UNIVERSITY *of York*

This is a repository copy of *High aboveground carbon stock of African tropical montane forests*.

White Rose
university consortium
Universities of Leeds, Sheffield & York

eprints@whiterose.ac.uk
https://eprints.whiterose.ac.uk/

1   **High above-ground carbon stock of African tropical montane forests**
2
3   Aida Cuni-Sanchez[1,2*], Martin J.P. Sullivan[3,4], Phil J. Platts[1,5], Simon L. Lewis[4,6], Rob Marchant[1], Gérard
4   Imani[7], Wannes Hubau[8,9], Iveren Abiem[10,11], Hari Adhikari[12], Tomas Albrecht[13,14], Janne Altman[15],
5   Christian Amani[7], Abreham B. Aneseyee[16,17], Valerio Avitabile[18], Lindsay Banin[19], Rodrigue
6   Batumike[20], Marijn Bauters[21],Hans Beeckman[8], Serge K. Begne[4,22], Amy C. Bennett[4], Robert
7   Bitariho[23], Pascal Boeckx[21], Jan Bogaert[24], Achim Bräuning[25], Franklin Bulonvu[26], Neil D. Burgess[27],
8   Kim Calders[28], Colin Chapman[29-31], Hazel Chapman[11,33], James Comiskey[34], Thales de Haulleville[35],
9   Mathieu Decuyper[36,37], Ben DeVries[38], Jiri Dolezal[15,39], Vincent Droissart[22,40], Corneille Ewango[41],
10   Senbeta Feyera[42], Aster Gebrekristos[43], Roy Gereau[44], Martin Gilpin[4], Dismas Hakizimana[45], Jefferson
11   Hall[46], Alan Hamilton[47], Olivier Hardy[48], Terese Hart[49], Janne Heiskanen[12,50], Andreas Hemp[51], Martin
12   Herold[37], Ulrike Hiltner[52,53], David Horak[54], Marie-Noel Kamdem[22], Charles Kayijamahe[55], David
13   Kenfack[46], Mwangi J. Kinyanjui[56], Julia Klein[57], Janvier Lisingo[41], Jon Lovett[4], Mark Lung[58], Jean-Remy
14   Makana[59], Yadvinder Malhi[60], Andrew Marshall [1,61,62], Emanuel H. Martin[63], Edward T.A. Mitchard[64],
15   Alexandra Morel[65], John T. Mukendi[8], Tom Muller[66], Felix Nchu[67], Brigitte Nyirambangutse[68,69],
16   Joseph Okello[21,70,71], Kelvin S.-H. Peh[72,73], Petri Pellikka[12,74], Oliver L. Phillips[4], Andrew Plumptre[75], Lan
17   Qie[76], Francesco Rovero[77,78], Moses N. Sainge[79], Christine B. Schmitt[80,81], Ondrej Sedlacek[54], Alain S.K.
18   Ngute[61,82], Douglas Sheil[83], Demisse Sheleme[84], Tibebu Y. Simegn[85], Murielle Simo-Droissart[22],
19   Bonaventure Sonké[22], Teshome Soromessa[16], Terry Sunderland[86,87], Miroslav Svoboda[88], Hermann
20   Taedoumg[89,90], James Taplin[91], David Taylor[92], Sean C. Thomas[93], Jonathan Timberlake[94], Darlington
21   Tuagben[95], Peter Umunay[96], Eustrate Uzabaho[55], Hans Verbeeck[28], Jason Vleminckx[97], Göran Wallin[69],
22   Charlotte Wheeler[64], Simon Willcock[98,99], John T. Woods[100], Etienne Zibera[68]
23
24   **Abstract**
25   Tropical forests store 40-50% of terrestrial vegetation carbon[1]. Spatial variations in aboveground live
26   tree biomass carbon (AGC) stocks remain poorly understood, in particular in tropical montane
27   forests[2]. Because of climatic and soil changes with increasing elevation[3], AGC stocks are lower in
28   tropical montane compared to lowland forests[2]. 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   Network[4] and about 70% and 32% higher than averages from plot networks in montane[2,5,6] and
33   lowland[7] forests in the Neotropics, respectively. Notably, our results are two-thirds higher than the
34   IPCC default values for these forests in Africa[8]. We find that the low stem density and high
35   abundance of large trees of African lowland forests[4] 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

Main text

Tropical forests cover less than 10% of the global land area yet store 40–50% of terrestrial vegetation carbon[1] and contribute more than one third of primary productivity[11] so are a key component of the global carbon cycle[12,13]. There is substantial variation in carbon stocks across the biome, with lowland forests in Africa and Borneo storing more carbon per unit area than lowland forests in the Neotropics[4,7]. This variation arises partly from structural differences: the signature feature of African forests is their low stem density but relatively high abundance of large trees (>70 cm diameter) which store large quantities of carbon, while Bornean forests are characterised by high stem density and basal area[4,14,15].

Despite increased understanding of biogeographic differences in tropical lowland forests, patterns of spatial variation in carbon stocks remain poorly understood in the 880,000 km^2 of tropical montane forests located ≥ 1,000 m asl[2]. Montane forests are expected *a priori* to have lower aboveground live tree biomass carbon (AGC) stocks than lowland forests because (1) temperature decreases with increasing elevation, reducing net primary productivity and slowing nutrient recycling, (2) long periods of cloud immersion in montane forests suppresses productivity, (3) soil waterlogging slows nutrient recycling and (4) high epiphyte load, local wind exposure in crests and nutrient-limited soils limit tree size and increase investment in roots over shoots[3]. While forest inventory plots provide some support for these assumptions[2] data from African mountain regions are exceptionally sparse. Indeed, in the most recent IPCC guidelines, there is no specific AGC default value for old-growth montane forests in Africa: the value given of 89.3 Mg C ha^{-1} is simply a mean of secondary and old-growth forests found ≥ 1,000 m asl[8]. Mountain areas also pose special challenges for remote-sensing approaches for estimating carbon stocks, as radar data are affected by geometric distortions[16] while steep slopes bias spaceborne LiDAR estimates towards overestimating canopy height[17]. These issues are reflected in the limited correlation between estimates of AGC-stocks at mountain locations from different recent remote-sensing derived carbon maps (Supplementary Information Table S1).

Better understanding of montane carbon stocks is important for many African countries, particularly in eastern Africa where montane forests represent most of the extant evergreen old-growth forest cover. Quantifying carbon stocks in these ecosystems is critical for estimating national carbon losses from deforestation and forest degradation[18]. Quantifying carbon stocks in old-growth montane forests also serves to constrain potential carbon uptake by restored natural forests, given the high commitment of most African nations to the Bonn Challenge effort to restore 150 million ha of degraded and deforested lands by 2020 (see Table 1), and 350 million by 2030.

Here we measured, compiled and analysed an unprecedented dataset of 226 plot inventories spanning 44 sites in 12 African countries, covering most major mountain regions on the continent (the "AfriMont" dataset). Plots range from 800 to 3,900 m asl to include submontane forests (800-1,000 m asl) in smaller mountains closer to the ocean[19,20]. For all plots, stem diameter and species were recorded for each tree ≥10 cm diameter at breast height (or above buttress) following standard methods[21]. Tree height was sampled in 23 montane sites, allowing variation in height-diameter allometry to be incorporated into the calculation of aboveground biomass. A total of 72,336 stems with diameter ≥10 cm were measured. For each tree, we computed AGC (in Mg C ha^{-1}) according to standard procedures (see methods).

We find that the mean plot-level AGC-stock across sampled African tropical montane forests is 149.4 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 estimates are robust to subsampling our dataset (Extended Data Fig. 1) and excluding small plots (Extended Data Fig. 2) and are not affected by the sampling strategy used to establish plots in each study site (Extended Data Fig. 2). Comparing our dataset to previous syntheses of montane[2,5,6] and lowland[7] 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).

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 tropics[4]) 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 m^{2}ha^{-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≥0.24, Table S3),
114   although greater variation among plots is observed in montane forests (Fig. 2).

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 effect[22] (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).

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   regions[23], leading to regression dilution[24], 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.

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   nutrients[25]. 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 forests[4]. For
163   example, tropical cyclones are largely absent in mainland Africa (except in Mozambique[28]) and lava
164   flows are limited even in the active volcano of Mt Cameroon[29]. 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 Asia[30]. If forests have been ecologically stable over evolutionary timescales, tree species
168   may be adapted to grow slowly but potentially reaching great sizes[31]. On Mt Kilimanjaro
169   *Entandrophragma* individuals reach enormous heights and ages[32]. This low frequency of large-scale
170   abiotic disturbances contrasts with the Andes and several mountains in Southeast Asia (e.g. Barisian
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 conifers[33]. 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 resources[34]. Podocarpaceae can be found in montane forests across the tropics[35]. Despite
179   having fewer species in Africa than in other continents[36], 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   Neotropics[37], 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 Kenya[40]. 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 runoff[9]. They also regulate local temperatures[41] and provide
206 numerous other services to people in the surrounding landscapes[9]. 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 Congo[42]. Protected areas are known to help
210 reduce deforestation in the tropics[43]. 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 Cameroon[44]
216 and in the Usambara Mts, Tanzania[45]).
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 accumulation[46]. 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.
241
242

Figures main document

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

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

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

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

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.
295
296

References

1. Erb, K., et al. Unexpectedly large impact of forest management and grazing on global vegetation biomass. *Nature* **553**, 73–76 (2018).
2. Spracklen, D.V. & Righelato, R. Tropical montane forests are a larger than expected global carbon store. *Biogeosciences* **11**, 2741-2754 (2014).
3. Fahey, T. J., Sherman, R. E. & Tanne, E. V. J. Tropical montane cloud forest: environmental drivers of vegetation structure and ecosystem function. *J. Trop. Ecol.* **32**, 355–367 (2016).
4. Lewis, S. L. et al. Above-ground biomass and structure of 260 African tropical forests. *Phil. Trans. R. Soc. Lond. B* **368**, 20120295 (2013).
5. Vilanova, E. et al. Environmental drivers of forest structure and stem turnover across Venezuelan tropical forests. *PLoS ONE* **13**(6): e0198489 (2018).
6. Alvarez-Davila, E. et al. Forest biomass density across large climate gradients in northern South America is related to water availability but not with temperature. *PLoS ONE* **12**(3): e0171072 (2017).
7. Sullivan, M. J. P., et al. Long-term thermal sensitivity of Earth's tropical forests. *Science* **368**, 869–874 (2020).
8. IPCC. Chapter 4: Forest land. In: D. Blain, F. Agus, M. A. Alfaro & H. Vreuls (Eds.), 2019 Refinement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories. (Vol. 4): Agriculture, Forestry and Other Land Use (p. 68)(2019).
9. United Nations Environment Programme (UNEP) African Mountains Atlas. UNEP, Nairobi, Kenya (2014).
10. Rahbek, C., et al. Humboldt's enigma: What causes global patterns of mountain biodiversity? *Science* **365**, 1108–1113 (2019).
11. Pan, Y. et al. A large and persistent carbon sink in the world's forests. *Science* **333**, 988–993 (2011).
12. Booth, B. B. B. et al. High sensitivity of future global warming to land carbon cycle processes. *Environ. Res. Lett.* **7**, 024002 (2012).
13. Hubau, W., et al. Asynchronous carbon sink saturation in African and Amazonian tropical forests. *Nature* **579**, 80–87 (2020).
14. Feldpausch, T. R. et al. Tree height integrated into pantropical forest biomass estimates. *Biogeosciences* **9**, 3381–3403 (2012).
15. Bastin, J.-F., et al. Pan-tropical prediction of forest structure from the largest trees. *Global Ecol. Biogeogr.* **27**, 1366–1383 (2018).
16. CCI BIOMASS Product User Guide Year 1 Version 1.0. (2019) https://climate.esa.int/sites/default/files/biomass_D4.3_Product_User_Guide_V1.0.pdf
17. Lefsky, M. A., Keller, M., Pang, Y., de Camargo, P. & Hunter, M. O. Revised method for forest canopy height estimation from the Geoscience Laser Altimeter System waveforms. J. *Appl. Remote Sens.* **1**, 013537 (2007).
18. Willcock, S., et al. Quantifying and understanding carbon storage and sequestration within the Eastern Arc Mountains of Tanzania, a tropical biodiversity hotspot. *Carbon Balance Manage.* **9**, 2 (2014).
19. Bussmann, R.W. Vegetation zonation and nomenclature of African Mountains – An overview. *Lyonia* **11**, 41–66 (2006).
20. Hamilton, A. Vegetation, climate and soil, altitudinal relationships on the East Usambara Mountains of Tanzania. *J. E. Afr. Nat. Hist.* **87**, 1-5 (1998).
21. Phillips, O., Baker, T., Brienen, R. & Feldpausch, T. RAINFOR field manual for plot establishment and remeasurement. http://www.rainfor.org/upload/ManualsEnglish/RAINFOR_field_manual_version_2016.pdf (Univ. Leeds, 2016).
22. Jarvis, A. & Mulligan, M., The climate of cloud forests. *Hydrol. Process.* **25**, 327–343 (2011).

347 23. Platts, P.J., Omeny, P.A. & Marchant, R. AFRICLIM: high-resolution climate projections for
348   ecological applications in Africa. *Afr. J. Ecol.* **53**, 103–108 (2015).
349 24. McInerny, G. J., Purves, D. W. Fine-scale environmental variation in species distribution
350   modelling: Regression dilution, latent variables and neighbourly advice. *Methods Ecol. Evol.*
351   **2**, 248–257 (2011).
352 25. Poulsen, J.R., et al. Ecological consequences of forest elephant declines for Afrotropical
353   forests. *Conserv. Biol.* **32**, 559–567 (2018).
354 26. Berzaghi, F., et al. Carbon stocks in central African forests enhanced by elephant
355   disturbance. *Nat. Geosci.* **12**, 725–729 (2019).
356 27. Enquist, B.J., et al. The megabiota are disproportionately important for biosphere
357   functioning. *Nat. Commun.* **11**, 699 (2020).
358 28. Lin, T.-C., Hogan, J.A. & Chang, C.T. Tropical Cyclone Ecology: A Scale-Link Perspective.
359   *Trends Ecol. Evol.* **35**, 594–604 (2020).
360 29. Favalli, M., et al. Lava flow hazard and risk at Mt. Cameroon volcano. *Bull. Volcanol.* **74**, 423–
361   439 (2012).
362 30. Stanley, T. & Kirschbaum, D.B. A heuristic approach to global landslide susceptibility
363   mapping. *Nat. Hazards* **87**, 145–164 (2017).
364 31. Lovett, J. C. Elevational and latitudinal changes in tree associations and diversity in the
365   Eastern Arc mountains of Tanzania. *J. Trop. Ecol.* **12**, 629–650 (1996).
366 32. Hemp, A., et al. Africa's highest mountain harbours Africa's tallest trees. *Biodiv. Conserv.* 26,
367   103–113 (2016).
368 33. Culmsee, H., Leuschner, C., Moser, G. & Pitopang, R., Forest aboveground biomass along an
369   elevational transect in Sulawesi, Indonesia, and the role of Fagaceae in tropical montane rain
370   forests. *J. Biogeogr.* **37**, 960–974 (2010).
371 34. Enright, N.J. & Ogden, J. The southern conifers - a synthesis. Ecology of the southern conifers
372   (ed. by N.J. Enright & Hill R.S.), pp. 271–287. Melbourne University Press, Melbourne (1995).
373 35. Neale, D. B. & Wheeler, N. C. The Conifers. In: The Conifers: Genomes, Variation and
374   Evolution (eds. Neale, D. B. & Wheeler, N. C.) pp 1–21. Springer International Publishing
375   (2019).
376 36. Mill, R. R. Towards a Biogeography of the Podocarpaceae. In IV International Conifer
377   Conference, R. R. Mill, ed. *Acta Hort.* **615**, 137–147 (2003).
378 37. Helmer, E.H., Gerson, E.A., Baggett, L.S., Bird, B.J., Ruzycki, T.S. & Voggesser, S.M.
379   Neotropical cloud forests and paramo to contract and dry from declines in cloud immersion
380   and frost. PLoS ONE **14**(4): e0213155 (2019).
381 38. Hansen, M. C., et al. High-Resolution Global Maps of 21st-Century Forest Cover Change.
382   *Science* **342**, 850-853 (2013).
383 39. Turubanova, S., Potapov, P., Tyukavina, A. & Hansen M. Ongoing primary forest loss in Brazil,
384   Democratic Republic of the Congo, and Indonesia. *Environ. Res. Lett.* **13**, 074028 (2018).
385 40. Pellikka, P. K. E., Lötjönen, M., Siljander, M. & Lens, L. Airborne remote sensing of
386   spatiotemporal change (1955–2004) in indigenous and exotic forest cover in the Taita Hills,
387   Kenya. *Int. J. Appl. Earth Obs.* **11**, 221–232 (2009).
388 41. Zeng, Z. et al. Deforestation-induced warming over tropical mountain regions regulated by
389   elevation. *Nat. Geosci.* (2020). https://doi.org/10.1038/s41561-020-00666-0
390 42. Spira, C., Kirkby, A., Kujirakwinja, D. & Plumptre, A. J. The socio-economics of artisanal
391   mining and bushmeat hunting around protected areas: Kahuzi– Biega National Park and
392   Itombwe nature reserve, eastern Democratic Republic of Congo. *Oryx* **53**, 136–144(2017).
393 43. Bebber, D.P. & Butt, N. Tropical protected areas reduced deforestation carbon emissions by
394   one third from 2000-2012. *Sci. Rep.* **7**, 14005 (2017).
395 44. Tegha, K. C. & Sendze, Y. G., Soil organic carbon stocks in Mt Cameroon National Park under
396   different land uses. *J. Ecol. Nat. Environ.* **8**, 20–30, (2016).

397 45. Munishi, P.K.T. & Shear, T.H. Carbon storage in afromontane rain forests of the eastern arc
398   mountains of Tanzania: their net contribution to atmospheric carbon. *J. Trop. For. Sci.* **16**,
399   78–98 (2004).
400 46. Wheeler, C.E., et al. Carbon sequestration and biodiversity following 18 years of active
401   tropical forest restoration. *Forest Ecol. Manage.* **373**, 44–55 (2016).
402 47. Avitabile, V., Baccini, A., Friedl, M.A. & Schmullius, C. Capabilities and limitations of Landsat
403   and land cover data for aboveground woody biomass estimation of Uganda. *Remote Sens.*
404   *Environ.* **117**, 366–380 (2012).
405 48. Aneseyee, B A., Soromessa, T. & Belliethathan, S. Carbon Sock of Gambella National Park:
406   Implication for Climate Change Mitigation. *Int. J. Adv. Life Sci.* **35**, 41–56 (2015).
407 49. Lisboa, S.N., et al. Biomass allometric equation and expansion factor for a mountain moist
408   evergreen forest in Mozambique. *Carbon Balance Manage.* **13**, 23 (2018).
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 network[52], 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 ≥800m 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 biomass[55]. 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 AGC[59]. 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 boundaries[60]. 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 WorldClimV2[61] 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°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　climatology[63]. Values for soil variables (cation exchange capacity, CEC, representing soil fertility, and
495　percentage clay representing soil texture) were extracted from SoilGrids[64] (~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 map[66]
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 SD_{70} were natural-log transformed (a small constant was added to SD_{70} 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 (ΔAIC<4) models (using dredge
563 and movel.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.

References Methods

50. Lopez-Gonzalez, G., Lewis, S. L., Burkitt, M. & Phillips, O. L. ForestPlots.net: a web application and research tool to manage and analyse tropical forest plot data. *J. Veg. Sci.* **22**, 610–613 (2011).
51. Lopez-Gonzalez, G., Lewis, S. L., Burkitt, M., Baker, T. R. & Phillips, O. L. ForestPlots.net Database http://www.forestplots.net (2009).
52. Cavanaugh, K., et al. Carbon storage in tropical forests correlates with taxonomic diversity and functional dominance on a global scale. *Global Ecol. Biogeogr.* **23**, 563-573 (2014).
53. Lewis, S. L., et al. 2009 Increasing carbon storage in intact African tropical forests. *Nature* **457**, 1003–1006 (2009).
54. Chave, J. et al. Improved allometric models to estimate the aboveground biomass of tropical trees. *Glob. Change Biol.* **20**, 3177–3190 (2014).
55. Martin, A. R., Doraisami, M. & Thomas, S. C. Global patterns in wood carbon concentration across the world's trees and forests. *Nat. Geosci.* **11**, 915–920 (2018).
56. Chave, J. et al. Towards a worldwide wood economics spectrum. *Ecol. Lett.* **12**, 351–366 (2009).
57. Zanne, A. E. et al. Towards a Worldwide Wood Economics Spectrum https://doi.org/10.5061/dryad.234 (Dryad Digital Repository, 2009).
58. Feldpausch, T. R. et al. Tree height integrated into pantropical forest biomass estimates. *Biogeosciences* **9**, 3381–3403 (2012).
59. Clark, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q., Thomlinson, J.R., Ni, J. & Holland, E.A. Net primary production in tropical forests: an evaluation and synthesis of existing field data. *Ecol. Appl.* **11**, 371–384 (2001).

598   60. Paul, T.S.H., Kimberley, M.O. & Beets, P.N. Thinking outside the square: Evidence that plot
599   shape and layout in forest inventories can bias estimates of stand metrics. *Methods Ecol.*
600   *Evol.* **10**, 381–388 (2019).
601   61. Fick, S.E. & Hijmans, R.J., WorldClim 2: new 1-km spatial resolution climate surfaces for
602   global land areas. *Int. J. Climatol.* **37**, 4302–4315 (2017).
603   62. Wilson, A.M. & Jetz, W. Remotely sensed high-resolution Global Cloud Dynamics for
604   predicting ecosystem and biodiversity distributions. *PLoS Biol* **14**(3): e1002415 (2016).
605   63. Albrecht, R., Goodman, S., Buechler, D., Blakeslee R. & Christian, H. LIS 0.1 Degree Very High
606   Resolution Gridded Lightning Climatology Data Collection. Data sets available online
607   [https://ghrc.nsstc.nasa.gov/pub/lis/climatology/LIS/] from the NASA Global Hydrology
608   Resource Center DAAC, Huntsville, Alabama, U.S.A. doi:
609   http://dx.doi.org/10.5067/LIS/LIS/DATA306
610   64. Hengl, T., et al. SoilGrids250m: Global gridded soil information based on machine learning.
611   *PLoS ONE* **12**(2): e0169748 (2017).
612   65. Harris, N. L. et al. Global maps of twenty-first century forest carbon fluxes. *Nat. Clim. Change*
613   **11**, 234–240 (2021).
614   66. Santoro, M. & Cartus, O. ESA Biomass Climate Change Initiative (Biomass_cci): Global
615   datasets of forest above-ground biomass for the year 2017, v1. Centre for Environmental
616   Data Analysis, 2019. doi:10.5285/bedc59f37c9545c981a839eb552e4084
617   67. Saatchi, S., et al. Benchmark map of forest carbon stocks in tropical regions across three
618   continents. *PNAS* **108**, 9899-9904 (2011).
619   68. Avitabile, V., et al. An integrated pan-tropical biomass map using multiple reference
620   datasets. *Glob. Change Biol.* **22**, 1406–1420 (2016).
621   69. Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. nlme: Linear and Nonlinear
622   Mixed Effects Models. R package version 3.1-151, https://CRAN (2020).
623   70. Bates, D. Maechler, M., Bolker B. & Walker, S. Fitting Linear Mixed-Effects Models Using
624   lme4. *J. Stat. Softw.* **67**, 1–48 (2015).
625   71. Lüdecke, D., Ben-Shachar, M., Patil, I. & Makowski, D. Parameters: extracting, computing
626   and exploring the parameters of statistical models using R. *J. Open Source Softw* **5**, 2445
627   (2020).
628   72. Hothorn, T., Bretz, F. & Westfall, P. Simultaneous Inference in General Parametric Models.
629   *Biometrical Journal* **50**, 346–363 (2008).
630   73. Barton, K. 2020. MuMIn: Multi-Model Inference. R package version 1.43.17.
631   74. Hakizimana, D., Huynen, M.-C. & Hambuckers, A. Structure and floristic composition of Kibira
632   rainforest, Burundi. *Trop. Ecol.* **57**, 739–749 (2016).
633   75. Sainge, M.N., Lyonga, N.M. & Jailughe, B. Floristic diversify across the Cameroon Mountains:
634   The case of Bakossi National Park and Mt Nlonako. Technical report to the Rufford Small
635   Grant Foundation UK, by Tropical Plant Exploration Group (TroPEG) Cameroon (2018).
636   76. Hořák, D., et al. Forest structure determines spatial changes in avian communities along an
637   elevational gradient in tropical Africa. *J. Biogeodgr.* **46**, 2466–2478 (2019).
638   77. Ngute, A.S.K., et al. Investigating above-ground biomass in old-growth and secondary
639   montane forests of the Cameroon Highlands. *Afr. J. Ecol.* **58**, 503–513 (2020).
640   78. Sainge, M.N., et al. Vegetation, floristic composition and structure of a tropical montane
641   forest in Cameroon. *Bothalia* **49**, 1 (2019).
642   79. Imani, G., et al. Height-diameter allometry and above ground biomass in tropical montane
643   forests: Insights from the Albertine Rift in Africa. *PLoS ONE* **12**, e0179653 (2017).
644   80. Schmitt, C.B., Senbeta, S., Woldemariam, T., Rudner, M. & Denich, M. Importance of regional
645   climates for plant species distribution patterns in moist Afromontane forest. *J. Veg. Sci.* **24**,
646   553–568 (2013).
647   81. DeVries, B., Avitabile, V., Kooistra, L. & Herold, M. Monitoring the impact of REDD+
648   implementation in the UNESCO Kafa Biosphere Reserve, Ethiopia. In Proceedings IEEE

649   International Geoscience and Remote Sensing Symposium (IGARSS 2012), 22-27 July,
650   Munich, Germany (pp. 145–146).
651 82. Hiltner, U., Bräuning, A., Gebrekirstos, A., Huth, A. &Fischer, R. Impacts of precipitation
652   variability on the dynamics of a dry tropical montane forest. *Ecol. Model.* **320**, 92–101
653   (2016).
654 83. Maina, E.W., Odera, P.A. & Kinyanjui, M.J. Estimation of Above Ground Biomass in Forests
655   Using Alos Palsar Data in Kericho and Aberdare Ranges. *Open J. forest.* **7**, 79–96 (2017).
656 84. Cuni-Sanchez, A., et al. New insights on above ground biomass and forest attributes in
657   tropical montane forests. *For. Ecol. Manage.* **399**, 235–246 (2017).
658 85. Kinyanjui, M.J., Latva-Käyrä, P., Bhuwneshwar, P.S., Kariuki, P., Gichu, A. & Wamichwe, K. An
659   inventory of the above ground biomass in the Mau Forest ecosystem, Kenya. *Open J. Ecol.* **4**,
660   619–627 (2014).
661 86. Adhikari, H., Heiskanen, J., Siljander, M., Maeda, E., Heikinheimo, V. & Pellikka, P. K.E.
662   Determinants of aboveground biomass across an Afromontane Landscape Mosaic in Kenya.
663   *Remote Sens*. **9**, 827 (2017).
664 87. Abiem, I. Arellano, G., Kenfack, D. & Hazel, C., Afromontane forest diversity and the role of
665   grassland-forest transition in tree species distribution. *Diversity* **12**, 30 (2020).
666 88. Nyirambangutse, B., Zibera, E., Uwizeye, F.K., Nsabimana, D., Bizuru, E., Pleijel, H., Uddling,
667   J., Wallin, G. Carbon stocks and dynamics at different successional stages in an Afromontane
668   tropical forest. Biogeosciences 14, 1285–1303 (2017).
669 89. Ensslin, A., Rutten, G., Pommer, U., Zimmermann, R., Hemp, A., Fischer, M. Effects of
670   elevation and land use on the biomass of trees, shrubs and herbs at Mount Kilimanjaro.
671   *Ecosphere* **6**, 1–15 (2015).
672 90. Sheil, D., Jennings, S., Savill, P. Long-term permanent plot observations of vegetation
673   dynamics in Budongo, a Ugandan rain forest. *J. Trop. Ecol.* **16**, 865–882 (2000).
674 91. Taylor, D., Hamilton, A.C., Lewis, S.L. & Nantale, G. Thirty-eight years of change in a tropical
675   forest: plot data from Mpanga forest reserve, Uganda. *Afr. J. Ecol.* 46, 655–667 (2008).
676 92. Sheil, D. & Salim, A. Forest tree persistence, elephants, and stem scars. *Biotropica* **36**, 505–
677   521 (2004).
678

748
749   **Author Contributions**

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)

763 **Data availability**
764 Source data to generate figures and tables are available from:
765 https://doi.org/10.5521/forestplots.net/2021_5

767 **Code availability**
768 R code to generate figures and tables is available from:
769 https://doi.org/10.5521/forestplots.net/2021_5

771 **Affiliations**
772 [1]Department of Environment and Geography, University of York, York, UK. [2]Department of
773 International Environmental and Development Studies (NORAGRIC), Norwegian University of Life
774 Sciences, Ås, Norway. [3]Department of Natural Sciences, Manchester Metropolitan University,
775 Manchester, UK. [4]School of Geography, University of Leeds, Leeds, UK. [5]Climate Change Specialist
776 Group, Species Survival Commission, International Union for Conservation of Nature, Gland,
777 Switzerland. [6]University College London, Department of Geography, London, UK. [7]Biology
778 Department, Université Officielle de Bukavu, Bukavu, DRC. [8]Service of Wood Biology, Royal Museum
779 for Central Africa, Tervuren, Belgium. [9]Department of Environment, Laboratory of Wood Technology
780 (Woodlab), Ghent University, Ghent, Belgium. [10]University of Jos, Jos, Nigeria. [11]Nigerian Montane
781 Forest Project, Taraba State, Nigeria. [12]Department of Geosciences and Geography, University of
782 Helsinki, Finland. [13]Department of Zoology, Faculty of Science, Charles University, Prague, Czech
783 Republic. [14]Institute of Vertebrate Biology, Czech Academy of Sciences, Brno, Czech Republic.
784 [15]Institute of Botany of the Czech Academy of Science, Třeboň, Czech Republic. [16]College of Natural
785 and Computational Science, Addis Ababa University, Addis Ababa, Ethiopia. [17]Department of Natural
786 Resource Management, College of Agriculture and Natural Resource, Wolkite University, Wolkite,
787 Ethiopia. [18]European Commission, Joint Research Centre, Ispra, Italy. [19]UK Centre for Ecology &
788 Hydrology, Edinburgh, UK. [20]Université du Cinquantenaire Lwiro, Département de sciences de
789 l'environnement, Kabare, Suk-Kivu, DRC. [21]Isotope Bioscience Laboratory (ISOFYS), Ghent University,
790 Ghent, Belgium. [22]Plant Systematic and Ecology Laboratory, Higher Teachers' Training College,
791 University of Yaoundé I, Yaoundé, Cameroon. [23]Institute of Tropical Forest Conservation, Mbarara
792 University of Science and Technology, Uganda. [24]Biodiversity and Landscape Unit, Gembloux Agro-
793 Bio Tech, Université de Liege, Liège, Belgium. [25]Institut for Geography, Friedrich-Alexander-
794 Universität, Erlangen-Nürnberg, Germany. [26]Institut Supérieur d'Agroforesterie et de Gestion de
795 l'Environnement de Kahuzi-Biega (ISAGE-KB); Département de Eaux et Forêts, Kalehe, DRC. [27]UN
796 Environment World Conservation Monitoring Center (UNEP-WCMC), Cambridge, UK.
797 [28]Computational & Applied Vegetation Ecology (CAVElab), Faculty of Bioscience Engineering, Ghent
798 University, Ghent, Belgium. [29]Department of Anthropology, George Washington University,
799 Washington DC, USA. [30]School of Life Sciences, University of KwaZulu-Natal, Scottsville,
800 Pietermaritzburg, South Africa. [31]Shaanxi Key Laboratory for Animal Conservation, Northwest

801 University, Xi'an, China. [32]International Centre of Biodiversity and Primate Conservation, Dali
802 University, Dali Yunnan, China. [33]University of Canterbury, New Zealand. [34]Inventory & Monitoring
803 Program, National Park Service, Fredericksburg, USA. [35]University of Ghent, Belgium. [36]World
804 Agroforestry (ICRAF), Nairobi, Kenya. [37]Laboratory of Geo-Information Science and Remote Sensing,
805 Wageningen University, Wageningen, the Netherlands. [38]Geography, Environment & Geomatics,
806 University of Guelph, Canada.[39]Faculty of Science, University of South Bohemia, České Budějovice,
807 Czech Republic. [40]AMAP Lab, Université de Montpellier, IRD, CNRS, INRAE, CIRAD, Montpellier,
808 France.[41]Faculté de Gestion de Ressources Naturelles Renouvelables, Université de Kisangani,
809 Kisangani, DRC. [42]College of Development Studies, Addis Ababa University, Ethiopia.
810 [43]Dendrochronology Laboratory, World Agroforestry Centre (ICRAF), Kenya. [44]Missouri Botanical
811 Garden, St. Louis, Missouri, USA. [45]Department of Biology, University of Burundi, Burundi.
812 [46]Smithsonian Institution Forest Global Earth Observatory (ForestGEO), Smithsonian Tropical
813 Research Institute, Washington DC, USA. [47]Kunming Institute of Botany, Kunming, China. [48]Université
814 Libre de Bruxelles, Brussels, Belgium. [49]Division of Vertebrate Zoology, Yale Peabody Museum of
815 Natural History, New Haven, CT, USA. [50]Institute for Atmospheric and Earth System Research, Faculty
816 of Science, University of Helsinki, Finland. [51]Department of Plant Systematics, University of Bayreuth,
817 Germany. [52]Institute for Geography, Friedrich-Alexander-University Erlangen-Nuremberg, Germany.
818 [53]Helmholtz-Centre for Environmental Research (UFZ), Leipzig, Germany. [54]Department of Ecology,
819 Faculty of Science, Charles University, Prague, Czech Republic. [55]International Gorilla Conservation
820 Programme, Musanze, Rwanda. [56]Department of Natural Resources, Karatina University, Kenya.
821 [57]Dept. Ecosystem Science & Sustainability, Colorado State University, Fort Collins, USA.
822 [58]Eco2librium LLC, Boise, USA. [59]Department of Ecology, Université de Kisangani, Kisangani, DRC.
823 [60]Environmental Change Institute, School of Geography and the Environment, University of Oxford,
824 Oxford, UK. [61]Tropical Forests and People Research Centre, University of the Sunshine Coast,
825 Australia. [62]Flamingo Land Ltd., North Yorkshire, UK. [63]College of African Wildlife Management,
826 Mweka, Tanzania. [64]School of GeoSciences, University of Edinburgh, UK. [65]Department of Geography
827 and Environmental Sciences, University of Dundee, Dundee, UK. [66]Independent Botanist, Harare,
828 Zimbabwe. [67]Department of Horticultural Sciences, Faculty of Applied Sciences, Cape Peninsula
829 University of Technology, Bellville, South Africa. [68]Biology Department, University of Rwanda,
830 Rwanda. [69]Department of Biological and Environmental Sciences, University of Gothenburg, Sweden.
831 [70]Mountains of the Moon University, Fort Portal, Uganda. [71]National Agricultural Research
832 Organisation, Mbarara Zonal Agricultural Research and Development Institute, Mbarara, Uganda.
833 [72]School of Biological Sciences, University of Southampton, Southampton, UK. [73]Conservation
834 Science Group, Department of Zoology, University of Cambridge, Cambridge, UK. [74]State Key
835 Laboratory of Information Engineering in Surveying, Mapping and Remote Sensing, Wuhan
836 University, China. [75]Key Biodiversity Areas Secretariat, BirdLife International, Cambridge, UK.
837 [76]School of Life Sciences, University of Lincoln, UK. [77]Department of Biology, University of Florence,
838 Sesto Fiorentino, Italy. [78]Tropical Biodiversity Section, Museo delle Scienze, Trento, Italy. [79]Tropical
839 Plant Exploration Group (TroPEG) Cameroon. [80]Center for Development Research (ZEF), University of
840 Bonn, Germany. [81]Conservation and Landscape Ecology, University of Freiburg, Germany.[82]Applied
841 Biology and Ecology Research Unit, University of Dschang, Dschang, Cameroon. [83]Forest Ecology and
842 Forest Management Group, Wageningen University, Wageningen, The Netherlands. [84]Water and
843 Land Resources Center, Addis Ababa University, Addis Ababa, Ethiopia. [85]African Wildlife Foundation
844 (AWF), Biodiversity Conservation and Landscape Management Program, Simien Mountains National
845 Park, Debark, Ethiopia. [86]Faculty of Forestry, University of British Columbia, Vancouver, Canada.
846 [87]Center for International Forestry Research (CIFOR), Bogor, Indonesia. [88]Department of Forest
847 Ecology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Prague, Czech
848 Republic. [89]Department of Plant Biology, Faculty of Sciences, University of Yaoundé I, Cameroon.
849 [90]Bioversity International, Yaoundé, Cameroon. [91]UK Research & Innovation, UK. [92]Department of
850 Geography, National University of Singapore, Singapore. [93]Institute of Forestry and Conservation,
851 University of Toronto, Toronto, Canada.[94]Biodiversity Foundation for Africa, East Dean, East Sussex,

UK. [95]Forestry Development Authority of the Government of Liberia (FDA), Monrovia, Liberia. [96]School of Forestry and Environmental Studies, Yale University, New Haven, USA. [97]Department of Biological Sciences, Florida International University, Florida, USA. [98]School of Natural Sciences, University of Bangor, Bangor, UK. [99]Rothamsted Research, Harpenden, UK. [100]University of Liberia, Monrovia, Liberia. *corresponding author: a.cuni-sanchez@york.ac.uk

Extended Data

Extended Data Fig. 1 | Sensitivity of mean aboveground carbon stock estimates to data subsampling. AfriMont plot data were resampled at different sample sizes either at plot level (sampling with replacement) or at site level (sampling without replacement). N = 1,000 resamples for each sample size.

Extended Data Fig. 2 | Effect of plot area, aggregation procedure and plot design on estimates of aboveground carbon stocks across the AfriMont plot network. (**a**) Relationship between aboveground carbon stocks and plot area of plots prior to aggregation. The red line shows the fit of a locally weighted regression model (span = 0.75) relating these variables, with dashed lines showing the standard errors. (**b**) Variation in aboveground carbon stocks using either all plots prior to aggregation (unaggregated), plots prior to aggregation but excluding those < 0.2 ha (unaggregated, > 0.2 ha) or the aggregated plots used in the main analyses (aggregated). (**c**) Effects of plot design on aboveground carbon stocks (each site represents one dot). Sampling strategies include random or stratified random, plots positioned along transects, plots established within elevation bands, subjective measures such as choosing an area of forest considered representative of the wider area, and other strategies (one plot sampled per site or unclear strategy). Carbon stocks (log-transformed) did not differ significantly between sites with different sampling strategies (ANOVA: $F_{4,39}$ = 0.432, P = 0.785). For specific site information see Table S5.

Extended Data Fig. 3 | Robustness of differences in tropical montane forest aboveground carbon (AGC) stocks among continents based on plot networks to differences in elevation. (**a**) Elevations of montane forests plots sampled in each continent. Violin plots show the distribution of data, with boxplots showing the median and interquartile range of elevation in each continent. (**b**) Effect of removing submontane plots (800-1,000 m asl) and high elevation plots (> 2,200 m asl, approximately the upper quartile of elevations for the African montane plot dataset) on AGC-stocks in montane forests sampled by plot networks in each continent. Mean AGC-stocks and 95% confidence intervals are shown as estimated by models using i) all data, ii) excluding plots 800-1,000 m, and iii) restricting plots to 1,000-2,200 m. Means for all plots differ from the analysis in Fig. 1 as literature plots without elevation data (plots in Colombia) were excluded from this analysis. Point symbols are proportional to square-root plot area. N = 324 plots.

Extended Data Fig. 4 | Relationship between aboveground carbon (AGC) stocks and elevation for tropical montane forests in each continent based on plot networks. Dashed lines show relationships from a linear mixed-effects model of log-transformed AGC-stocks as a function of elevation, continent and their interaction. Site was included as a random effect, and AGC-stock – elevation relationships allowed to vary among sites. Lines show fitted slopes across sites. Neither the overall relationship between elevation and AGC-stocks (slope = -0.039 [95% CI -0.127 – 0.057], P = 0.420) nor interactions between elevation and continent (Southeast Asia, change in slope = -0.074 [-0.294 – 0.149], P = 0.503; Neotropics, change in slope = 0.006 [-0.132 – 0.149], P = 0.913) are statistically significant. N = 324 plots.

Extended Data Fig. 5 | Environmental drivers of aboveground carbon stocks across the AfriMont plot network. Coefficients are from a linear mixed-effects model with site as a random intercept.

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

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

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

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

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

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

a

b

c

Primary Humid Tropical Forests

Lowland forest circa 2018

Montane (incl. submontane) forest

Countries with montane plot data

Bars: % montane versus lowland (left axis)
Points: % lost since 2000 (right axis)

★ AfriMont plot network