

## 1 **High resilience of tropical rainforests to climate change.**

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46 **There is uncertainty in how tropical forest carbon stocks might alter in response to**  
47 **changes in climate and atmospheric composition. Existing studies<sup>1-3</sup> demonstrate large**  
48 **differences due to alternative representations of vegetation processes. Others<sup>4</sup>**  
49 **investigate more the impact of ranges in climate projections of adjusted patterns of**  
50 **temperature and rainfall. Carbon loss has importance for the efficacy of Reducing**  
51 **Emissions from Deforestation and Degradation (REDD). Here we present a systematic**  
52 **exploration of these sources of uncertainty and that associated with different emissions**  
53 **scenarios, for all three major tropical forest regions: (i) Americas, i.e. Amazonia and**  
54 **Central America, (ii) Africa and (iii) Asia. Using driving data from 22 climate models**  
55 **and the MOSES-TRIFFID land surface scheme, only one<sup>5</sup> of these simulations projects**  
56 **biomass loss by the end of the 21<sup>st</sup> Century, and then only for the Americas. However**  
57 **when comparing to alternative models of plant physiological processes<sup>1,2</sup> we find the**  
58 **latter to be a larger uncertainty, the next largest related to future emissions scenario,**  
59 **with uncertainties in climate projection being significantly smaller. Despite this, there is**  
60 **evidence of forest resilience for the three regions.**

61

62 Tropical forests store approximately 470 billion tonnes of carbon in their biomass and soil<sup>6</sup>,  
63 are responsible for about one-third of global terrestrial primary productivity<sup>7</sup>, regulate local  
64 meteorology and house a disproportionate amount of global biodiversity<sup>8</sup>. A number of  
65 previous analyses have investigated potential vulnerability of tropical forests under climate  
66 change (Table A1, Supp Info). Some, based on future projections by the HadCM3 climate  
67 model e.g. Ref<sup>5</sup>, suggest anthropogenically-induced climate change across Amazonia could  
68 cause catastrophic losses of forest cover and biomass ('die-back'). This is true when using  
69 outputs from that climate model to drive a number of vegetation models<sup>1</sup>. More recently,  
70 multiple climate models have been used to force particular vegetation models, hence utilising  
71 an ensemble of climate forcings<sup>4</sup>. In other analyses, alteration of the biogeographical extent  
72 of tropical forests is estimated solely by predicting regions that will have meteorological  
73 conditions similar to those of present day and where forest exists (bioclimatic envelope  
74 modelling)<sup>9,10</sup>. When forced by General Circulation Models (GCMs) other than HadCM3,  
75 vegetation models have usually simulated lower or even no losses of Amazonian forest cover.  
76 There are far fewer assessments of possible climate change impacts on tropical regions  
77 outside of Amazonia. Two existing studies<sup>10,11</sup> suggest significant parts of tropical Africa  
78 and Asia may be less sensitive to climate change.

79

80 We study projected uncertainty of biomass stocks for the three major tropical forest regions  
81 of: the Americas (i.e. Central America and the Amazonia Basin *sensu lato*), Africa and Asia,  
82 and with initial emphasis on a version of the land surface model (MOSES-TRIFFID) similar  
83 to Ref<sup>5</sup> (Methods). This is forced with bias-corrected climate change projections for the  
84 tropics based on the 22 climate models used by the IPCC 4<sup>th</sup> Assessment. We isolate  
85 meteorological drivers and hence the relationship between biomass and changes in  
86 temperature<sup>3</sup>, precipitation and direct “fertilisation” influence of raised [CO<sub>2</sub>]. Simulations  
87 are compared to recent measurements of tropical forest biomass stocks, by extrapolating  
88 forest plot networks<sup>12,13</sup>.

89

90 Figure 1 shows the geographical distribution of rainforest cover predicted for the initial  
91 contemporary state of our land surface model (Methods) forced with Climate Research Unit  
92 (CRU) climatology. We find general agreement between the modelled rainforest distribution  
93 and the observed distribution. Figure 2 presents simulated terrestrial vegetation carbon  
94 content defined as the carbon in above ground biomass and live roots,  $C_v$  (Mg ha<sup>-1</sup>). This is  
95 for the three tropical regions, to year 2100 and driven with atmospheric [CO<sub>2</sub>] concentrations  
96 and non-CO<sub>2</sub> radiative forcing pathways representative of the Special Report on Emissions  
97 Scenarios (SRES) A2 “business-as-usual” anthropogenic emissions scenario. These  
98 predictions have been constructed by emulating the changes in surface meteorology predicted  
99 by the 22 climate models, all in the combined climate and land surface impacts system  
100 IMOGEN<sup>14</sup> (Methods). Such changes of climate are added to the CRU climatology, taken as  
101 representative of pre-industrial conditions and removing significant model biases (Figure S1).  
102 For the contemporary period,  $C_v$  increases in all simulations and regions, and is compared to  
103 normalised forest inventory data (Methods) as the three short black curves for Americas and  
104 Africa. The three curves correspond to changes at the 97.5% confidence level, mean change  
105 and 2.5% level (Refs<sup>12,13</sup>). There is agreement tropical forests are gaining biomass, although  
106 the observational data suggest the increases have been larger than that modelled for the recent  
107 period. The magnitude of the increase in tropical forest biomass from plot networks is the  
108 subject of some debate<sup>15</sup>. However the contemporary increase in tropical forest biomass is  
109 consistent with the large and increasing carbon sink on Earth’s land surface derived from the  
110 mass-balance implications of fossil fuel CO<sub>2</sub> emissions and atmospheric CO<sub>2</sub> measurements,  
111 along with the global role of woody tissue as the location of a large fraction of the terrestrial  
112 carbon sink<sup>6</sup>.

113

114 Forest biomass carbon stocks in Asia and Africa are projected to be greater in year 2100 than  
115 at the present-day, in all simulations. This is true for the Americas/Amazon, except for the  
116 HadCM3 climate model. There is however a decreasing ability to sequester carbon in  
117 biomass; many pathways have a  $C_v$  peak towards the end of the 21<sup>st</sup> Century. Figure 2 grey  
118 columns are “commitment” simulations where climate forcing (here that predicted for 2100)  
119 is maintained at that level for a sufficient period that terrestrial ecosystems fall in equilibrium  
120 with that amount of climate change. Generally this increases the spread of simulations, where  
121 those with higher vegetation carbon at the end of the 21<sup>st</sup> Century show an even higher uptake  
122 for the committed period, and simulations peaking earlier in the century show a further  
123 reduction. Particularly large differences between the final year of the transient simulations  
124 and committed values of  $C_v$  are, for Americas: (i) major biomass loss for HadCM3  
125 (confirming the analysis of Ref<sup>16</sup>); and (ii) the MPI ECHAM 5 model predicts less  $C_v$  than  
126 that estimated in pre-industrial times.

127

128 We perform sensitivity simulations where only single patterns of meteorological change are  
129 added to the CRU climatology. This aids understanding of the mechanisms responsible for  
130 the changes in  $C_v$ . Figure 3 shows these changes, years 1860 to 2100, for the  
131 Americas/Amazon region, and decomposes them into the individual effects of temperature,  
132 rainfall and atmospheric  $[CO_2]$ . Predictions are most sensitive to changes in temperature and  
133 atmospheric  $[CO_2]$ , with a lower sensitivity to precipitation alteration (Figure S4 shows the  
134 small sensitivity to other drivers e.g windspeed change). Future changes in temperature  
135 would lead to reduced  $C_v$ , if not for our modelled positive response of vegetation to elevated  
136 atmospheric carbon dioxide<sup>17,3</sup>. Hence the likelihood of die-back could be altered depending  
137 on the future balance of raised greenhouse-gas concentrations, with non- $CO_2$  gases such as  
138 methane having no fertilisation effect<sup>18</sup>. Identical plots (Figures S2 and S3) for African and  
139 Asian forests show again a balance predominantly between the effects of  $CO_2$ -fertilisation  
140 and increased temperature, although there the temperature-only changes are generally smaller  
141 in magnitude.

142

143 To place our analysis in the broader context of uncertainty in ecosystem description, we  
144 extract changes in biomass for the same three regions from ecological Parameter Perturbation  
145 Experiments (PPE) which use the HadCM3C climate model<sup>2</sup>, and from a Dynamic Global  
146 Vegetation Model (DGVM) inter-comparison study<sup>1</sup>. The latter includes inter-DGVM  
147 structural differences (and different  $CO_2$ -fertilisation responses), also with climate change

148 drivers from HadCM3. Figure 4 (a-c) presents these changes in  $C_v$  by 2100, compared to  
149 1860, for our 22-GCM simulations (values could be inferred from Figure 3; red bars are  
150 HadCM3 model), then for PPE (forced with SRES A1B emissions, a scenario with strong  
151 similarities to SRES A2), and finally the DGVM inter-comparison study (five models, four  
152 SRES scenarios). The red bars in the DGVM values are for MOSES/TRIFFID, and these and  
153 the PPE simulations are for “fixed- $Q_{10}$ ” representation of maintenance respiration. This  
154 corresponds to lower year 2100 biomass contents, particularly for the Americas and HadCM3  
155 driving model (Figure SI-5). Figure 4d shows “vectors” of uncertainty, comparing estimates  
156 of Standard Deviation (SD) in climate uncertainty and SD between SRES scenarios, both  
157 plotted against SDs due to DGVM differences. The DGVM response uncertainty dominates  
158 over variation between climate models and emission scenarios. Limited but illustrative  
159 overall statistics are based on combining these three SDs to estimate uncertainty, and a  
160 calculated mean of the DGVM/SRES simulations offset by the HadCM3 difference from 22-  
161 GCM mean (from first columns, Figure 4a-c). Fitting a normal distribution, this returns  
162 across ecosystem model, scenario and climate model probabilities of biomass decrease by  
163 year 2100 of 40% for the Americas, and 7% for both Africa and Asia (Methods). An  
164 alternative statistic, SRES A2 only, is to adopt the MOSES-TRIFFID simulation from our 22-  
165 GCMs simulations (red bar, first columns of Figure 4a-c) to replace that from the DGVM  
166 intercomparison (red bar, A2 DGVM column). Then the probabilities of biomass decrease by  
167 year 2100, after similar mean offset, become 16% for the Americas, 2% for Africa and 4%  
168 for Asia (Methods).

169

170 With the largest uncertainty being land surface description, then the timing and magnitude of  
171 any projections of tropical forest cover will depend strongly on modelled response to higher  
172 temperatures, elevated  $[CO_2]$  concentrations and changes in precipitation regimes. Figure 4  
173 complements other studies; for instance the LPJ ecosystem model predictions of Amazon die-  
174 back forced across climate models<sup>4</sup> includes one configuration showing less resilience<sup>19</sup>.  
175 Reducing this ecological uncertainty requires many parameters to be refined and possibly  
176 new process depiction. Free Air  $CO_2$  Enrichment (FACE) experiments artificially maintain  
177 carbon dioxide at raised concentrations<sup>20</sup>, and do demonstrate a  $CO_2$ -fertilisation effect in  
178 temperate post-disturbance forests. However, at present there are no such experiments in  
179 tropical forests. Other studies<sup>20</sup> indicate that productivity may eventually become constrained  
180 by nutrient limitation, which could therefore increase vulnerability to climate change. For  
181 tropical ecosystems there is good evidence that soil phosphorus is the dominant limiting

182 nutrient (more limiting than nitrogen)<sup>21,22</sup>. However the magnitude of this constraint remains  
183 uncertain, with several mechanisms potentially allowing extra phosphorus to be taken up  
184 from the soil to support at least some increased rates of plant growth at higher [CO<sub>2</sub>]<sup>23</sup>.

185

186 Uncertainty exists in physiological response to elevated temperatures<sup>3,17</sup>. We describe  
187 vegetation maintenance respiration as following a roughly “bell”-shaped response to  
188 temperature (or a “declining-  $Q_{10}$ ”<sup>24</sup>), and peaking around 32°C. Other versions of MOSES-  
189 TRIFFID have assumed an exponential “fixed- $Q_{10}$ ” increase with increasing temperatures  
190 and existing Amazon studies<sup>3,25</sup> show this process representation has a large effect on future  
191 modelled carbon stocks. Figure S5 plots  $C_v$  for both and re-iterates that future values are  
192 significantly lower for a “fixed- $Q_{10}$ ” increase. Our peak temperature of 32°C is lower than  
193 some reports<sup>24</sup>, and as such Figure S5 can be regarded as providing upper and lower bounds  
194 on biomass implications due to this uncertainty in respiration response. There is also  
195 increasing evidence that the long-term temperature response of respiration is dynamic,  
196 capable of thermal acclimation<sup>26</sup>. Generally acclimation, again not yet included in any major  
197 land surface model, is believed to mitigate the rate of increase in respiration rates in the event  
198 of a transition to warmer temperatures. There are suggestions that photosynthesis can also  
199 acclimate to rising temperatures<sup>27</sup> although the extent to which this might occur in tropical  
200 forest species remains unknown. Although our sensitivity simulations suggest that elevated  
201 temperature could be more detrimental to forest biomass than any climate model-predicted  
202 decrease in rainfall, recent field data suggests that tropical forest function may be impeded in  
203 unusually dry years due to strong seasonal moisture deficits. Using a basin-wide plot network  
204 in Amazonia<sup>12</sup> an increased mortality was observed in areas affected by the year 2005  
205 Amazon drought<sup>28</sup>. More details expanding on current uncertainties are presented in  
206 Supplementary Information.

207

208 We find the possibility of climate-induced (i.e. not direct deforestation) damage to tropical  
209 rainforests in the period to year 2100, even under SRES A2 “business-as-usual” emissions  
210 scenario, might be lower than some earlier studies suggest. For instance, our MOSES-  
211 TRIFFID model configuration predicts undisturbed tropical forests as always sequestering  
212 carbon to mid 21<sup>st</sup> Century, and possibly beyond for most climate models. Such a result has  
213 implications for the United Nation’s Reducing Emissions from Deforestation and  
214 Degradation+ (REDD+) scheme, which has previously been questioned due to concerns over  
215 the resilience of the carbon stored in tropical forests. Physiological processes, rather than

216 differences amongst climate projections, dominate uncertainties in the amount of future  
217 carbon accumulation in undisturbed tropical forests, but we anticipate that emerging data and  
218 ecological understanding will reduce this substantially in the next generation of land surface  
219 models.

220

## 221 **Methods**

222 Our land surface model for assessing climate uncertainty effects only is the Met Office Surface Exchange  
223 Scheme 2.2 (MOSES) coupled to DGVM Top-down Representation of Interactive Foliage and Flora Including  
224 Dynamics (TRIFFID); now part of the JULES model<sup>29</sup>. MOSES-TRIFFID has been used in previous ‘Amazon-  
225 dieback’ investigations<sup>3,5,25</sup>, but here are two differences. First soil parameterisations include new values  
226 reported. Second dark respiration has the same temperature response as the maximum rate of carboxylation,  
227  $V_{c,max}$ . This is the  $R_d$  term of Eqn (13) in Ref<sup>29</sup> and its influence on the canopy level plant respiration fluxes is in  
228 Eqn (39)-(42), also Ref<sup>29</sup>. For broad-leaved trees, we used the JULES formulation for  $V_{c,max}$ , peaking at leaf  
229 temperature around 32°C. Many earlier studies set leaf respiration monotonically increasing with temperature  
230 following an exponential  $Q_{10}$  function, where  $Q_{10} = 2.0$ . Respiration peaking in temperature is more appropriate  
231 because (in photosynthetic and non-photosynthetic organs) it is known to ultimately decline as temperatures  
232 increase.<sup>24</sup> Data on peak temperature of tropical tree leaf respiration is limited. Our relatively low peak value  
233 versus the  $Q_{10} = 2.0$  formulation, may provide bounds on this uncertainty.

234 MOSES-TRIFFID is forced by a common base climatology plus patterns of changing meteorological conditions  
235 fitted against the 22 CMIP3 climate models. We employ “pattern-scaling” to calculate change, where regional  
236 and seasonal changes are assumed linear in global warming<sup>30</sup>. An energy balance model calculates global  
237 warming amount, also fitted to the CMIP3 ensemble. Precipitation patterns however are normalised against the  
238 CRU dataset. For geographical position, month and a unit of global warming, each climate model predicts a  
239 percentage change in rainfall compared to its estimate of pre-industrial rainfall values. We then calculate the  
240 anomaly pattern as that percentage change applied to the CRU climatology estimate of precipitation. This  
241 combined impacts system, IMOGEN<sup>14</sup>, is forced with historical followed by a standard pathway in atmospheric  
242 CO<sub>2</sub> concentrations associated with “business-as-usual” SRES A2 emissions scenario, reaching 867ppm in  
243 2100. For non-CO<sub>2</sub> greenhouse gases and aerosols, an additional radiative forcing change is prescribed to the  
244 energy balance model. The modelling system is operated with a disturbance fraction for each gridbox  
245 appropriate for end of the last Century. This is assumed invariant in to the future, and hence we do not take in to  
246 account any future potential direct deforestation.

247

248 Adding anomalies of change to the CRU dataset removes model biases. We estimate pre-industrial state as  
249 averaged monthly CRU values for 1960 to 1989, recognising these include anthropogenically-induced climate  
250 change up to that date. We assumed this error to be smaller than errors through using much earlier years in the  
251 CRU climatology, due to the presence of many more contributing tropical meteorological measurements. This  
252 discrepancy is certainly much smaller than the large biases removed from the climate models (Figure S1). For

253 the Americas, all 22 climate models have rainfall predictions that are too low. These biases can be as large as  
254 predicted change in climate (compare to temperature and rainfall magnitudes, left side Figure 3).

255

256 Biomass inventory data are from the RAINFOR network across South America<sup>12</sup> (measurements from 123  
257 plots) and from the AfriTRON network across Africa<sup>13</sup> (79 plots). Geographical spread of measurements for  
258 South America is not as large as the Americas region depicted in Figure 1. There are only a few plots in the  
259 Central Congo basin for the African dataset. These datasets are relatively sparse compared to the extent of  
260 tropical forest, but are currently the most geographically widespread measurements of tropical biomass  
261 available. To compare with model outputs, corrections were applied to include stems smaller than those  
262 measured in each plot (< 100 mm diameter). We do not consider necromass (coarse woody debris). For South  
263 America, measurements used are 1980 to 2005; measurements following the 2005 drought indicate a reduced  
264 rate of sequestration<sup>6,12</sup> but it is unknown if this is a short-term perturbation or the beginning of a lower rate of  
265 net carbon uptake. African measurements used are 1987 to 1997, the mean start and end census dates of the 79  
266 plots. We normalise spatially-averaged inventory numbers to equal mean  $C_v$  across the 22 simulations in years  
267 1980 (South America) and 1987 (Africa). Yearly percentage changes in mean, and 97.5% and 2.5% confidence  
268 levels equal those measured, and these normalised changes are plotted in Figure 1.

269

270 Variance of changes in  $C_v$  between DGVMs (square of SDs in Figure 4d) is the average of, for each SRES  
271 scenario, expected variance across the five models. Similarly variance between SRES scenarios is calculated by  
272 averaging, for each DGVM, the variance across scenarios. Adding these two values to the additional variance  
273 across the 22-GCM simulations gives total variance. An overall mean is calculated across the 20 DGVM  
274 simulations (5 models, 4 scenarios). We account for the HadCM3 climate model only being used in the DGVM  
275 intercomparison study by offsetting the overall mean by the difference between the mean of the 22 climate  
276 simulations and the HadCM3 simulation (red bar versus mean value of the “22-GCM” columns; Figure 4a-c).  
277 These mean and variance provide the first illustrative probabilities of biomass loss under an assumption of  
278 normal distribution. The second set of probabilities are similarly calculated, with our HadCM3-forced MOSES-  
279 TRIFFID simulation replacing that in the DGVM-study for SRES A2. Now the mean is calculated across the  
280 SRES A2 DGVM simulations, and offset as above. Variance is the sum of variance across SRES A2 DGVMs  
281 combined with that across the 22-GCM runs.

282

283 Supplementary Information gives additional discussion of methods and ecological uncertainties.

284

## 285 **References**

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378

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392

### 393 **Author Contributions**

394

395 C.H. designed the overall paper; P.Z. built the climate patterns; D.G. and L.M.M. created the  
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404 conclusions. All authors contributed to the writing of the manuscript.

405

## 406 **Figure Legends**

407

408 **Figure 1:** Map of tropical forest. Shown are tropical land regions and model gridboxes predicted to  
409 have more than 85% cover of forest for pre-industrial climate (continuous and dashed black outlines).  
410 The green dots are from satellite retrievals of where there is mainly evergreen tropical forest, based on  
411 the GLC2000 land cover map. The gridboxes used in our analysis have continuous black outlines. The  
412 15 gridboxes outlined with dashed lines were not included in our analysis as these areas contain little  
413 (<10%) observed forest cover, despite the model predicting higher coverage.

414

415 **Figure 2:** Tropical forest biomass predictions for (a) Americas, (b) Africa and (c) Asia by the  
416 MOSES-TRIFFID model forced by 22 climate models. Climate models emulated are colour-coded,  
417 from dark blue to dark red for decreasing year 2100 values of  $C_v$ . Grey regions are “committed”  $C_v$   
418 values with climate constant at year 2100 values, and small dashes link back to same model in  
419 transient predictions. Committed equilibrium values are year-independent, hence the “x”-axis break  
420 (small vertical bars). Normalised estimates of  $C_v$  from inventory data (2.5%, mean and 97.5%  
421 confidence levels) are the short black curves for Americas and Africa. Horizontal lines (large dashes)  
422 are estimated pre-industrial values, year 1860.

423

424 **Figure 3:** Sensitivity of changes in biomass of Americas to different climate model drivers. Plot of  
425 changes to  $C_v$  for year 2100 minus 1860, for each climate model emulated. Included are sensitivity  
426 simulations for temperature change only, rainfall change only,  $CO_2$  change only, and for comparison  
427 against these, for all forcings. Also presented, as numbers on the plot, are the average yearly changes  
428 across the Amazon in the climatology associated with each sensitivity simulation.

429

430 **Figure 4:** Contributions of model uncertainties. For the three regions (panels a-c), spread of changes  
431 in  $C_v$ , 2100 value minus 1860. “22-GCM” the transient simulations presented in Figure 2 with the  
432 HadCM3 climate model in red. Similar calculations for the Perturbed Parameter Experiments with  
433 HadCM3C (“PPE”) 3C and the HadCM3-forced DGVM intercomparison simulations (“DGVMs”;

434 SRES scenarios as marked and MOSES/TRIFFID red). “PPE” and MOSES/TRIFFID for “DGVMs”  
435 are fixed  $Q_{10}$  maintenance respiration. Panel (d) presents for all three regions, estimates of standard  
436 deviations between climate models (cyan axis) and between SRES scenarios (blue axis), plotted  
437 against standard deviations between the DGVM models.  
438