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### ► To cite this version:

Almut Arneth, Stephen Sitch, Julia Pongratz, B. D. Stocker, Philippe Ciais, et al.. Historical carbon dioxide emissions caused by land-use changes are possibly larger than assumed. *Nature Geoscience*, 2017, 10 (2), pp.79-84. 10.1038/NGEO2882. hal-01681571

**HAL Id: hal-01681571**

**<https://hal.science/hal-01681571>**

Submitted on 14 May 2018

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1 **Historical carbon dioxide emissions due to land use changes possibly larger than assumed**

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37 **The terrestrial biosphere absorbs about 20% of fossil fuel CO<sub>2</sub> emissions. The overall**  
38 **magnitude of this sink is constrained by the difference between emissions, the rate of**  
39 **increase in atmospheric CO<sub>2</sub> concentrations and the ocean sink. However, the land sink**  
40 **is actually composed of two largely counteracting fluxes that are poorly quantified:**  
41 **fluxes from land-use change and CO<sub>2</sub> uptake by terrestrial ecosystems. Dynamic global**  
42 **vegetation model simulations suggest that CO<sub>2</sub> emissions from land-use change have**  
43 **been substantially underestimated because processes such as tree harvesting and land-**  
44 **clearing from shifting cultivation have not been considered. Since the overall terrestrial**  
45 **sink is constrained, a larger net flux as a result of land-use change implies that**  
46 **terrestrial uptake of CO<sub>2</sub> is also larger, and that terrestrial ecosystems might have**  
47 **greater potential to sequester carbon in the future. Consequently, reforestation projects**  
48 **and efforts to avoid further deforestation could represent important mitigation**  
49 **pathways, with co-benefits for biodiversity. It is unclear whether a larger land carbon**  
50 **sink can be reconciled with our current understanding of terrestrial carbon cycling. In**  
51 **light of our possible underestimation of the historical residual terrestrial carbon sink**  
52 **and associated uncertainties, we argue that projections of future terrestrial carbon**  
53 **uptake and losses are more uncertain than ever.**

54

55 The net atmosphere-to-land carbon flux ( $F_L$ ) is typically inferred as the difference between relatively  
56 well-constrained terms of the global carbon cycle: fossil fuel and cement emissions, oceanic carbon  
57 uptake and atmospheric growth rate of CO<sub>2</sub> (see Textbox) <sup>1</sup>. In contrast, very large uncertainties exist  
58 in how much anthropogenic land-use and land-cover change ( $F_{LULCC}$ ) contributes to  $F_L$ , which  
59 propagates into large uncertainties in the estimation of the residual carbon flux ( $F_{RL}$ ) (Box 1). The lack  
60 of confidence in separating  $F_L$  into its component fluxes diminishes the predictive capacity for  
61 terrestrial carbon cycle projections into the future. It restricts our ability to estimate the capacity of

62 land ecosystems to continue to mitigate climate change, and to assess land management options for  
63 land-based mitigation policies.

64 As land-use change emissions and the residual sink are spatially closely enmeshed, global-scale  
65 observational constraints do not exist for estimating  $F_{LULCC}$  or  $F_{RL}$  separately. Dynamic Global  
66 Vegetation Models (DGVMs) have over recent years been used to infer the magnitude and spatial  
67 distribution of  $F_{LULCC}$  as well as of  $F_{RL}$ , while  $F_{LULCC}$  has traditionally been also derived from data-  
68 driven approaches such as the bookkeeping method<sup>1-3</sup> (Box 1). Although large, for some sources of  
69 uncertainties in  $F_{LULCC}$  (such as differences in baseline years used for calculation, how environmental  
70 effects have been considered, or assumptions about wood products) there is no good reason to believe  
71 that these would introduce a systematic under- or overestimation<sup>4-6</sup>. However, until recently, most  
72 processes related to land management and the subgrid-scale dynamics of land-use change have been  
73 ignored in large-scale assessments of the terrestrial carbon balance, and we argue here that including  
74 these missing processes might systematically increase the magnitude of  $F_{LULCC}$ . In turn, an upward  
75 revision of  $F_{LULCC}$  implies through the global budget the existence of a substantially higher  $F_{RL}$  and  
76 raises the question whether this is plausible given our understanding of the response of ecosystems to  
77 changing environmental conditions.

#### 78 **Gross land-cover transitions such as shifting cultivation**

79 Opposing changes in different land-use types can take place simultaneously within a region (see  
80 Methods and Supplementary Figure 1), for example: an area might be converted from natural to  
81 managed land, whereas an equal area within the same region might be abandoned or reforested,  
82 equating to a net-zero land-cover change. The magnitude of these bi-directional changes depends on  
83 the size of the area investigated. Over thousands of kilometres squared (the typical resolution of  
84 DGVMs), ignoring sub-grid changes can have a substantial effect on the simulated carbon cycle, since  
85 accounting for the gross changes (for example, the parallel conversion to, and abandonment of,  
86 agricultural land in the same grid-cell) includes (rapid) carbon losses from deforestation, (slow) loss  
87 from post-deforestation soil-legacy effects, and (slow) uptake in areas of regrowth. In sum this leads to

88 younger mean stand age, smaller biomass pools and thus higher  $F_{LULCC}$  compared to net area-change  
89 simulations.

90 Gross area transitions are fundamental to land-use land-cover change (LULCC) dynamics in areas of  
91 shifting cultivation (SC) in the tropics<sup>7</sup>, but also occur elsewhere<sup>8</sup>. Gross forest loss far exceeding net  
92 area loss can be demonstrated from remote-sensing products globally<sup>9</sup>, although these products in  
93 themselves cannot distinguish effects of logging from natural disturbance events such as fire or  
94 storms. Secondary forests in the tropics can return to biomass carbon stocks comparable to old-growth  
95 forest within five to six decades<sup>10</sup>, but the same is not the case for soil carbon. Also, fallow lengths in  
96 SC systems tends to be shorter, and show a decreasing trend in many regions<sup>11</sup>. These dynamics result  
97 in the degraded vegetation and reduced soil carbon stocks commonly observed in disturbed forest land  
98 <sup>12</sup>.

## 99 **Wood harvesting**

100 Until recently, global DGVM studies that accounted for LULCC concentrated on the representation of  
101 conversion of natural lands to croplands and pastures, while areas under forest cover were represented  
102 as natural forest, and hence by each model's dynamics of establishment, growth and mortality. Two-  
103 thirds to three-quarters of global forests have been affected by human use, which is mainly due to  
104 timber harvest; but forests are also a source of firewood or secondary products; or used for recreational  
105 purposes<sup>13</sup>. Between 1700-2000 an estimated 86 PgC has been removed globally from forests due to  
106 wood harvesting (WH)<sup>14</sup>. WH leads to reduced carbon density on average in managed forests<sup>15</sup> and  
107 can ultimately result in degradation in the absence of sustainable management strategies. Furthermore,  
108 the harvest of wood can reduce litter input, which lowers soil pools<sup>13</sup>. Bringing a natural forest under  
109 any harvesting regime probably will lead to net-CO<sub>2</sub> emissions to the atmosphere – with a magnitude  
110 and time-dependency conditionnal on harvest intensity and frequency, regrowth and the fate and  
111 residence time of the wood products.

## 112 **Grazing and crop harvesting, and cropland management**

113 Management is not only fundamental for the carbon balance of forests, but also for pasture and  
114 cropland. As with forests, accounting for management processes on arable lands has only recently  
115 been included in DGVMs (see Methods). Regular grazing and harvesting (GH), and more realistic  
116 crop management processes (MC) such as flexible sowing and harvesting, or tillage, will enhance  
117  $F_{LULCC}$  (ref. 16). Over decadal timescales, conversion of forest to cropland has been observed to reduce  
118 soil carbon pools by around 40% (ref. 17), resulting from reduced vegetation litter soil inputs and  
119 enhanced soil respiration in response to tillage, although the effect and magnitude of the latter is being  
120 debated<sup>18</sup>. Conversion to pasture often has either little effect, or may even increase soil carbon<sup>17</sup>.

## 121 **Impacts of land-management processes on the carbon cycle**

122 The few published DGVM studies that account for the management of land more realistically<sup>16,19-21</sup>  
123 consistently suggest a systematically larger  $F_{LULCC}$  over the historical period compared to estimates  
124 that ignored these processes, with important implications for our understanding of the terrestrial  
125 carbon cycle and its role for historical (and future) climate change. In order to assess if results from  
126 these initial experiments hold despite differences among models, we compile here results from a wider  
127 set of DGVMs (and one DGVM “emulator”, see Methods and Supplementary Table 1), adopting the  
128 approach described in ref. 2.  $F_{LULCC}$  was calculated as the difference between a simulation in which  
129 CO<sub>2</sub> and climate were varied over the historical period, at constant (pre-industrial) land use, and one in  
130 which land use was varied as well.

131 When accounting for SC and WH,  $F_{LULCC}$  was systematically enhanced (Fig. 1). Shifting-  
132 cultivation, assuming that no shade-trees remain in cultivated areas, results in increased cumulative  
133  $F_{LULCC}$  over the period 1901-2014 on average by  $35 \pm 18$  PgC (Fig. 1, Supplementary Table 2).  
134 Although three DGVMs had demonstrated this effect previously<sup>19-21</sup>, an upward shift of  $F_{LULCC}$  was  
135 also found in the other models that performed additional SC simulations for this study. Including WH  
136 caused  $F_{LULCC}$  to increase over the same time period by a similar magnitude to SC:  $30 \pm 21$  PgC.

137 Trends in WH-related  $F_{LULCC}$  over time differed between models (Fig. 1) probably due to different  
138 rates of post-harvest regrowth, and assumptions about residence time in different pools<sup>22</sup>. Including the  
139 harvesting of crops and the grazing of pastures also resulted in larger  $F_{LULCC}$ , as carbon harvested or  
140 grazed is consumed and released as CO<sub>2</sub> rapidly instead of decaying slowly as litter and soil organic  
141 matter. Beyond harvest, accounting for more realistic MC such as tillage processes also showed, with  
142 one exception (in which tillage effects were not modelled, see methods) an enhancement of  $F_{LULCC}$   
143 emissions.

144 When ignoring the additional land-use processes investigated here, average  $F_{LULCC}$  is  $119 \pm 50$  PgC  
145 (Supplementary Table 2). Adding effects of SC, WH, GH and MC enhance land-use change emissions  
146 by, on average, 20-30% each (Fig. 2; Supplementary Table 1), with individually large uncertainties.  
147 The combined effects on  $F_{LULCC}$  are difficult to judge as models do not yet account for all land-use  
148 dynamics. For instance, SC and WH effects are expected to enhance  $F_{LULCC}$  additively as there is little  
149 overlap in the input dataset used by DGVMs regarding the areas that are assumed to be under SC, and  
150 areas where other types of forest harvesting occur<sup>7</sup>. But in the case of accounting for harvesting and  
151 other management on arable lands and pastures, carbon cycle interactions with SC and WH cannot be  
152 excluded because subsequent transitions could occur in a grid location, between primary vegetation  
153 and cropland, pastures or secondary forests. The overall enhancement of  $F_{LULCC}$  therefore, will need to  
154 be explored with model frameworks that include all dynamic land-use-change processes. DGVMs  
155 currently contributing to the annual update of the global carbon budget account for some of the  
156 processes examined here, but as of yet not at all comprehensively, and we thus expect DGVM-based  
157  $F_{LULCC}$  to increase substantially compared to results reported in ref. 1. As a consequence, the  
158 discrepancy to bookkeeping estimates of  $F_{LULCC}$  will become larger, although results in ref. 23 call for  
159 a broader range of bookkeeping approaches as well.

## 160 **Implications for the historical residual land sink**

161 In order to match  $F_L$  in the global carbon budget (Box 1) for the historical period a substantially larger  
162  $F_{LULCC}$  would need to be balanced by a corresponding increase in  $F_{RL}$ , which could be either due to



163 underestimated historical increase in gross primary production (GPP) and vegetation biomass,  
164 overestimated heterotrophic carbon loss, or both. The question arises if such a discrepancy is credible  
165 in light of today's understanding. For instance, by compiling a number of observations Pan et al.<sup>24</sup>  
166 suggested a forest sink that is in line with total carbon budget estimates<sup>1</sup>. However, their study  
167 excluded savannahs, grasslands, and woodlands and in semi-arid regions alone carbon uptake was  
168 estimated to be about 20% of the terrestrial sink (plus around another 30% from other non-forested  
169 ecosystems), which also dominate the recent positive trend in carbon uptake<sup>25</sup>. Reconstructing the  
170 Austrian historical forest sink from inventory data also suggested a much larger residual sink,  
171 compared with (bookkeeping) model results<sup>26</sup>.

172 The response of photosynthesis to increasing CO<sub>2</sub> could underlie more than half of today's land carbon  
173 sink<sup>27</sup>. Several recent lines of observation-based evidence suggest that GPP may have undergone much  
174 stronger enhancement over the last century than currently calculated by DGVMs. These studies  
175 include isotopic analysis of herbarium plant samples, of stable oxygen isotope ratios in atmospheric  
176 CO<sub>2</sub>, and accounting for the effect of leaf mesophyll resistance to CO<sub>2</sub> (refs 28-30). Ciais *et al.*<sup>31</sup>  
177 inferred a pre-industrial GPP of 80 PgC a<sup>-1</sup> based on measurements of oxygen isotopes in ice-core air,  
178 indicative for a 33% difference to the often-used present-day GPP benchmark of ~120 PgC a<sup>-1</sup> (ref. 32)  
179 and independently consistent with the 35% increase suggested by ref. 28. In contrast, the participating  
180 DGVMs in this study show an average increase of GPP by only 15% between the first and last ten  
181 years of the simulation (not shown).

182 Whether or not enhancements in GPP translate into increased carbon storage depends on other factors  
183 such as nutrient and water supply, seen for instance in the mixed trends in stem growth found in forest  
184 inventories<sup>33,34</sup>. Much work remains to better understand the response of ecosystem carbon storage to  
185 increasing atmospheric CO<sub>2</sub> concentration<sup>35</sup>. Ultimately, carbon turnover time determines whether or  
186 not enhanced growth will only result in increasing carbon pools<sup>22</sup>. Besides GPP and heterotrophic  
187 ecosystem respiration, lateral carbon flows play an important role in the ecosystem carbon sink.  
188 Recent syntheses that combined a range of observations, inventories of carbon stock changes, trade

189 flows and transport in waterways, estimated dissolved organic carbon losses to account for a flux of >  
190 1.0 PgC a<sup>-1</sup>, with an unknown historical trend<sup>36,37</sup>. The fate of this carbon is highly uncertain, but its  
191 inclusion would enhance the calculated residual sink via an additional loss term (Box 1, equation (1)).  
192 Taken together, a number of candidates for underestimated  $F_{RL}$  in today's models are plausible, and a  
193 combination of the above listed processes likely. It remains to be seen whether a larger  $F_{LULCC}$  can be  
194 supported by observation-based estimates. Several lines of evidence suggest that a common low-bias  
195 in the historic  $F_{LULCC}$  could affect all DGVMs, and the challenge of resolving the many open issues  
196 will stay with us for some years to come.

### 197 **Unknowns in historical LULCC reconstructions**

198 Patterns and historical trends of deforestation, cropland and pasture management, or WH are  
199 uncertain. Land-use reconstructions differ substantially in terms of the time, location and rate of  
200 LULCC (see ref. 38 and reference therein). The DGVM and climate science community has mostly  
201 relied on the LUH1 dataset by Hurtt et al.<sup>7</sup>, chiefly because it provides the needed seamless time series  
202 from the historical period into future projections at the spatial resolution required by DGVMs. Clearly  
203 such a globally applicable gridded dataset must necessarily include simplifications. For instance, the  
204 assumed uniform 15-year turnover in tropical SC systems<sup>7</sup> cannot account for the known variation  
205 between a few years and one to two decades, or trends towards shorter fallow periods in some regions  
206 (see ref. 11 and references therein), although there is also an increasing proportion of permanent  
207 agriculture. Likewise, not only the amount of WH but also the type of forestry (coppice, clear-cut,  
208 selective logging, fuel-wood) will vary greatly in time and space, which is difficult to hindcast<sup>39,40</sup>.

209 In upcoming revisions to LUH1 (LUH-2, <http://luh.umd.edu/data.shtml>), forest-cover gross  
210 transitions are now constrained by the remote sensing information<sup>9</sup>, and have overall been re-estimated  
211 (Fig. 3). Whether or not this will result in reduced SC carbon loss estimates in recent decades remains  
212 to be seen. At the same time, these historical estimates consider large gross transitions of land-cover  
213 change only for tropical regions even though there is good reason to believe that bi-directional  
214 changes occur elsewhere<sup>41</sup>. For Europe alone, a recent assessment that is relatively impartial to spatial

215 resolution estimated twice the area having undergone land-use transitions since 1900 when accounting  
216 for gross *vs.* net area changes<sup>8</sup>. This leads to substantial increase in the calculated historical European  
217  $F_{LULCC}$ , both in a bookkeeping-model and DGVM-based study<sup>42</sup>. Historical land carbon cycle  
218 estimates therefore are not only highly uncertain due to missing LULCC processes, but equally so due  
219 to the LULCC reconstructions *per se*. However, for a given reconstruction, accounting for additional  
220 processes discussed here will always introduce a unidirectional enhancement in  $F_{LULCC}$  compared to  
221 ignoring these processes.

## 222 **Implications for the future land carbon mitigation potential**

223 Our calculated increases in  $F_{LULCC}$ , in absence of a clear understanding of the processes underlying  
224  $F_{RL}$ , notably strengthen the existing arguments to avoid further deforestation (and all ecosystem  
225 degradation) – an important aspect of climate change mitigation, with considerable co-benefits to  
226 biodiversity and a broad range of ecosystem service supply. One could also conjecture whether or not  
227 a larger historical carbon loss through LULCC would imply a larger potential to sequester carbon  
228 through reforestation, than thought so far. However, assessments of mitigation potentials must  
229 consider the often relatively slow carbon gain in regrowing forests (compared to the rapid, large loss  
230 during deforestation), in particular the sluggish replenishment of long-term soil carbon storage<sup>43,44</sup>.  
231 What is more, trees grow now, and will in future, under very different environmental conditions  
232 compared to the past. A warmer climate increases mineralisation rates and hence enhances nutrient  
233 supply to plant growth, supporting the CO<sub>2</sub> fertilisation effect, but also stimulates heterotrophic decay  
234 of existing soil carbon and/or flow of dissolved carbon, with as yet no agreement about the net  
235 effects<sup>3,45</sup>. Regrowing forests might also in future be more prone to fire risk, and other episodic events  
236 such as wind-throw or insect outbreaks<sup>46,47</sup>, crucial ecosystem features not yet represented well in  
237 models<sup>48</sup>. This question of “permanence” has been an important point of discussion at conferences  
238 under the UNFCCC, and also endangers the success of payment-for-ecosystem-services schemes that  
239 target conservation measures, as it is unclear how an increasing risk of losing carbon-uptake potential  
240 can be accounted for<sup>49,50</sup>.

241 Given that we may be greatly underestimating the present-day  $F_{RL}$ , and therefore missing or  
242 underestimating the importance of key driving mechanisms, projections of future terrestrial carbon  
243 uptake and losses appear more fraught with uncertainty than ever. In the light of the findings  
244 summarized here, this poses not only a major challenge when judging mitigation efforts, but also for  
245 the next generation of DGVMs and Earth System models to assess the future global carbon budget.  
246 Future work therefore needs to concentrate on representing the interactions between physiological  
247 responses to environmental change in ecosystems with improved representations of human land  
248 management.

249

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#### 370 **Acknowledgements**

371 AA, ADB and TAMP acknowledge support from EU FP7 grants LUC4C (grant no. 603542) and  
372 OPERAS (grant no.308393), and the Helmholtz Association in its ATMO programme and its impulse  
373 and networking fund. MF, WL, CY and SS were also funded by LUC4C. JP and JEMSN were  
374 supported by the German Research Foundation's Emmy Noether Program (PO 1751/1-1). EK was  
375 supported by the ERTDF (S-10) from the Ministry of the Environment, Japan. ER was funded by  
376 LUC4C and by the Joint UK DECC/Defra Met Office Hadley Centre Climate Programme (GA01101).  
377 SZ has received funding from the European Research Council (ERC) under the European Union's  
378 Horizon 2020 research and innovation programme (grant agreement no. 647204; QUINCY). BDS is

379 supported by the Swiss National Science Foundation and FP7 funding through project EMBRACE  
380 (282672). PC received support from the ERC SyG project IMBALANCE-P ‘Effects of phosphorus  
381 limitations on Life, Earth system and Society’ Grant agreement no.: 610028.’

382

### 383 **Author contributions**

384 AA, SS, JP, BS conceived the study. BP, LC, AB, MF, EK, JEMN, ADB, ML, TAMP, ER, TG, NV,  
385 CY, SZ made changes to model code and provided simulation results. AA and SS analysed results.  
386 BS, PC, WL provided Fig. 3. AA wrote the first draft, all authors commented on the draft and  
387 discussion of results.

### 388 **Additional information**

389 Supplementary information is available in the online version of the paper. Reprints and permissions  
390 information is available online at [www.nature.com/reprints](http://www.nature.com/reprints). Correspondence and requests for  
391 materials should be addressed to A.A.

392

### 393 **Box 1: Calculations of global terrestrial carbon uptake and removal**

394 The net atmosphere-to-land carbon flux ( $F_L$ ) is generally inferred as the difference between other  
395 terms of the global carbon cycle perturbation:

$$396 \quad F_L = F_{FFC} - F_O - \frac{dA_{CO_2}}{dt} \quad (1)$$

397 where  $F_{FFC}$  are fossil fuel and cement emissions,  $F_O$  is the atmosphere-ocean carbon exchange  
398 (currently an uptake) and  $\frac{dA_{CO_2}}{dt}$  is the atmospheric growth rate of  $CO_2$  (equation 1).  $F_{FFC}$  and  $\frac{dA_{CO_2}}{dt}$  are  
399 well known, and the estimate of the decadal global ocean carbon sink is bounded by a range of  
400 observations<sup>1</sup> such that the net land carbon flux is relatively well constrained. By contrast, there is

401 much less confidence in separating  $F_L$  into a carbon flux from anthropogenic land use and land cover  
402 change ( $F_{LULCC}$ ), and a residual carbon flux to the land ( $F_{RL}$ , (equation 2)) which is typically calculated  
403 as the difference from the other carbon-cycle components:

$$404 \quad F_L = F_{RL} - F_{LULCC} \quad (2)$$

405  $F_{LULCC}$  and  $F_{RL}$  are both made up of source and sink fluxes. Uncertainties in  $F_{LULCC}$  and  $F_{RL}$  are around  
406 35% - 40% over the period 1870-2014 (when expressed as % of the cumulative mean absolute values),  
407 compared to 13% for the cumulative ocean sink and 5% for fossil fuel burning and cement emissions<sup>1</sup>.

408  $F_{LULCC}$  has been modelled by the bookkeeping method (combining data-driven representative carbon  
409 stocks trajectories and/or, for the satellite period, remote-sensing information on carbon density for  
410 different biomes, with estimates of land-cover change), or by dynamic global vegetation models  
411 (DGVMs; calculating carbon density of ecosystems with process-based algorithms; see Methods).  
412 DGVMs can also be used to calculate explicitly the magnitude and spatial distribution of  $F_{RL}$  (refs 1,  
413 3) instead of deducing its global value as a difference between  $F_L$  and  $F_{LULCC}$  as done in global budget  
414 analyses. The bookkeeping approach has the advantage that carbon densities and carbon response  
415 functions that describe the temporal evolution and fate of carbon after a LULCC disturbance can be  
416 based directly on observational evidence<sup>6,23</sup>, but has to assume that local observations can be  
417 extrapolated to regions/countries or biomes, thus partly ignoring spatial edaphic and climatic gradients  
418 of carbon stocks. The DGVM-based simulations have the advantage to account for environmental  
419 effects on carbon stocks through time, and account for spatial heterogeneity, but are poorly  
420 constrained by data. DGVMs and bookkeeping models have similarly large degree of uncertainties<sup>1</sup>.

## 421 **Figure captions**

422 Figure 1: Difference in LULCC emission flux ( $\Delta F_{LULCC}$ ) due to individual processes. **a**, Wood harvest.  
423 **b**, Shifting cultivation. **c**, Harvest (using the grass functional type). **d**, Full crop representation.  
424 Coloured lines represent different models, grey symbols and hairlines are average  $\pm$  one standard  
425 deviation.

426 Figure 2: Response ratio of cumulative  $F_{LULCC,1}$  and  $F_{LULCC,0}$ . See also Supplementary Table 1 and  
427 methods for individual processes and models.

428 Figure 3: Comparison of net (a) and gross (b) forest / natural land change (million km<sup>2</sup>) between  
429 different LULCC data sets. Changes in LUH1 data <sup>7</sup> represents the change of natural land because  
430 there is no separate forest type in LUH1 while change in the other data sets indicates the forest change.

## 431 **Methods**

### 432 **General simulation setup**

433 Carbon fluxes from land-use change are derived as the difference between a simulation with  
434 historically varying observed climate, atmospheric CO<sub>2</sub> concentration and land-cover change (S3) and  
435 one in which land-cover change was held constant (S2)<sup>1,2</sup>. Land-cover changes were taken from  
436 HYDE<sup>51</sup> or LUH1<sup>7</sup>. In S2, land-cover distribution was fixed. Gridded historical estimates of gross-  
437 transitions (shifting cultivation (SC) in the tropics) and wood harvesting (WH) were taken from ref. 7.

438 Spin-up used repeated climate from the first decades of the twentieth century, and constant CO<sub>2</sub>  
439 concentration and land-cover distribution (for details, see the individual description below). Upon  
440 achieving steady-state, land-cover distribution and CO<sub>2</sub> concentration were allowed to evolve  
441 transiently, whereas transient climate evolution began at 1901. Atmospheric CO<sub>2</sub> concentration was  
442 taken from ice core data until roughly mid-twentieth century, when atmospheric measurements  
443 became available<sup>1</sup>. A “baseline” carbon flux related to land-use change ( $F_{LULCC,0}$ ; see Supplementary  
444 Table 1) is defined as excluding gross transitions and wood harvest, and using the grass plant  
445 functional type to represent crop areas. Data in this Perspective were from previously published work,  
446 supplemented by additional, new simulations. In cases where more than one of the processes that are  
447 under investigation here were assessed by one model, several S3 experiments were provided.  
448 Although spin-up and model configurations differed between models, for S2 and S3 simulations of  
449 any one individual model the setup was the same, which allows to identify the effect of adding the  
450 individual processes. We describe briefly the relevant aspects of models and simulational protocol, in  
451 particular where they differ from their previously published versions.

452 **JULES model.** Here, to implement crop harvest, four additional PFTs were added: C3 crops, C4  
453 crops, C3 pasture and C4 pasture, with identical parameter sets as the C3 and C4 grass PFTs. Lotka-  
454 Volterra equations<sup>52</sup> are used three times to calculate the vegetation distribution in natural areas, crop  
455 and pasture areas, with the calculations in each area being independent of the others. Crop-harvest is

456 represented by diverting 30% of crop litter to the fast product pool instead of to the soil; the fast  
457 product pool has a rapid decay timescale of 1 year. Pasture is not harvested.

458 The model is forced by crop and pasture area from the Hyde 3.2 dataset<sup>1</sup> and by CRU-NCEP  
459 climate<sup>1,2</sup>, both at 1.875x1.25 degrees, using an hourly time-step, and updating vegetation distribution  
460 every ten days. 1080 years of spin-up were run by fixing crop and pasture areas at 1860 levels and by  
461 repeating 1901-1920 climate and CO<sub>2</sub> concentrations.

462 **JSBACH model.** The JSBACH version used here is similar to the version in ref.1. S3 experiments  
463 include gross land-use transitions and WH<sup>21</sup>.  $F_{LULCCc,0}$  in Supplementary Table 2 were calculated by  
464 subtracting the individual contributions of these processes. Net transitions are derived from the gross  
465 transition implementation, but by minimizing land conversions<sup>21</sup>. WH<sup>7</sup> is taken not only from forest  
466 PFTs but also shrubs and natural grasslands are harvested. Upon harvest, 20% of the carbon is  
467 immediately released to the atmosphere; the rest is transferred into the litter and subject to soil  
468 dynamics. JSBACH simulations were conducted at 1.9°x1.9° forced with remapped 1° LUH1 data  
469 from 1860-2014 and daily climate calculated from the 6-hourly 0.5° CRU-NCEP product<sup>1</sup> for the  
470 years 1901-2014. The initial state in 1860 is based on a spin-up with 1860 CO<sub>2</sub> concentrations (286.42  
471 ppm), cycling (detrended) 1901-1921 climate and constant 1860 LUH1 WH amounts. From 1860  
472 annual CO<sub>2</sub> forcing was used, and after 1901 climate was taken from CRU-NCEP. In the no-harvest  
473 simulation the 1860 WH amounts were applied throughout the whole simulated period.

474 **LPJ-GUESS model.** SC: For implementing SC, recommendations followed those by ref.7, with  
475 rotation periods of 15 years. Simulations used the coupled carbon-nitrogen version of the model<sup>16,53</sup>  
476 spin-up used constant 1701 land-cover and CO<sub>2</sub> concentration, and 1901-1930 recycled climate. Upon  
477 steady-state land-cover and CO<sub>2</sub> were allowed to change from 1701, and climate from 1901 onwards<sup>42</sup>.  
478 When land is cleared, 76% of woody biomass and 71% of leaf biomass is removed and oxidised  
479 within one year, with a further 21% of woody biomass assigned to a product pool with 25 year  
480 turnover time<sup>42</sup>. Upon abandonment a secondary forest stand is created and recolonization of natural

481 vegetation takes place from a state of bare soil. With forest rotation, young stands (above a minimum  
482 age of 15 years) are preferentially converted.

483 GH/MC: Simulations are taken from ref. 16, using the carbon-only version of the model. 68% of  
484 deforested woody biomass and 75% of leaf biomass is oxidised within one year, with a further 30% of  
485 woody biomass going to the product pool. In the GH case, 50% of the above-ground biomass are  
486 annually removed from the ecosystem. In MC, 90% of the harvestable organs and an additional 75%  
487 of above-ground crop residues are removed each year. Simulations ran from 1850 to 2012, with 1850  
488 land-cover and CO<sub>2</sub> concentrations, and recycled climate (1901-1930) being used for spin-up. All LPJ-  
489 GUESS simulations used CRU TS 3.23 climate<sup>54</sup>.

490 **LPJ model.** Compared to previous versions, the model now uses the World Harmonization Soils  
491 Database v.1.2 for soil texture and Cosby equations<sup>55</sup> to estimate soil water holding capacity. Further  
492 developments allow for gross land-use transitions and WH to be prescribed. Changes include: (1) the  
493 primary grid-cell fraction only decreases in size; (2) secondary grid-cell fractions can decrease or  
494 increase in size by combining with other secondary forest fractions, recently abandoned land, or  
495 fractions with recent WH; (3) deforestation that results in an immediate flux to the atmosphere equal  
496 to 100% of heartwood biomass and 50% of sapwood biomass; root biomass enters belowground litter  
497 pools, while 100% leaf and 50% of sapwood biomass becomes part of aboveground litter.

498 WH demand<sup>7</sup> on primary or secondary lands was met by the biomass in tree sapwood and heartwood  
499 only. Only whole trees were harvested (that is, tree-density was reduced); wood from deforestation  
500 was not included to meet WH demand. 100% of leaf biomass and 40% of the sapwood and heartwood  
501 enters the aboveground litter, and 100% of root biomass enters the belowground litter pools; 60% of  
502 sapwood and heartwood are assumed to go into a product pool. Of these, 55% go to the 1-year product  
503 pool (emitted in the same year), 35% go to the 10-year product pool (emitted at rate 10% per year) and  
504 10% go to the 100-year product pool (emitted at rate 1% per year). These delayed pool-emission  
505 fluxes are part of the LULCC fluxes. After harvest, the harvested fraction is mixed with existing  
506 secondary forest fraction, or a secondary fraction is created if none exists, while fully conserving

507 biomass. For simulations with SC, grid-cell fractions that underwent land-use change were not mixed  
508 with existing managed lands or secondary fractions until all land-use transitions had occurred.

509 Simulations were performed using monthly CRU<sup>54</sup> (TS v.3.23) climate at 0.5° degrees, and finished in  
510 year 2013. Spin-up was done using recycled 1901-20 climate, and using 1860 land-cover and CO<sub>2</sub>.  
511 Upon steady-state, land cover and CO<sub>2</sub> varied after 1860 and climate varied after 1900.

512 **LPJmL model.** The LPJmL version used was as described in refs 56-58. In the baseline scenario all  
513 crops were simulated as a mixture of C3 and C4 managed grasslands, 50% of the aboveground  
514 biomass is transferred to the harvest compartment and assumed to be respired in the same year.  
515 Climate data was 1901-2014 CRU TS v.3.23 monthly datasets and land-use patterns from the HYDE  
516 3.2 dataset. Simulations were performed at 0.5° spatial resolution. Model spin-up used recycled  
517 climate data from 1901-1920, and with land use patterns and CO<sub>2</sub> concentrations fixed to the 1860  
518 value. Simulations from 1861-2014 were done with varying annual CO<sub>2</sub> concentration values, and  
519 varying land use patterns according to the HYDE dataset, and with transient climate from 1901 until  
520 2014.

521 **LP3X model.** Land-use change, including SC and WH, is implemented as described in ref. 20,  
522 using the full land-use transition and wood harvesting data provided<sup>7</sup>. Wood (heartwood and  
523 sapwood) removed by harvesting and land conversion is diverted to products pools with  
524 turnover rates of 2 years (37.5%) and 20 years (37.5%). The rest, including slash from roots  
525 and leaves is respired within the same year.

526 Simulation results shown here are based on employing the GCP 2015 protocol and input  
527 data<sup>1</sup>. LPX includes interactive C and N cycling with N deposition and N fertiliser inputs<sup>59</sup>.  
528 Simulations with SC and WH were spun up to equilibrium under land-use transitions and WH  
529 of year 1500<sup>20</sup>. Varying land-use transitions and WH was included from 1500 onwards, with  
530 CO<sub>2</sub> and N deposition of year 1860 and recycled climate from CRU TS v.3.23, years 1901-  
531 1931. All simulations are done on a 1 x 1 degree spatial resolution and make use of monthly



532 climate input. Original GCP standard input files were aggregated to 1 x 1 degrees conserving  
533 area-weighted means (climate input) or absolute area of cropland and pasture (land use input).

534 **OCN model.** The OCN version used here is applied as in the framework of the annual carbon budget<sup>1</sup>.  
535 OCN includes interactive C and N cycling with N deposition and N fertiliser inputs<sup>60</sup>. Wood harvest  
536 was implemented by first satisfying the prescribed wood extraction rate from wood production due to  
537 land-use change, and then removing additional biomass proportionally from forested tiles. Wood  
538 (heartwood and sapwood) removed by harvesting and land conversion is diverted to products pools  
539 with turnover rates of 1 years (59.7%), 10 years (40.2% for tropical, and 29.9% for extratropical trees)  
540 and 100 years (10.4 % for extratropical trees)<sup>61</sup>. The remainder enters the litter pools. In case OCN's  
541 forest growth rate did not suffice to meet the prescribed wood extraction rate, harvesting was limited  
542 to 5% of the total stand biomass and assumed to stop if the stand biomass density fell below 1 kg C m<sup>-2</sup>.  
543 These limits were set to account for offsets in annual wood production between OCN's predicted  
544 biomass growth and the assumptions in the Hurtt et al. database<sup>7</sup>. These limits may lead to lower than  
545 prescribed WH rates in low productive areas. An additional run was performed with keeping WH  
546 constant at 1860s level.

547 Simulations with WH were spun up to equilibrium using harvesting of the year 1860<sup>1</sup>. Varying land-  
548 use transitions or WH was included from 1860 onwards, with CO<sub>2</sub> and N deposition of year 1860 and  
549 recycled climate from CRU-NCEP, years 1901-1931. All simulations are done on a 1 x 1 degree  
550 spatial resolution and make use of daily climate input, which is disaggregated to half-hourly values by  
551 means of a weather generator<sup>62</sup>. Original GCP standard input files were aggregated to 1 x 1 degrees  
552 conserving area-weighted means (climate input) or absolute area of cropland and pasture (land use  
553 input).

554

555 **ORCHIDEE model.** WH: Developments to the version included in ref.1 include annual WH, the total  
556 wood harvested of a grid cell is removed from above-ground biomass of the different forest PFTs  
557 proportional (i) to its fraction in the gridcell and (ii) also to its relative biomass among forest PFTs.

558 This results in harvesting more wood in biomass-rich forests. In cases of inconsistencies between the  
559 Orchidee and Hurtt forest fraction, and to avoid forest being degraded from excessive harvest we  
560 assume that no more than 20% of the total forest biomass of a gridcell can be harvested in one year.  
561 Hence the biomass actually harvested each year can be slightly lower than prescribed<sup>7</sup>. The harvested  
562 biomass enters three pools of 1, 10 and 100 residence years respectively (and is part of  $F_{LULCC}$ ). Model  
563 runs were done at  $0.5^\circ \times 0.5^\circ$  resolution. Spin-up used recycled climate of 1901-1910.  $CO_2$   
564 concentration, land-cover and WH of the year 1860. The model was run until the change in mean total  
565 carbon of 98% of grid-points over a ten-year spin-up period was  $< 0.05\%$ .

566 SC: Land cover transition matrices are upscaled from  $0.5^\circ$  LUH1 data<sup>7</sup> so no transition information is  
567 lost in the low-resolution run. The minimum bi-directional fluxes between two land cover types in  
568 LUH1 were treated as shifting cultivation. The model was forced with CRU-NCEP forcing (v5.3.2),  
569 re-gridded to  $5^\circ$  resolution from the original  $0.5^\circ$  resolution. Spin-up simulation used recycled climate  
570 data for 1901-1910 with atmospheric  $CO_2$  held at 1750 level, and land cover fixed at 1500. Transient  
571 runs started from 1501 until 2014, with  $CO_2$  varying from 1750 and climate varying from 1901. In the  
572 transient run for the control simulation, land cover is held constant at 1500; for the SC run, land cover  
573 varies by applying annual land use transition matrices of SC. All runs have been performed with  
574 outputs on annual temporal resolution but forcing data is 6-hourly.

575 **OSCAR model.** A complete description of OSCAR v2.2 is provided by ref. 63. OSCAR is not a  
576 DGVM, but a compact Earth system model calibrated on complex models. Here, it is used in an  
577 offline setup in which the terrestrial carbon-cycle module is driven by exogenous changes in  
578 atmospheric  $CO_2$  (IPCC AR5 WG1 Annex 2), climate (CRU TS v.3.23), and land-use and land cover  
579 (HYDE v.3.2).

580 The global terrestrial biosphere is disaggregated into nine regions (detailed by ref. 64) and subdivided  
581 into five biomes (bare soil, forest, shrubland+grassland, cropland, pasture). The carbon-cycle in each  
582 of these 45 subparts is represented by a three-box model whose parameters are calibrated on DGVMs.  
583 The preindustrial equilibrium (carbon densities and fluxes) is calibrated on TRENDY models<sup>2</sup>. The

584 transient response of NPP, heterotrophic respiration and wildfires to CO<sub>2</sub> and/or climate is calibrated  
585 on CMIP5 models<sup>65</sup>. The impact of land-use and land-cover change on the terrestrial carbon-cycle is  
586 modelled using a bookkeeping approach. Coefficients used to allocate biomass after land-use or land-  
587 cover change are based on ref. 66.

588 Since OSCAR v2.2 is meant to be used in a probabilistic setup we made an ensemble of 2400  
589 simulations in which the parameters (for example, preindustrial equilibrium, transient responses,  
590 allocation coefficients) are drawn randomly from the pool of available parameterizations. See ref. 63  
591 for more details. The resulting OSCAR values discussed and shown in the main text are the median of  
592 this ensemble.

593 **VISIT model.** Implementation of climate, land-use change (gross transitions, SC) and WH has not  
594 changed from<sup>1</sup>. Land-use, land-use change, and WH data for 1860-2014 were from LUH1<sup>7</sup>. For WH,  
595 the amount of harvested biomass prescribed in ref. 7 were transferred from simulated stem biomass to  
596 1-year product pool (emitted in entirety in same year of wood harvest), 10-year product pool, and 100-  
597 year product pool in a same manner as in the cleared biomass with land-use change described in ref.  
598 67. The non-harvested part of biomass remains in the ecosystem. The fluxes from WH pools are  
599 included in the NBP calculations.

600 Climate data was 1901-2014 monthly CRU TS v.3.23 and all simulations were conducted with 0.5°  
601 spatial resolution. The model spin-up was performed recycling climate data from 1901-1920, and with  
602 land use patterns and CO<sub>2</sub> concentrations fixed to the 1860 value. Simulations from 1860-2014 were  
603 done with varying annual CO<sub>2</sub> concentration values, varying land use patterns according to LUH1,  
604 recycling the climate from 1901-1920 in the period 1860-1900, and with transient climate from 1901  
605 until 2014.

606

607 **Data in Fig. 3.** Data for net forest change from the Food and Agriculture Organization (FAO)<sup>68</sup> is  
608 calculated as the difference of forest area between 2000 and 2010 in each region. The same data were

609 also used in the Houghton et al. bookkeeping model<sup>6</sup>. The net forest change from Hansen et al.<sup>69</sup> is  
610 based on satellite observations, and is their difference between gross forest gain and gross forest loss  
611 during 2000-2012. Because the LUH1 dataset<sup>7</sup> only has one type of natural vegetation, and does not  
612 separate natural forest from natural grassland, the change in Fig. 3 represents the total change of  
613 natural land. In Fig. 3b, for LUH1 the gross loss includes transitions from primary/secondary  
614 vegetation to cropland / pasture, while the gross gain is the sum of transitions from cropland and  
615 pasture to secondary land. With grasslands and forests treated as separate land-cover types in LUH2  
616 (<http://luh.umd.edu/>), the change includes transitions from primary / secondary forest to cropland /  
617 pasture (gross loss) and transitions from cropland / pasture to secondary forest (gross gain). The net  
618 change for LUH1 or LUH2 is the difference between gross loss and gross gain. To be consistent with  
619 ref. 69, the period calculated for LUH1 and LUH2 is also from 2000 to 2012. The products shown in  
620 Figure 3 use definitions of forest loss and gain, and interpretation of differences between products  
621 should therefore take these into consideration.

622

623 **Data and code availability.** The data that support the findings of this study are available upon  
624 request, for access please contact [almut.arneth@kit.edu](mailto:almut.arneth@kit.edu) and [s.a.sitch@exeter.ac.uk](mailto:s.a.sitch@exeter.ac.uk). We are unable to  
625 make the computer code of each of the models associated with this paper freely available because in  
626 many cases the code is still under development. However, individual groups are open to share code  
627 upon request, in case of interest please contact the co-authors for specific models. Access for LUH1 &  
628 LUH2 is under <http://luh.umd.edu/data.shtml>; the HYDE data are accessible via  
629 <http://themasites.pbl.nl/tridion/en/themasites/hyde/download/index-2.html>

630

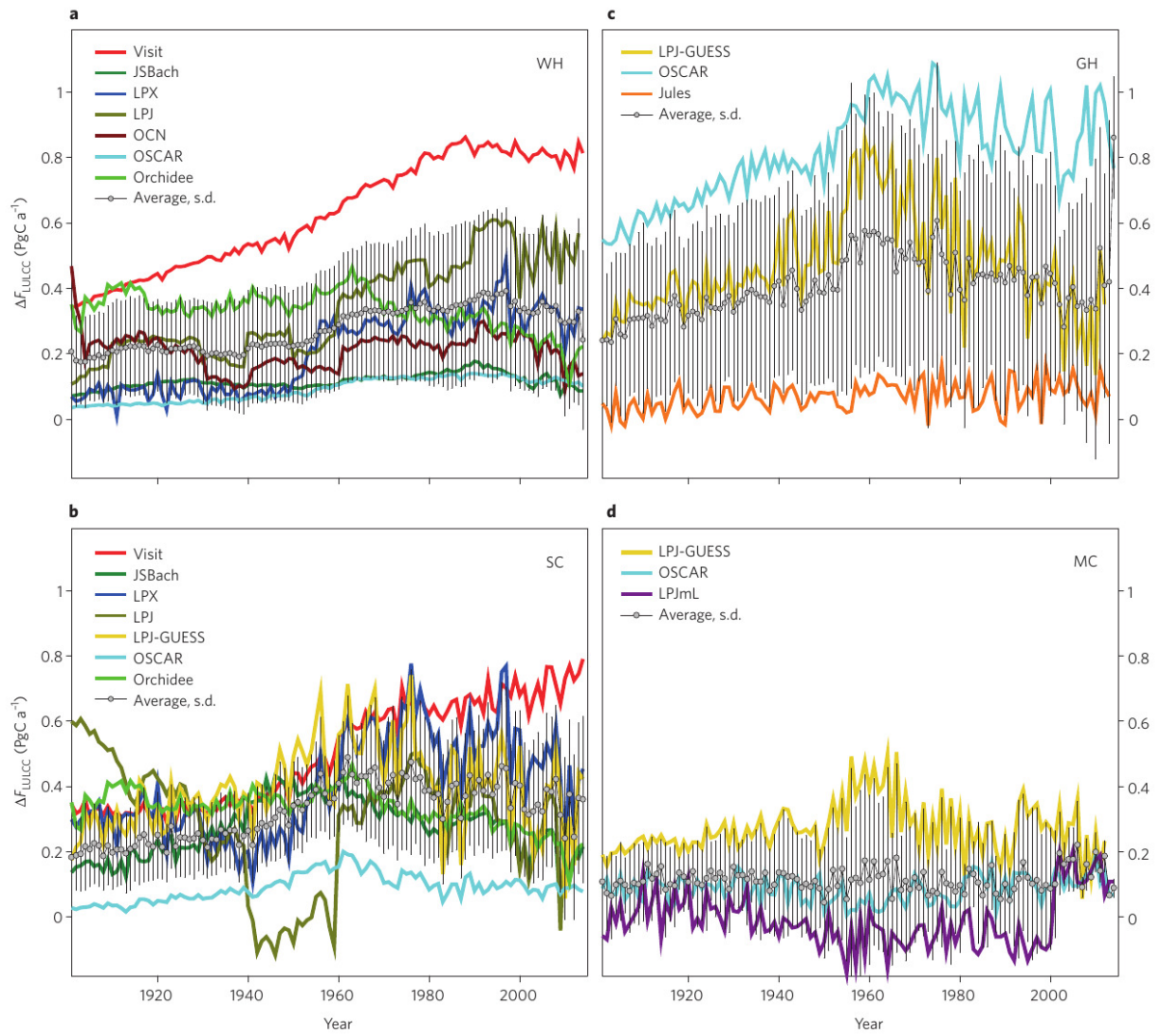
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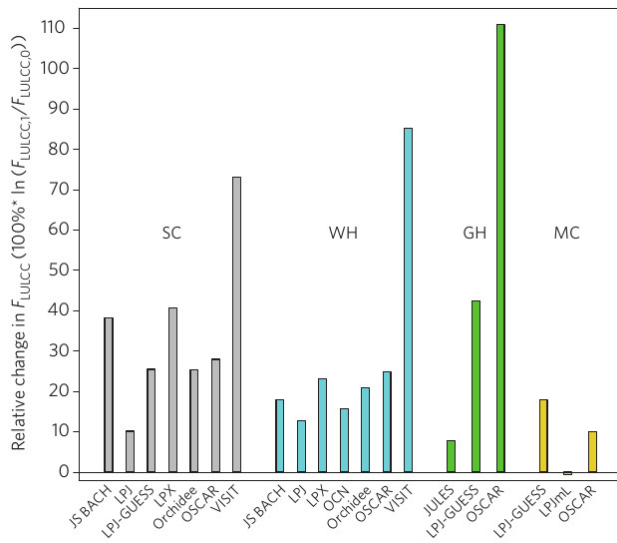
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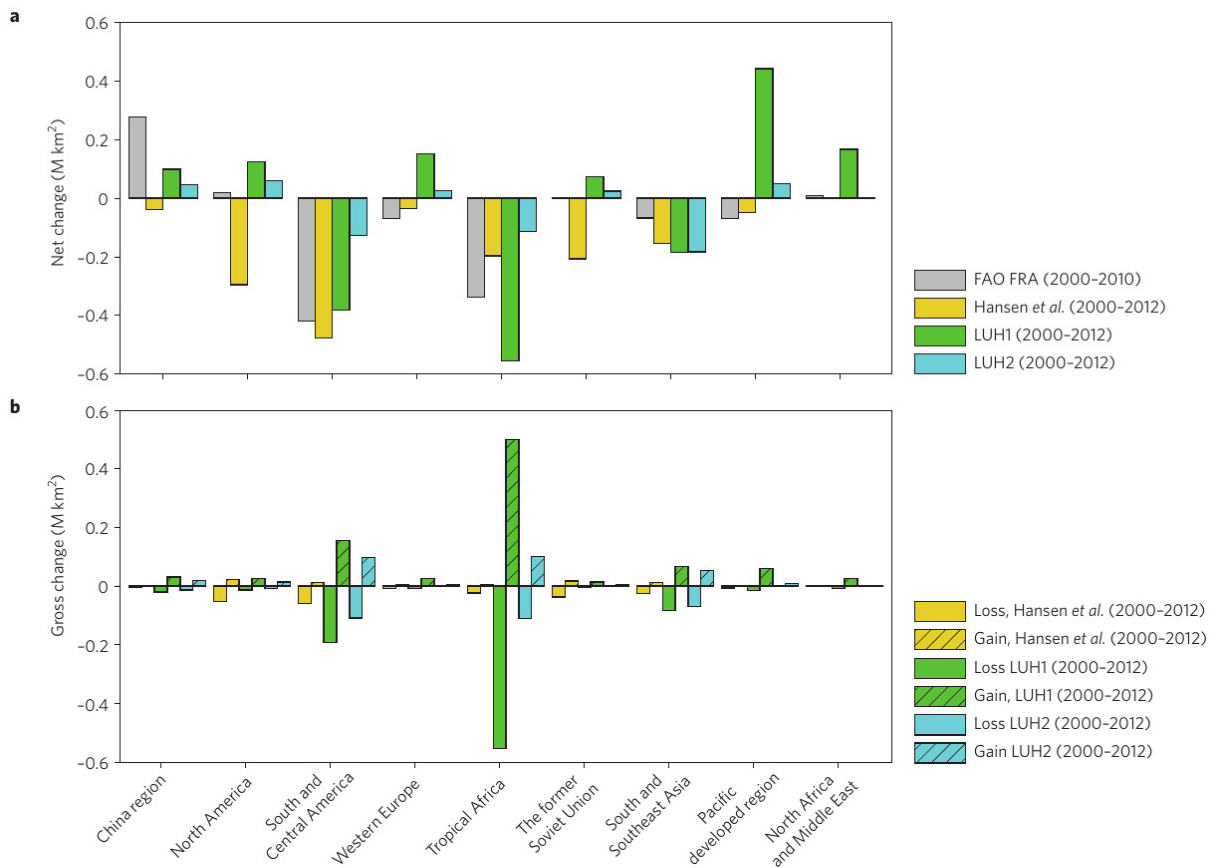


682 Figure 2



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684 Figure 3



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