. There is substantial variation in carbon stocks across the
46 biome, with lowland forests in Africa and Borneo storing more carbon per unit area than lowland
47 forests in the Neotropics^{4,7}. This variation arises partly from structural differences: the signature
48 feature of African forests is their low stem density but relatively high abundance of large trees (>70
49 cm diameter) which store large quantities of carbon, while Bornean forests are characterised by high
50 stem density and basal area^{4,14,15}.

51

52 Despite increased understanding of biogeographic differences in tropical lowland forests, patterns of
53 spatial variation in carbon stocks remain poorly understood in the 880,000 km² of tropical montane
54 forests located $\geq 1,000$ m asl². Montane forests are expected *a priori* to have lower aboveground live
55 tree biomass carbon (AGC) stocks than lowland forests because (1) temperature decreases with
56 increasing elevation, reducing net primary productivity and slowing nutrient recycling, (2) long
57 periods of cloud immersion in montane forests suppresses productivity, (3) soil waterlogging slows
58 nutrient recycling and (4) high epiphyte load, local wind exposure in crests and nutrient-limited soils
59 limit tree size and increase investment in roots over shoots³. While forest inventory plots provide
60 some support for these assumptions² data from African mountain regions are exceptionally sparse.
61 Indeed, in the most recent IPCC guidelines, there is no specific AGC default value for old-growth
62 montane forests in Africa: the value given of 89.3 Mg C ha⁻¹ is simply a mean of secondary and old-
63 growth forests found $\geq 1,000$ m asl⁸. Mountain areas also pose special challenges for remote-sensing
64 approaches for estimating carbon stocks, as radar data are affected by geometric distortions¹⁶ while
65 steep slopes bias spaceborne LiDAR estimates towards overestimating canopy height¹⁷. These issues
66 are reflected in the limited correlation between estimates of AGC-stocks at mountain locations from
67 different recent remote-sensing derived carbon maps (Supplementary Information Table S1).

68

69 Better understanding of montane carbon stocks is important for many African countries, particularly
70 in eastern Africa where montane forests represent most of the extant evergreen old-growth forest
71 cover. Quantifying carbon stocks in these ecosystems is critical for estimating national carbon losses
72 from deforestation and forest degradation¹⁸. Quantifying carbon stocks in old-growth montane
73 forests also serves to constrain potential carbon uptake by restored natural forests, given the high
74 commitment of most African nations to the Bonn Challenge effort to restore 150 million ha of
75 degraded and deforested lands by 2020 (see Table 1), and 350 million by 2030.

76

77 Here we measured, compiled and analysed an unprecedented dataset of 226 plot inventories
78 spanning 44 sites in 12 African countries, covering most major mountain regions on the continent
79 (the “AfriMont” dataset). Plots range from 800 to 3,900 m asl to include submontane forests (800-
80 1,000 m asl) in smaller mountains closer to the ocean^{19,20}. For all plots, stem diameter and species
81 were recorded for each tree ≥ 10 cm diameter at breast height (or above buttress) following
82 standard methods²¹. Tree height was sampled in 23 montane sites, allowing variation in height-
83 diameter allometry to be incorporated into the calculation of aboveground biomass. A total of
84 72,336 stems with diameter ≥ 10 cm were measured. For each tree, we computed AGC (in Mg C ha⁻¹)
85 according to standard procedures (see methods).

86

87 We find that the mean plot-level AGC-stock across sampled African tropical montane forests is 149.4
88 Mg C ha⁻¹ (95% CI 137.1-164.2), two-thirds more than the IPCC default value of 89.3 Mg C ha⁻¹. Our
89 estimates are robust to subsampling our dataset (Extended Data Fig. 1) and excluding small plots
90 (Extended Data Fig. 2) and are not affected by the sampling strategy used to establish plots in each
91 study site (Extended Data Fig. 2). Comparing our dataset to previous syntheses of montane^{2,5,6} and
92 lowland⁷ forest plot networks reveals that tropical montane forests in Africa have significantly higher

93 AGC-stocks per unit area than both montane (95% CI = 50.4 – 71.9 Mg C ha⁻¹) and lowland (95% CI =
94 124.0 – 147.9 Mg C ha⁻¹) forests in the Neotropics, and that they do not differ significantly from
95 lowland forests in Africa (95% CI = -27.6 – 9.6 Mg C ha⁻¹, Fig. 1, Table S2). The similar AGC-stocks in
96 montane and lowland forests in Africa contrasts with the Neotropics and Southeast Asia, where
97 carbon stocks are lower in montane forests than lowland forests (albeit not significantly different in
98 Southeast Asia due to the small sample size, Fig. 1). These differences are robust to accounting for
99 differences in elevation among montane datasets: removing African plots 800-1,000 m asl slightly
100 reduces estimated montane forest AGC-stock to 145.0 Mg C ha⁻¹ (95% CI 129.6 – 163.2), but
101 observed differences in AGC-stock among continents remain when plots are restricted to elevations
102 well represented in all continents (Extended Data Fig. 3).

103

104 The characteristic structural properties of lowland African forests (relatively low stem density and
105 greater importance of large trees compared to elsewhere in the tropics⁴) are also evident in the
106 African montane forests we sampled. In these montane forests mean stem density is 483.3 stems ha⁻¹
107 (± 177.7 s.d.) and mean basal area is 39 m²ha⁻¹ (± 14.8 s.d.). We find a high density of large stems
108 (>70 cm diameter, 19.1 stems ha⁻¹ ± 15.4 s.d.) which contribute 35.3% (95% CI = 29.6 – 41.8 %) to
109 plot-level AGC-stock (Fig. 2). The contribution of large trees to plot-level AGC-stock is also similar in
110 montane and lowland Africa (95% CI of difference in square-root transformed proportional
111 contribution of large trees between lowland and montane forests = -0.100 - 0.075, $P = 0.80$). There
112 was no significant difference in the proportional contribution of any other size class to AGC-stocks
113 between our montane dataset and 132 lowland plots from the AfriTRON network ($P \geq 0.24$, Table S3),
114 although greater variation among plots is observed in montane forests (Fig. 2).

115

116 To investigate if elevation affected AGC or forest structure, we modelled these variables as functions
117 of elevation using random slopes mixed-effects models. This approach allows intercepts and
118 relationships to vary among sites, which would be expected as mountains can have very different
119 climate at the same elevation due to proximity to the ocean (generally the further, the drier) and
120 because of the mass-elevation or telescopic effect²² (larger mountains are better at warming the
121 atmosphere above them). We found that AGC, stem density or density of large stems (>70 cm
122 diameter) were not significantly related to elevation (Fig. 3, Table S4). Across sites these non-
123 significant relationships were all negative, although there was some variation in strength and
124 direction amongst sites (Fig. 3). Similarly, in the Neotropics and Southeast Asia montane forest plot
125 datasets, AGC was not significantly correlated with elevation (Extended Data Fig. 4).

126

127 To assess potential environmental drivers of AGC-stock variation across the AfriMont plot network,
128 we related AGC to climate, soil and topography. We found that AGC-stocks increased with annual
129 precipitation (albeit not statistically significantly), decreased with soil fertility and were higher in
130 plots which were locally at higher elevation than their surroundings (Extended Data Fig. 5).
131 Relationships with other environmental variables were non-significant (Extended Data Fig. 5).
132 Although global datasets might not capture fine-scale variation in climate or soils in mountain
133 regions²³, leading to regression dilution²⁴, the general absence of strong climate effects combined
134 with the lack of significant effect of elevation on AGC-stocks suggest that the high AGC-stock of
135 African montane forests is a pervasive phenomenon across a wide environmental gradient.

136

137 Although the AfriMont dataset covers most major mountain areas in tropical Africa (Fig. 4), some
138 areas remain under-sampled relative to forest extents (Extended Data Fig. 6), resulting in some
139 differences between the environmental conditions sampled by our plot network and the wider
140 montane forest biome in Africa (Extended Data Fig. 7). Notably, the absence of plots from montane
141 forests of eastern Democratic Republic of the Congo (Fig. 4, Extended Data Fig. 6) means that the
142 AfriMont dataset samples forests that are, on average, at higher elevations, and that are cooler and
143 cloudier than the wider montane forest biome in Africa (Extended Data Fig. 7). Using relationships

144 with environmental variables (Extended Data Fig. 5) to predict AGC-stocks in each 1-km grid cell
145 containing montane forest gives a mean (weighted by remaining forest cover) AGC-stock of 176.9
146 Mg C ha⁻¹ (± 32.0 s.d.) for the tropical montane forest biome in Africa. This indicates that the
147 estimate we report based on our AfriMont plot network data (149.4 Mg C ha⁻¹) is conservative.

148

149 Several mechanisms could explain the high AGC-stock of montane forests in the AfriMont plot
150 network. Firstly, large herbivores such as elephants (*Loxodonta* spp.) can have profound effects on
151 forest structure by consuming biomass, destroying small stems, dispersing seeds and transporting
152 nutrients²⁵. Studies for lowland forests suggest that elephants can increase carbon stocks^{26,27}. We
153 tested if AfriMont plots with known elephant presence as of 2019 had significantly higher AGC-
154 stocks, but found that they had significantly lower AGC-stocks, although significant differences were
155 not observed in some countries (Extended Data Fig. 8). While the initial ecosystem response to
156 elephant removal might be greater AGC-stocks due to reduced biomass consumption and small-stem
157 destruction, the longer-term effects might differ. We were unable to fully disentangle such effects,
158 as we lacked details on both i) time since elephant extirpation, and ii) elephant abundance and its
159 determinants (see Table S5).

160

161 A second potential explanation is a relatively low frequency of large-scale abiotic disturbances,
162 allowing trees time to grow large and stands to self-thin, as is seen in lowland African forests⁴. For
163 example, tropical cyclones are largely absent in mainland Africa (except in Mozambique²⁸) and lava
164 flows are limited even in the active volcano of Mt Cameroon²⁹. Although fine-scale variability in
165 landslide risk limits comparisons across large spatial scales, there are fewer areas with high landslide
166 susceptibility in mountains in tropical Africa than in the Andes and most mountain ranges in
167 Southeast Asia³⁰. If forests have been ecologically stable over evolutionary timescales, tree species
168 may be adapted to grow slowly but potentially reaching great sizes³¹. On Mt Kilimanjaro
169 *Entandrophragma* individuals reach enormous heights and ages³². This low frequency of large-scale
170 abiotic disturbances contrasts with the Andes and several mountains in Southeast Asia (e.g. Barisan
171 mountains in western Sumatra), which are tectonically active, so the trees there are adapted to
172 sudden disturbance followed by intense competition to get established and grow. Future monitoring
173 of the AfriMont plot network will help determine the extent to which the high biomass of African
174 tropical montane forests results from them being dynamic and productive, or adapted to stability.

175

176 A third potential explanation could be the presence of conifers³³. Mixed conifer/broad-leaved forests
177 tend to have greater basal area than purely broad-leaved forests due to a more effective use of light
178 and other resources³⁴. Podocarpaceae can be found in montane forests across the tropics³⁵. Despite
179 having fewer species in Africa than in other continents³⁶, these could be more abundant at the site-
180 level. However, there is no pantropical comparative study on Podocarpaceae abundance in tropical
181 montane forests. In our dataset there was no significant correlation between plot-level AGC-stock
182 and conifer (Podocarpaceae) abundance (Extended Data Fig. 9). Other explanations could be
183 continental differences in mountain terrain (more gentle slopes or plateau regions in Africa) or types
184 of montane forests investigated (less cloud forest existing/sampled in Africa). Within our dataset,
185 slope did not have a significant effect on AGC-stocks (Extended Data Fig. 5). Contrary to the
186 Neotropics³⁷, there is no high-resolution map of cloud forests available for Africa, so while we found
187 no relationship between AGC-stock and cloud frequency (Extended Data Fig. 5), we were unable to
188 investigate differences in AGC-stock between cloud forest vs non-cloud forest plots.

189

190 To understand the policy implications of our findings for African countries, we calculated montane
191 (≥800 m asl) forest cover change between 2000 and 2018, using forest cover from ref.³⁸ clipped to
192 'primary humid forest' from ref.³⁹. We show that tropical montane forests represent most - or all-
193 evergreen old-growth forests found in ten African countries (Fig. 4), and that the Democratic
194 Republic of the Congo has two thirds of the remaining 16 million ha of montane forests in Africa.

195 Over 0.8 million ha (5%) have been lost in Africa since 2001, with the highest losses in the
196 Democratic Republic of the Congo (536,000 ha), Uganda (65,000 ha) and Ethiopia (62,000 ha) (Fig. 4,
197 Table 1). In terms of percentage, Mozambique and Côte d'Ivoire lost over 20% of their montane
198 forests over this period (Fig. 4, Table 1). In some sites, however, a larger proportion of montane
199 forests was lost before 2000, e.g. in Taita Hills in Kenya⁴⁰. If absolute country-level deforestation
200 rates continue, a further 0.5 million ha of tropical montane forests will be lost by 2030.

201
202 African tropical montane forests are not only carbon-rich, but they also harbour some of the highest
203 concentrations of biodiversity and endemism in the world^{9,10}. They are important 'water towers' as,
204 located at the headwaters of numerous river systems, including the Congo and the Nile, they
205 regulate timing and magnitude of runoff⁹. They also regulate local temperatures⁴¹ and provide
206 numerous other services to people in the surrounding landscapes⁹. Clearly, more should be done to
207 avoid the destruction of these important ecosystems. Logging, mining and clearing land for farming,
208 but also political unrest and militia presence have affected -and continue to affect- these forests, e.g.
209 in Itombwe Mts in the Democratic Republic of the Congo⁴². Protected areas are known to help
210 reduce deforestation in the tropics⁴³. Beyond protected areas, other forest conservation
211 mechanisms could be implemented, including effective carbon finance. Previous IPCC AGC-stock
212 estimates for montane forests in Africa (89.3 Mg C ha⁻¹) may have contributed to low incentives for
213 carbon finance mechanisms in these ecosystems. Our study shows the far greater carbon storage
214 potential in these tropical montane forests, which will be even higher if soil carbon stocks are
215 considered (e.g. > 200 Mg C ha⁻¹ of organic carbon occurs in the top 0-30 cm soil on Mt Cameroon⁴⁴
216 and in the Usambara Mts, Tanzania⁴⁵).

217
218 As well as conserving the remaining montane forests, efforts to restore them are critical. Forest
219 restoration at one of our sites, Kibale National Park in Uganda, indicates the potential for rapid AGC
220 accumulation⁴⁶. Our study shows the high potential AGC-stock these montane forests can attain. The
221 possible co-benefits of forest restoration, notably water regulation, control of soil erosion and
222 landslides and biodiversity conservation should also be considered. Most African nations are
223 committed to the Bonn Challenge; Ethiopia leading with 15 million ha committed (Table 1). We
224 provide country-specific estimates of potential AGC-stocks based on forests sampled in the AfriMont
225 dataset to help guide such interventions (Table 1, Extended Data Fig. 10). Caution is needed when
226 scaling-up our estimates to the landscape scale, as not all forests are closed-canopy old-growth and
227 structurally intact. Remote sensing or ancillary data (landcover maps, spatial environmental data)
228 could be used to identify e.g. exotic plantations, degraded or bamboo forests, and thus help create
229 detailed AGC maps at different spatial scales^{18,47}. A closer collaboration between air-borne, space-
230 borne and ground approaches (such as the AfriMont and AfriTRON plot networks) is key for accurate
231 quantification and monitoring of landscape-scale tropical forest AGC-stocks, particularly in mountain
232 regions.

233
234 Our newly compiled dataset and analysis has provided the first large-scale quantification of AGC-
235 stock in African tropical montane forests, indicating it to be on average substantially higher than
236 previously thought. While there is variation around this mean AGC-stock within and across sites, it is
237 not systematically related to elevation. Apart from helping refine country-level estimates, IPCC
238 guidelines and ground-calibration of remote-sensing estimates, continued on-the-ground monitoring
239 of the AfriMont plot network will help determine ecosystem dynamics and carbon residence time in
240 these extraordinarily carbon-rich forests, as well as their responses to climatic changes.

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242

243 **Figures main document**

244

245 **Fig. 1 | Pantropical variation in aboveground carbon stocks sampled by plot networks in montane**
246 **(≥ 800 m asl) and lowland (< 800 m asl) tropical forests.** Data from this study for African montane
247 forests ($n = 226$ plots), montane forests in the Neotropics ($n = 131$) and Southeast Asia ($n = 32$) from
248 ref.^{2,5,6}, lowland forests in Africa ($n = 290$), the Neotropics ($n = 416$) and Southeast Asia ($n = 60$) from
249 ref.⁷. Coloured points show the AGC-stock in each plot, with point size proportional to square-root
250 plot area. Black points show means for each continent-elevation category estimated using linear
251 mixed-effects models with site as a random effect, and lines show 95% confidence intervals around
252 means. Letters indicate significant differences between continent elevation category combinations
253 (linear mixed-effects models with site as a random effect, $P < 0.05$).

254

255

256 **Fig. 2 | Proportion of plot-level aboveground carbon stock and stems accounted for by each size**
257 **class in montane and in lowland forests in Africa.** Statistically significant differences in contribution
258 of each size class between montane and lowland forest plot networks are shown by asterisks (linear
259 mixed-effects model, $P < 0.05$). NS = non-significant difference. Montane ($n = 226$), lowland ($n =$
260 132).

261

262 **Fig. 3 | Relationship between elevation and (a) plot-level aboveground carbon stock, (b) stem**
263 **density and (c) stem density of large stems (>70 cm diameter) for the AfriMont dataset.** Note log-
264 scale of y-axis. Each response variable was log-transformed and modelled as a function of elevation
265 with a linear mixed-effect models with random slopes. The dashed line shows the relationship across
266 sites (non-significant in all cases, $P \geq 0.3$, Table S4), while the black lines show the relationship within
267 each site. Point sizes are proportional to square-root plot area. A polynomial model allowing a non-
268 linear relationship with elevation was also tested but not supported over the linear model in any
269 case ($P \geq 0.7$, Table S4). The absence of a significant relationship with elevation is robust to removing
270 the two highest elevation sites, RWE and VRG (Table S4).

271

272 **Fig. 4. | Old-growth evergreen humid forests in lowland and montane tropical Africa.** Forest
273 extends circa 2018. Note that montane includes submontane forests (800-1,000 m asl, light purple).
274 Montane forests represent most (or all) evergreen humid old-growth forest in ten African nations:
275 Burundi, Ethiopia, Kenya, Rwanda, Tanzania, Uganda and Zimbabwe (included in AfriMont); and
276 Zambia, Malawi and South Sudan (no plot data available). Forest cover extracted from ref.³⁸ and
277 clipped to 'primary humid forest' using ref.³⁹. See Table 1 for country-level absolute estimates.

278

279 **Table 1 | Remaining forest area and aboveground carbon estimates for montane and lowland**
 280 **tropical forests in Africa**
 281

Country	Montane (ha)	Montane lost (ha)	Montane AGC (Mg ha ⁻¹ , 95% CI)	Montane sites (plots)	Lowland (ha)	Lowland AGC (Mg ha ⁻¹ , 95% CI)	Lowland plots	Bonn Challenge by 2020 (ha)
Burundi	25,000	300	94 (47-176)	1 (7)	0		0	2 million
Cameroon	840,000	30,200	153 (121-195)	7 (37)	17.7 million	166 (151-185)	72	12 million
DRC	10.2 million	536,500	129 (84-202)	2 (37)	90 million	158 (135-183)	48	8 million
Ethiopia	1.7 million	62,100	165 (124-215)	8 (25)	145,000	^a	0	15 million
Guinea	29,000	1,700	314 (147-616)*	1 (2)	193,000	157 (122 – 206) ^c	24	2 million
Kenya	568,000	44,100	104 (79-136)	8 (38)	37,000		0	5.1 million
Mozambique	18,000	6,600**	226 (146-384)*	3 (4)	93,000	^b	0	1 million
Nigeria	42,000	1,400	120 (47-309)*	1 (1)	1.8 million	161 (105-262)	2	4 million
Rwanda	53,000	300	106 (65-168)	2 (11)	0		0	2 million
Tanzania	587,000	13,900	175 (129-234)	6 (29)	130,000	128 (101-163)	16	5.2 million
Uganda	427,000	64,600**	158 (111-209)	6 (23)	18,000		0	2.5 million
Zimbabwe	7,000	800**	203 (108-363)	1 (12)	<1,000		0	2 million

282

283 Forest cover circa 2018 was extracted from ref.³⁸ and clipped to 'primary humid forest' using ref.³⁹.

284 Montane forest lost covers the period 2000-2018. Mean aboveground carbon (AGC, in Mg C ha⁻¹)
 285 estimates for montane (or lowland) forests were estimated from AfriMont and AfriTRON plot
 286 network data. Mean AGC values are in boldface, 95% confidence intervals in parentheses. For details
 287 on sites and plots used see Table S5. Bonn Challenge pledges for 2030 not yet available.

288 ^a ref.⁴⁸ report 192 Mg C ha⁻¹ for lowland; ^b ref.⁴⁹ report 132.2 Mg C ha⁻¹ for lowland. ^c Data from
 289 neighbouring Liberia.

290 * few plots sampled, or very small plots sampled, AGC estimates may not be robust, see Extended
 291 data Fig. 10.

292 **Montane forest loss in Mozambique, Uganda and Zimbabwe represents 27%, 13% and 10% of the
 293 existing montane forest in 2001, respectively. Montane forest loss in Côte d'Ivoire (no plot data
 294 available) was estimated to be 21% for the same period.

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- 409

410 **Methods**

411 **AfriMont – montane Africa dataset**

412 We compiled forest inventory plot data from the African Tropical Rainforest Observatory Network
413 (AfriTRON; www.afritron.org), with data curated at www.ForestPlots.net^{50,51} and the TEAM
414 network⁵², as well as from numerous site-specific publications detailed in Table S5 and mapped in
415 Fig. 4. Plots were selected for the analysis when conforming to the following criteria: ≥800 m asl,
416 closed-canopy evergreen wet or moist tropical forest, geo-referenced, old-growth and structurally
417 intact (not impacted by recent selective logging, fire or coffee cultivation), with no exotic species
418 present (e.g. *Eucalyptus* or *Pinus* spp.), all trees ≥10 cm diameter measured and majority of stems
419 identified to species. We included plots from Virunga Massif in Rwanda/Uganda even when not
420 100% closed-canopy due to high abundance of naturally-occurring bamboo. In all plots, tree
421 diameter was measured at 1.3 m along the stem from the ground, or above buttresses if present. In
422 23 sites tree height was sampled in the field for some stems, using a clinometer or a laser. Families
423 and species names follow the African Plant Database (ville-ge.ch/cjb/bd/africa/). The AfriMont
424 dataset consists of 72,336 stems, of which 92.9% were identified to species, 98.4% to genus and
425 98.5% to family. This dataset represents a standardised safe long-term repository of valuable
426 historical data (four sites initially considered could not be included because tree-level data had
427 already been lost by data owners).

428

429 **AfriTRON – lowland Africa dataset**

430 The 132 lowland-forest plots are all from AfriTRON^{4,13,53}. They were selected using the same criteria
431 as above (but with elevation <800 m asl), restricted to countries for which we also had montane
432 plots plus neighbouring countries where the mountains span international borders (e.g. Mt Nimba
433 spans Guinea and Liberia). The dataset includes 51,305 stems, of which 89.6% were identified to
434 species, 97.3% to genus and 97.7% to family. The plot data were retrieved from forestplot.net on
435 06/01/2019. The plot locations and details are in Table S6.

436

437 **Literature dataset**

438 We compiled data on AGC-stocks in tropical lowland and montane forests to compare to the
439 AfriMont data. Data for lowland forests came from ref.⁷ and consisted of all multi- and single-census
440 plots that were <800 m asl. Data for montane forests were obtained from ref.², with additional data
441 from Venezuela (ref.⁵) and Colombia (ref.⁶). Montane plots were defined as ≥800 m asl; elevation
442 was not provided for the Colombian dataset so plots were selected based on the forest type, and
443 these plots were excluded from analyses requiring elevation. To avoid double counting plots,
444 Venezuelan and Colombian plots were removed from the ref.² dataset.

445

446 **Aboveground carbon**

447 For each tree in the montane dataset we used the published allometric equation by ref.⁵⁴ to
448 estimate aboveground biomass. This allometric equation was created using data from directly
449 harvested trees at 58 sites across the tropics, including eight sites with elevation ≥ 800 m asl (range
450 900-3,000m asl including sites in Africa). We then converted this biomass to carbon, assuming that
451 aboveground carbon (AGC, in Mg C ha^{-1}) is 45.6% of aboveground biomass⁵⁵. AGC for each plot was
452 estimated as the sum of the AGC of each living stem, divided by planimetric plot area (in hectares). If
453 field measurements of slope were unavailable, we converted surface to planimetric area extracting
454 slope from the SRTM product. We excluded tree ferns, bamboo and palms, as these were not
455 measured in all plots. Ref.⁵⁴ includes tree diameter, wood mass density and tree height. The best
456 taxonomic match wood density of each stem was extracted from a global database^{56,57} following
457 ref.⁵³. For some sites, all trees in a plot had been sampled for height. If this was not the case, but
458 some field measurements of height were available (typically ten stems per diameter class), we
459 constructed a site-specific height-diameter model, using a Weibull equation following ref.⁵⁸. If no
460 field measurements of height were available, we constructed a cluster-specific height-diameter
461 model, using a Weibull equation, as explained in Table S7 in Supplementary Information. The same
462 approach was used to calculate aboveground biomass for lowland forests. For these, height was
463 estimated using a Weibull equation following ref.⁵⁸.

464

465 **Small plots and data subsampling**

466 For 22 sites where plots were small (<0.2 ha), we aggregated plots to groups of about 0.2 ha based
467 on their geographic proximity, elevation, environmental affinity and the co-authors' knowledge of
468 the site, to help reduce the variation among plots at site level. This is because the presence of an
469 extremely large tree in a small plot can result in overestimates of AGC⁵⁹. We investigated if using the
470 aggregated-plot approach affected AGC-stock estimates at the site level, and this was not the case
471 (Extended Data Fig. 2). We also investigated if including small plots affected the continental mean
472 AGC-stock estimates, as small plots have greater edge surface, and there is a tendency of some field
473 teams to include large trees inside plots when laying out the boundaries⁶⁰. Including small plots did
474 not significantly affect our continental mean AGC-stock estimates (Extended Data Fig. 2). We also
475 explored the sensitivity of our continental mean AGC-stock estimates to data subsampling. Data
476 were resampled at different sample sizes either at plot level (sampling with replacement) or at site
477 level (sampling without replacement). The number of plots ($n=226$) and the number of sites ($n=44$)
478 we sampled indicate that our estimates of AGC-stock at the continental level are robust (Extended
479 Data Fig. 1). They are also not affected by the fact that we included plots 800-1,000 m asl (Extended
480 Data Fig. 3).

481

482 **Size classes**

483 For all plots, we computed the proportion of AGC which was distributed in each size-diameter class,
484 using the classes of ref.¹⁵. We also computed stem density, basal area, density of large trees (>70 cm
485 diameter, named SD_{70} in stems ha^{-1}) and Podocarpaceae abundance (in percentage of plot-level
486 basal area).

487

488 **Environmental variables and their effects**

489 Climate variables (temperature annual mean and seasonality, and precipitation mean and
490 seasonality, i.e. Bio1, 4, 12 and 15) were extracted from WorldClimV2⁶¹ at 30 arc-sec (~ 1 -km)
491 resolution. Mean temperature values were adjusted for the difference in elevation between the plot
492 and the wider 1-km grid cell using the lapse rate of $-0.005^\circ\text{C m}^{-1}$. We obtained data on cloud cover
493 from ref.⁶² and lightning frequency (0.1 degree, ~ 11 km) from the LIS very high resolution
494 climatology⁶³. Values for soil variables (cation exchange capacity, CEC, representing soil fertility, and
495 percentage clay representing soil texture) were extracted from SoilGrids⁶⁴ (~ 1 -km resolution) and a
496 depth-weighted mean taken for values from 0 to 30 cm depth to give a single value of each soil
497 variable per plot. Elevation was obtained from SRTM (at 3 arc-second resolution, ~ 90 m).

498 Topographic metrics were calculated from elevation data using the terrain function in the raster R
499 package. These were slope and topographic position index (TPI). TPI is the difference between the
500 elevation of the plot and the mean value of the eight surrounding grid cells – positive values indicate
501 locally high locations and negative values indicate locally low locations. Where small plots were
502 aggregated for analysis, environmental variables were extracted for the ungrouped plot locations,
503 and then an area-weighted mean taken to obtain a plot-level value.

504

505 **Elephant and conifer effects on AGC-stocks**

506 For the current elephant presence in the AfriMont plots, we created a binary variable
507 (presence/absence) based on co-authors knowledge of elephant ranges and elevation distribution at
508 each site as of 2019. Co-authors estimated that elephants were present in 2019 in 54 plots in 12
509 sites in five countries (see Table S5). For all plots which had at least one individual in the
510 Podocarpaceae family (47 plots, 16 sites, 7 countries), we computed the contribution of
511 Podocarpaceae to plot basal area and AGC-stock in terms of percentages.

512

513 **Estimating forest cover and loss**

514 We obtained estimates of forest cover and loss in the years 2000 through to 2018, using the ‘loss
515 year’ dataset of the Global Forest Change database, version 1.6 (ref.³⁸). To exclude plantation
516 forests, ‘dry’ forests (e.g. miombo woodland) and degraded forests, we applied the ‘primary humid
517 forest’ mask developed by ref.³⁹. We distinguished montane from lowland forests using an
518 elevational cut-off of 800-m elevation, using the SRTM v3 product at 1 arc-sec resolution (snapping
519 to the ref.³⁸ grid of the same resolution). Where there were gaps in the 1 arc-sec SRTM product, we
520 filled these using a 1 arc-sec bilinear interpolation of the (gapless) 3 arc-sec SRTM product. Areal
521 estimates of forest cover and loss were calculated at 30-m resolution using the Africa Sinusoidal
522 projection. To estimate future forest loss by year 2030, we extrapolated absolute country-level
523 deforestation rates for the period 2000-2018 (in ha per year).

524

525 **Investigating AfriMont representativeness**

526 To quantify AfriMont sampling effort within the montane forest biome in Africa, we used the map of
527 tropical montane forest extent (see above) and calculated the amount of remaining forest in each 1-
528 degree grid-cell. By dividing the area sampled in the AfriMont dataset by the proportion of this
529 biome in a grid-cell, we calculated the expected sampling intensity if sampling was proportional to
530 remaining forest extent. To assess how representative our plot network was of the environmental
531 conditions of the wider tropical montane forest biome in Africa, we extracted the environmental
532 data (climate and soil variables presented above) at ~1-km resolution from grid-cells that contained
533 montane forest. We then visually compared the distribution of each variable in our dataset to its
534 distribution across the biome (Extended Data Fig. 7).

535

536 **AfriMont vs global AGC maps**

537 We extracted alternative AGC estimates for the AfriMont plots (unaggregated, n=666) from four
538 different sources: Harris et al. (ref.⁶⁵) (30-m resolution, dated 2000), the ESA CCI Biomass map⁶⁶
539 (100-m resolution, 2017), Saatchi, et al. (ref.⁶⁷) (1-km resolution, 2007/8) and Avitabile et al. (ref.⁶⁸)
540 (1-km resolution, circa 2000-2010). Most of the AfriMont plots were sampled between 2000 and
541 2019 (Table S5). Where the plots were found within a single map pixel, we extracted that value.
542 Where plots were larger than the pixel size, we averaged the values from the surrounding pixels
543 weighted according to the proportion of the pixel that was in the plot.

544

545 **Statistical analysis**

546 Data were analysed using linear mixed-effects models, with site as a random effect. Site was
547 included as a random intercept in all models, and as a random slope where relationships were
548 assessed against elevation. Allowing the slope of the elevation effect to vary amongst sites in this

549 way captures the *a priori* expectation for slopes to differ among sites, for example due to mass
550 elevation effects. The effect of plot size on variation was accounted for by weighting observations by
551 a power transformation of plot size; this was estimated during model fitting using the varPower
552 function in the nlme R package (ref.⁶⁹), and then models refitted using the lme4 R package (ref.⁷⁰)
553 using these estimated weights. Confidence intervals and *P*-values for mixed effects models
554 parameters were estimated by bootstrapping models (1,000 iterations) using the
555 bootstrap_parameters function in the parameters R package (ref.⁷¹). AGC-stocks, stem density and
556 SD₇₀ were natural-log transformed (a small constant was added to SD₇₀ before log transforming to
557 avoid log-transforming zeros) to meet assumptions of normality and avoid heteroscedacity. Likewise,
558 the proportional contribution of each size class was square-root transformed. Differences in AGC-
559 stocks between all combinations of lowland and montane forests amongst continents were assessed
560 using Tukey post-hoc tests implemented in the multcomp R package (ref.⁷²). Relationships between
561 AGC-stocks and environmental variables were investigated by fitting all subsets of the full model
562 with all environmental covariates and averaging the best supported ($\Delta AIC < 4$) models (using dredge
563 and model.avg functions in the MuMIn R package (ref.⁷³)). We used these relationships with climate
564 and soil to predict AGC-stocks in each 1-km grid cell containing montane forests (holding
565 topographic variables at their dataset wide mean), and then took the forest-area weighted mean of
566 these to obtain a single mean for the tropical montane forest biome in Africa. Differences in AGC-
567 stocks between plots with and without elephants were tested using t-test with AGC-stocks natural-
568 log transformed. We investigated if Podocarpaceae abundance (in terms of basal area) and plot
569 AGC-stocks were significantly correlated using Spearman's rank correlation coefficient. To
570 investigate if sampling design affected AfriMont AGC-stock estimates we used ANOVA to test
571 whether site-level mean AGC-stocks differed according to the sampling strategy used to establish
572 plots at that site. To explore the relationship between AfriMont AGC-stock estimates and global
573 maps, and among these global maps, we used Spearman's rank correlation test.

574

575 **References Methods**

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750 A.C-S. conceived the study and assembled the AfriMont dataset. A.C-S. and M.J.P.S. analysed the
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755

756 **Competing interests** The authors declare no competing interests.

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758 **Additional information**

759 Supplementary information is available for this paper at XX (to be added)

760 Correspondence and requests for materials should be addressed to A. C-S.

761 Reprints and permissions information are available at XX (to be added)

762

763 **Data availability**

764 Source data to generate figures and tables are available from:

765 https://doi.org/10.5521/forestplots.net/2021_5

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767 **Code availability**

768 R code to generate figures and tables is available from:

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857

858 **Extended Data**

859

860 **Extended Data Fig. 1 | Sensitivity of mean aboveground carbon stock estimates to data**

861 **subsampling.** AfriMont plot data were resampled at different sample sizes either at plot level
862 (sampling with replacement) or at site level (sampling without replacement). $N = 1,000$ resamples
863 for each sample size.

864

865 **Extended Data Fig. 2 | Effect of plot area, aggregation procedure and plot design on estimates of**

866 **aboveground carbon stocks across the AfriMont plot network.** (a) Relationship between
867 aboveground carbon stocks and plot area of plots prior to aggregation. The red line shows the fit of a
868 locally weighted regression model (span = 0.75) relating these variables, with dashed lines showing
869 the standard errors. (b) Variation in aboveground carbon stocks using either all plots prior to
870 aggregation (unaggregated), plots prior to aggregation but excluding those < 0.2 ha (unaggregated, >
871 0.2 ha) or the aggregated plots used in the main analyses (aggregated). (c) Effects of plot design on
872 aboveground carbon stocks (each site represents one dot). Sampling strategies include random or
873 stratified random, plots positioned along transects, plots established within elevation bands,
874 subjective measures such as choosing an area of forest considered representative of the wider area,
875 and other strategies (one plot sampled per site or unclear strategy). Carbon stocks (log-transformed)
876 did not differ significantly between sites with different sampling strategies (ANOVA: $F_{4,39} = 0.432$, P
877 = 0.785). For specific site information see Table S5.

878

879 **Extended Data Fig. 3 | Robustness of differences in tropical montane forest aboveground carbon**

880 **(AGC) stocks among continents based on plot networks to differences in elevation.** (a) Elevations
881 of montane forests plots sampled in each continent. Violin plots show the distribution of data, with
882 boxplots showing the median and interquartile range of elevation in each continent. (b) Effect of
883 removing submontane plots (800-1,000 m asl) and high elevation plots (> 2,200 m asl, approximately
884 the upper quartile of elevations for the African montane plot dataset) on AGC-stocks in montane
885 forests sampled by plot networks in each continent. Mean AGC-stocks and 95% confidence intervals
886 are shown as estimated by models using i) all data, ii) excluding plots 800-1,000 m, and iii) restricting
887 plots to 1,000-2,200 m. Means for all plots differ from the analysis in Fig. 1 as literature plots without
888 elevation data (plots in Colombia) were excluded from this analysis. Point symbols are proportional
889 to square-root plot area. $N = 324$ plots.

890

891 **Extended Data Fig. 4 | Relationship between aboveground carbon (AGC) stocks and elevation for**

892 **tropical montane forests in each continent based on plot networks.** Dashed lines show
893 relationships from a linear mixed-effects model of log-transformed AGC-stocks as a function of
894 elevation, continent and their interaction. Site was included as a random effect, and AGC-stock –
895 elevation relationships allowed to vary among sites. Lines show fitted slopes across sites. Neither the
896 overall relationship between elevation and AGC-stocks (slope = -0.039 [95% CI = -0.127 – 0.057], P =
897 0.420) nor interactions between elevation and continent (Southeast Asia, change in slope = -0.074 [-
898 0.294 – 0.149], P = 0.503; Neotropics, change in slope = 0.006 [-0.132 – 0.149], P = 0.913) are
899 statistically significant. $N = 324$ plots.

900

901 **Extended Data Fig. 5 | Environmental drivers of aboveground carbon stocks across the AfriMont**

902 **plot network.** Coefficients are from a linear mixed-effects model with site as a random intercept.

903 Results are following all-subsets regression and model averaging, in which variables that do not
904 appear in well supported models are given coefficients of zero, leading to shrinkage in model
905 coefficients. Statistically significant relationships ($P < 0.05$) are indicated with asterisks. TPI refers to
906 topographic position index (positive values indicate higher than surroundings, negative values
907 indicate lower than surroundings).

908

909 **Extended Data Fig. 6 | Expected sampling effort if effort was distributed in proportion to the area**
910 **of tropical montane forest biome in Africa.** Data are summarised at 1-degree resolution. Upward
911 triangles show grid-cells where AfriMont sampling effort is more than double expected effort,
912 downward triangles show grid-cells where AfriMont sampling effort is less than half expected effort.
913 Circles denote AfriMont sampling effort being between half and double expected effort. The extent
914 of the tropical montane forest biome was defined as closed-canopy forests ≥ 800 m asl in December
915 2018, extracted from ref.³⁸ and clipped to 'primary humid forest' using ref.³⁹. This grided map differs
916 from Fig. 4 as numerous grids have very little tropical montane forest.

917

918 **Extended Data Fig. 7 | Differences in the environmental conditions sampled by the AfriMont plot**
919 **network and the tropical montane forest biome in Africa.** The extent of the biome was defined as
920 closed-canopy forests ≥ 800 m asl in December 2018, extracted from ref.³⁸ and clipped to 'primary
921 humid forest' using ref.³⁹. Environmental variables for the biome were extracted at ~ 1 -km
922 resolution.

923

924 **Extended Data Fig. 8 | Differences in aboveground carbon (AGC) stocks in AfriMont plots located in**
925 **montane forests with and without elephants.** (a) Differences across all plots. AGC-stocks are
926 statistically significantly lower in forests with elephants (t -test, $t = 3.5$, $df=83.5$, $P = 0.001$). (b)
927 Differences in countries where elephants are present in at least one of the montane sites studied.
928 Black squares show means in each country in forests with or without elephants – solid lines denote
929 statistically significant differences (t -tests, $P < 0.05$). Elephant presence in 2019 was estimated by co-
930 authors (see Table S5).

931

932 **Extended Data Fig. 9 | Relationship between aboveground carbon (AGC) stocks and**
933 **Podocarpaceae.** (a) Relationship between AGC-stocks and Podocarpaceae basal area across plots in
934 the AfriMont network, expressed as a percentage of total plot basal area. These variables are not
935 significantly correlated ($r_s = 0.083$, $n = 226$, $P = 0.212$). (b) Distribution of plots with at least 20%
936 basal area of Podocarpaceae (black points) in relation to elevation and AGC-stocks. AGC-stocks are
937 not significantly related to elevation or Podocarpaceae basal area (Linear mixed effects model, $P =$
938 0.152 and 0.132 respectively).

939

940 **Extended Data Fig. 10 | Within country variation in aboveground carbon stocks based on the**
941 **AfriMont plot network.** Error bars show means and 95% confidence intervals estimated by linear
942 mixed-effects models. Modelled means not shown for countries with fewer than five plots. Point size
943 is proportional to plot area.

944

945

946







