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Unexpectedly large impact of forest management and grazing on global vegetation biomass

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Carbon stocks in vegetation have a key role in the climate system^{1–4}. However, the magnitude, patterns and uncertainties of carbon stocks and the effect of land use on the stocks remain poorly quantified. Here we show, using state-of-the-art datasets, that vegetation currently stores around 450 petagrams of carbon. In the hypothetical absence of land use, potential vegetation would store around 916 petagrams of carbon, under current climate conditions. This difference highlights the massive effect of land use on biomass stocks. Deforestation and other land-cover changes are responsible for 53–58% of the difference between current and potential biomass stocks. Land management effects (the biomass stock changes induced by land use within the same land cover) contribute 42–47%, but have been underestimated in the literature. Therefore, avoiding deforestation is necessary but not sufficient for mitigation of climate change. Our results imply that trade-offs exist between conserving carbon stocks on managed land and raising the contribution of biomass to raw material and energy supply for the mitigation of climate change. Efforts to raise biomass stocks are currently verifiable only in temperate forests, where their potential is limited. By contrast, large uncertainties hinder verification in the tropical forest, where the largest potential is located, pointing to challenges for the upcoming stocktaking exercises under the Paris agreement.

The amount of carbon stored in terrestrial vegetation is a key component of the global carbon cycle⁴. Changes in carbon stored in vegetation biomass have a large effect on atmospheric CO₂ concentrations, due to either sequestering or release of carbon². The urgency to conserve and, where appropriate, enhance the carbon reservoirs of terrestrial vegetation has long been recognized and is reflected by, for example, the inclusion of the land sector in the report of the United Nations Framework Convention on Climate Change (UNFCCC), the program for Reducing Emissions from Deforestation and Forest Degradation (REDD+), and the acknowledgement of biomass stocks as an essential climate variable⁵. Therefore, monitoring changes in biomass stocks is key for securing progress towards the commitment of halting global warming below 1.5°C.

Although aboveground biomass stocks are straightforward to measure at the site level, their assessment at landscape-to-global scales is time consuming, costly and requires extrapolations⁵. Remote sensing is well-established for wall-to-wall mapping of biomass stocks, but the methodological differences between different remote-sensing products^{6–8} and their scale mismatch with ground data^{9–11} hamper their comparability. Consequently, and despite efforts to improve observational databases³, biomass stocks and their spatial distribution remain uncertain at the global scale (Extended Data Fig. 1).

Many studies of global changes focus on changes in vegetation biomass without quantifying absolute amounts of biomass stocks^{2,12}. Such approaches are indispensable for tracing the role of vegetation in the carbon cycle over time, but do not allow calculations of, for example, restoration potentials. Furthermore, large gaps in our knowledge remain concerning the impact of various land-use activities on biomass stocks^{1,2,13}.

Informed design, implementation, monitoring and verification of land-based climate-change mitigation strategies require comprehensive and systematic stocktaking of the carbon stored in vegetation¹⁴. Beyond accounts of carbon-stock changes, stocktaking also needs to consider the potential and actual biomass stocks of terrestrial vegetation; the full impact of land use on biomass stocks, that is, both land cover conversion and land management; and the uncertainty of biomass stock estimates. Here, we compile such information, complementary to current approaches that quantify actual biomass stocks^{6–8,15,16} (Extended Data Fig. 2).

We present seven global maps of the actual biomass stocks (Extended Data Fig. 3), here defined as the terrestrial, living, aboveground and belowground vegetation biomass measured in grams of carbon, based on remote sensing^{6–8} and inventory-derived information^{15,16}. Ecological literature on biomass stocks of natural zonal vegetation (Supplementary Tables 1, 2), and remote-sensing-derived information on natural vegetation remnants in ecozones, was combined with state-of-the-art biome maps (Methods), accounting for areas without vegetation, to obtain six reconstructions of potential biomass stocks, defined as biomass stocks that would exist without human disturbance under current environmental conditions (Methods, Extended Data Fig. 4). Because actual and potential biomass stocks both refer to the same environmental conditions, their difference isolates the effect of land use on biomass stocks (Methods).

Variation within both sets of maps was interpreted as an indicator of uncertainty, assuming that the uncertainty is the result of differences between approaches rather than measurement errors within a single approach. From the variation between the seven actual biomass estimates, we calculated a detection-limit map for stock changes (Methods). Permuting potential and actual maps resulted in 42 pairs, which enabled us to quantify the effects of land use on biomass stocks^{17,18}. Note that spatial variability in biomass stocks at the landscape level, for example, owing to age class structure, variation in soil fertility or soil-water availability, is accounted for differently in estimates of the potential and actual biomass stocks (Methods). This could introduce a bias of unknown sign and size when interpreting the fine-scale spatial patterns of the biomass-stock reduction maps.

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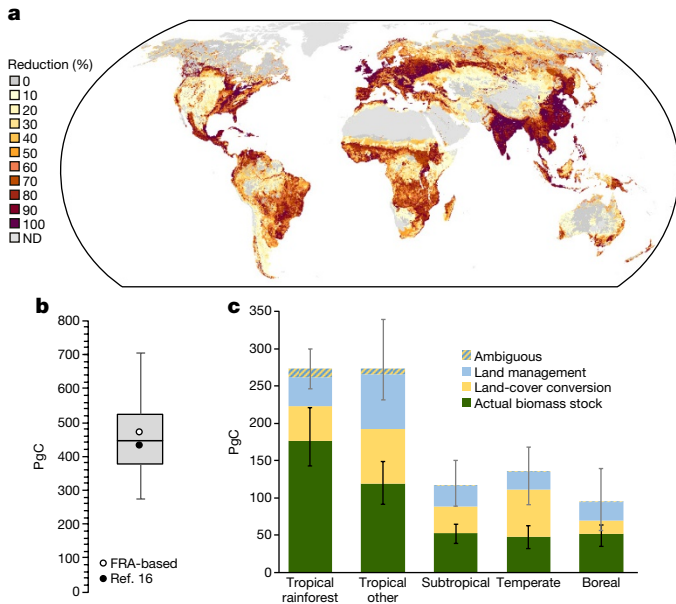


Figure 1 | Differences in biomass stocks of potential and actual vegetation induced by land use. **a**, Spatial pattern of land-use-induced biomass stock differences (expressed as a percentage of potential biomass stocks), mean of all 42 estimates. **b**, Box plot of all 42 estimates of global potential-actual biomass-stock difference. Whiskers indicate the range, the box shows the inner 50% percentiles, the line indicates the median of all estimates; the two dots represent the results of the two approaches used for the attribution of biomass stock differences to land-cover conversion and land management. **c**, Actual and potential biomass stocks in the world's major biomes (see Extended Data Fig. 5f), and role of land-cover conversion and management in explaining their difference. Error bars indicate the range of the estimates for potential (grey; $n = 6$) and actual (black; $n = 7$) biomass stocks. 'Ambiguous' denotes cases attributed differently in the assessments based on FRA and ref. 16.

Two of the actual biomass stock maps (based on the Global Forest Resource Assessment (FRA)¹⁵ and ref. 16) were established on the basis of a present-day land-use dataset (Methods) and therefore enabled the systematic separation of land-cover conversion effects, that is, change in the biomass stocks due to conversion of pristine ecosystems into artificial grassland, cropland or infrastructure; and land management effects, that is, management-induced changes that occur within unaltered land-cover types, such as forests, savannahs and other natural grasslands (Extended Data Fig. 2).

At the global scale, the biomass stocks of the currently prevailing vegetation have a mean of 450 petagrams of carbon (PgC; range of the seven estimates: 380–536 PgC, coefficient of variation: 11%). By contrast, biomass stocks of potential vegetation have a mean of 916 PgC (range of the six estimates, individually adjusted to actual biomass stock maps: 771–1,107 PgC, coefficient of variation: 12%). Therefore, our analysis suggests that land use halves the amount of carbon that is potentially stored in terrestrial biomass (Fig. 1). Irrespective of the climate zone, the difference in biomass between potential and actual stocks mostly follows the pattern of global agriculture, with hotspots in South and East Asia, and Europe, as well as the eastern part of North and South America (Fig. 1a). Considerable differences between potential and actual biomass stocks also occur in regions dominated by forest and natural grassland use (Extended Data Fig. 5a, b). Given that biomass stocks are a function of net primary production and turnover time, a 50% reduction in the turnover time¹⁸ and a 10% land-use-induced decrease in net primary production¹⁹ explains the reduced biomass stocks.

The 42 pairs of potential-actual biomass-stock differences have a median of 49%, with the inner quantiles ranging from 43 to 55%, which implies an average impact on biomass stocks of 447 PgC (median; inner quartiles: 375–525 PgC; Fig. 1b).

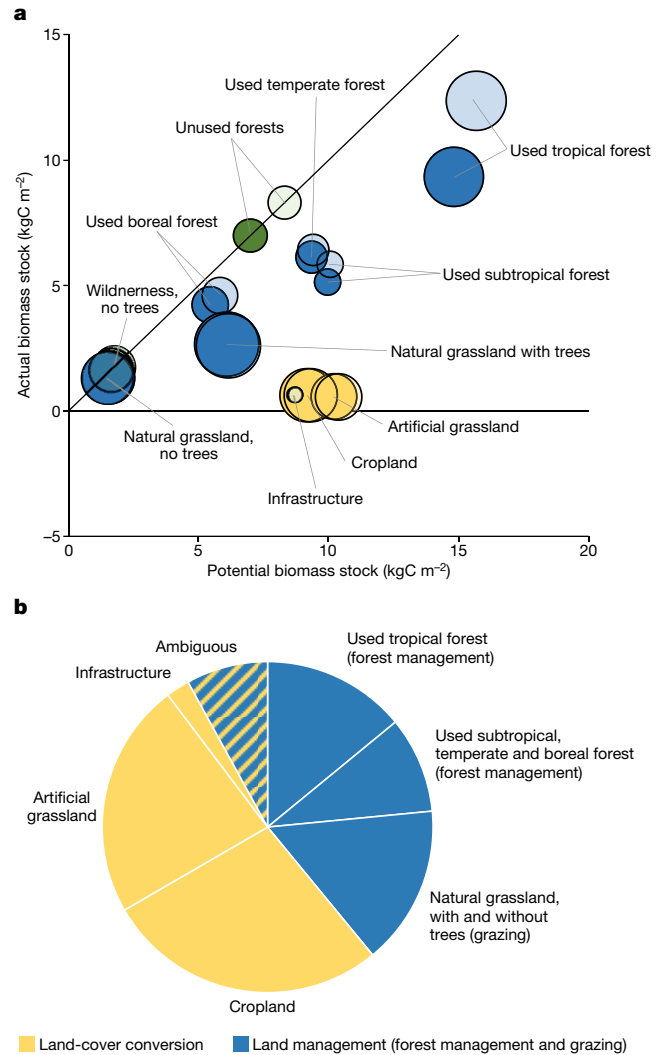


Figure 2 | Contribution of land-use types to the difference between potential and actual biomass stocks. **a**, Potential and actual biomass stock per unit area per land-use type for the assessment based on FRA (dark colours) and ref. 16 (light colours). Circle size is proportional to the global extent of the individual land use type. The diagonal line indicates the 1:1 relationship between actual and potential biomass stocks (no change, green colour). **b**, Relative contribution of land-cover conversion and land management to the difference between potential and actual biomass stocks, calculated on the basis of the assessments based on FRA and ref. 16. 'Ambiguous' denotes cases attributed differently in the two assessments (for absolute values refer to Extended Data Table 1).

The approaches based on FRA¹⁵ and ref. 16 enable the separation of effects of land-cover conversion and land management (Fig. 1c). Owing to land-cover conversion (Methods), actual biomass stocks reach only 10% of potential biomass stocks per unit area (Fig. 2a), affecting only a relatively small area of 28 million km^2 . By contrast, in an area of 56 million km^2 of managed, but not converted, ecosystems, the actual biomass stocks reach 60 to 69% of the potential biomass stock per unit area. As a consequence, land-cover conversion (53–58%) and land management (42–47%) contribute almost equally to the overall difference between potential and actual biomass stocks. Forest management contributes two-thirds and grazing one-third to the management-induced difference in biomass stocks (Fig. 2b and Extended Data Table 1).

The large impact of land management on vegetation biomass suggests that estimates of historical land-use change emissions are incomplete if only deforestation is considered (Extended Data Table 2). Contextualizing our results with accounts of the global terrestrial

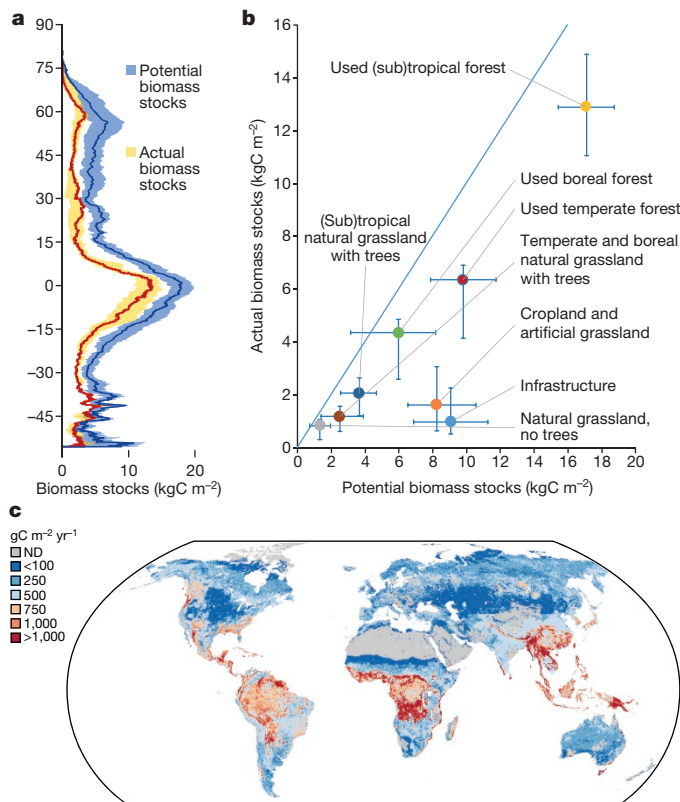


Figure 3 | Uncertainty of biomass stock estimates. **a**, Latitudinal profile of all seven actual (yellow) and all six potential (blue) biomass stock estimates, the lines indicate the respective median, shaded areas the range. **b**, Ranges of potential and actual biomass stocks per land-use type, intersected at the median ($n = 6$ for potential, $n = 7$ for actual biomass stocks). In the absence of consistent land-use information for all layers, biomass stock changes were estimated on grid cells dominated (>85%) by a land-use type and therefore deviate slightly from estimates displayed in Fig. 2. The diagonal line indicates the 1:1 relationship where actual and potential biomass stocks are equal. **c**, Detection limit of annual changes in actual biomass stocks. Changes in biomass stocks need to exceed the detection limit in order to be detectable, for example, in monitoring or stocktaking efforts such as foreseen in the Paris Agreement.

carbon balance suggests that pre-industrial land-use impacts on biomass stocks were considerable (115–425 PgC of the total difference of 375–525 PgC; Extended Data Table 3), corroborating model-based findings²⁰; these larger pre-industrial emissions are consistent with recent estimates of the global carbon budget considering strong but uncertain processes of natural sinks, such as the build-up of peat (see Supplementary Information).

Alternatively—or in addition—they indicate an underestimation of the strength of the current terrestrial carbon sink, as suggested by model-based studies^{12,13}. In order to reduce the large uncertainty range of current estimates, future research will need to scrutinize the role of land management, in particular in non-forest ecosystems, which are often ignored in global carbon studies. It is important to note that the difference between potential and actual biomass stocks represents only a rough proxy for cumulative emissions from land use. Firstly, it does not include soil carbon and product pools. Including soil carbon would probably increase the difference, whereas including products would decrease it. There are large uncertainties for these two components, but their effects are generally estimated to be small in comparison to biomass changes^{12,21}. Secondly, the difference between actual and potential carbon stocks is not identical to stock changes between two points in time. Both actual and potential biomass stocks refer to the same environmental conditions, therefore, their difference integrates two effects: cumulative land-use emissions and land-use induced

reductions in carbon sequestration that would result from environmental changes (Extended Data Fig. 2 and Supplementary Information). Therefore, cumulative emissions are probably smaller than the overall impact of land use on biomass stocks, depending on the uncertain^{13,20} strength of the environmental effect.

The large importance of land management for terrestrial biomass stocks has far-reaching consequences for climate-change mitigation. The difference between actual and potential biomass stocks can be interpreted as the upper boundary of the carbon-sequestration potential of terrestrial vegetation. Long-term changes in growth conditions, for example, due to large-scale alterations in hydrological conditions or severe soil degradation, could lower this potential. Conversely, climate change could increase the future potential biomass stocks of ecosystems, but this effect is highly uncertain^{13,22,23}. Managing vegetation carbon so that it reaches its current potential would store the equivalent of 50 years of carbon emissions at the current rate of 9 PgC per year (PgC yr^{-1}), but that is not feasible, because it would mean taking all agricultural land out of production. More plausible potentials are much lower (Extended Data Table 4); for example, restoring used forests to 90% of their potential biomass would absorb fossil-fuel emissions for 7–12 years. However, such strategies would entail severe reductions in annual wood harvest volumes, because optimizing forest harvest reduces forest biomass compared to potential biomass stocks²⁴. By contrast, widely supported plans to substantially raise the contribution of biomass to raw material and energy supply, for example, in the context of the so-called bioeconomy²⁵, imply a need for increased harvests²⁴. From the perspective of greenhouse gas emissions, the challenge for land managers is to maintain or increase biomass productivity while at the same time maintaining or even enhancing biomass stocks.

Although the uncertainty ranges of actual and potential biomass stocks are typically around 35% of the median estimate, the estimates rarely overlap across the latitudinal north–south gradient (Fig. 3a). Although the potential biomass stock shows a similar uncertainty level across most relevant biomes, uncertainty patterns are noteworthy for the actual biomass stock. Actual biomass-stock estimates are particularly uncertain in the tropics (Fig. 3b, c), a region that contains more than half of the current global biomass stocks (Fig. 1c).

The spatial uncertainty patterns are relevant for designing and monitoring climate-change mitigation efforts such as carbon-stock restoration. Whereas industrialized countries have access to much finer and more robust data than those used here, most developing countries have to rely on global data, such as those used in this study^{5,16}. The uncertainty range could be narrowed if a single robust, validated method would be applied continuously in the stocktaking efforts. Indeed, technical facilities for deriving improved estimates of actual biomass stocks will soon become available (for example, the Biomass mission of the European Space Agency²⁶, the Global Ecosystem Dynamics Investigation mission of the National Aeronautics and Space Administration²⁷ as well as integration efforts (<http://globbiomass.org/>)). The current planning, however, suggests that this capacity will not be fully operational before the inception of the stocktaking processes, and until then, restoration planning and monitoring will have to rely on existing global datasets and their present-day uncertainties.

In boreal and temperate forests, restoration efforts would be detectable even with the present-day uncertainties (Fig. 3c). But three-quarters of the global restoration potential can be found in tropical regions (Fig. 1c and Extended Data Table 4), where biomass stocks would need to increase by over $750 \text{ gC m}^{-2} \text{yr}^{-1}$ for 10 consecutive years to be detectable against variation between global data. A large threat to biomass-stock conservation comes from the use of dry tropical forests and savannahs, in particular in Africa, where these biomes have been identified as having a high potential for increasing global agricultural production, to improve global food security or bioenergy supply²⁸. Given current detection limits for tropical biomes, both the intensification of land use in dry tropical forests and savannahs and the restoration efforts in tropical forests are questionable because of the

possibility of undetectable carbon debts from land-use intensification²⁹ or unverifiable gains from carbon restoration measures.

Our analysis suggests that land-use impacts were pronounced already in the pre-industrial period and reveals that effects of forest management and grazing on vegetation biomass are comparable in magnitude to the effects of deforestation. Therefore, a focus on biomass stocks helps to recognize options for land-based greenhouse gas mitigation beyond the mere conservation of forest area. Our findings also suggest that important trade-offs in climate-change mitigation need to be tackled. The scientific and political focus on forest protection and productivity increases needs to be complemented by analyses of the interactions between land use and the carbon state of ecosystems.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Supplementary Information is available in the online version of the paper.

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Author Contributions K.-H.E., T.K., C.P. and S.L. designed the study and performed the research, A.L.S.B., N.C., T.F., S.G., H.H., C.L., M.N., M.T. and J. P. contributed and analysed data and results, and all authors contributed substantially to the analysis, interpretation of results and writing of the manuscript.

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METHODS

We established six datasets for potential biomass stocks and seven datasets for actual biomass stocks. All maps were constructed at the spatial resolution of five arc minutes. Datasets were chosen on the basis of their coverage (that is, only maps covering large parts of the globe were included) and their plausibility. Given that most datasets did not cover all land-use types, all regions of the globe, or all relevant biomass stocks, some completion exercises were performed to generate consistently comparable datasets. These relied on different types of evidence, such as land-use information, information from census statistics, remotely-sensed information, and modifications of assumptions on biomass-stock density of different land-use categories and ecozones. The construction of the individual maps is described below.

Actual biomass-stock maps 1 and 2. Actual biomass-stock maps 1 and 2 (based on FRA and ref. 16, respectively; see Extended Data Fig. 3a, b) enabled the isolation of the effect of individual land uses. They were based on a consistent land-use dataset, derived and modified from previous work³⁰. The dataset was adjusted to newly available statistical data on the national extent of forests¹⁵ and cropland³¹. Information on cropland types³² was used to identify permanent crops, other trees within cropland³³ are not included in the cropland layer, complying with FAO definitions³¹. Unused land was identified on the basis of previous assessments (for example, delineating unproductive land with a productivity threshold of $20 \text{ gC m}^{-2} \text{ yr}^{-1}$)^{19,30}, information on permanent snow from a land cover product³⁴, a thematic footprint map³⁵ and a map on intact forests³⁶. All land not classified as infrastructure, cropland or forestry was defined as grazing land. Grazing land was split into three layers: (1) Artificial grasslands, that is, grasslands on potentially forested areas; (2) natural grasslands with trees, including savannahs and other wooded land; and (3) natural grasslands without trees (for example, temperate steppes), on the basis of land cover information on the extent of land under agricultural management³⁴, biome maps^{37–39} and MODIS data⁴⁰ on fractional tree cover, applying a tree cover of 5% at the resolution of 500 m to discern grazing land with and without trees, in fractional cover representation. The final land-use dataset discerns the following classes. Unused land: (1) non-productive and snow; (2) wilderness, no trees; (3) unused forests. Used land: (4) infrastructure; (5) cropland; (6) used forests; (7) artificial grassland; (8) natural grassland, no trees; (9) natural grassland with trees.

To each land-use unit, typical biomass-stock density values from the literature or census statistics were assigned. For forests, the FRA-based map uses national-level data from the global Forest Resource Assessment¹⁵. By contrast, the map based on ref. 16 uses data from forest inventories and site data. The estimate from ref. 16 is higher, particularly in the tropical forests, but slightly lower in boreal forest biomass stocks, resulting in overall higher total forest biomass stocks (361 PgC in contrast to 298 PgC, for forests only). National forest biomass stock data were downscaled to the grid using information on tree height from a global database⁴¹, following the finding that tree height is among the critical factors determining biomass stocks and it can thus serve as proxy for the spatial allocation of biomass stock densities at large scales^{18,42}. Minimum biomass-stock density for forests was set to 3 kgC m^{-2} to discern forests from scrub vegetation and other wooded land. For grassland–tree mosaics, no census data on biomass stocks is available. For some countries, data on wood stocking (in m^3) of other wooded land is available¹⁵, showing a range between 0.4% and 21% (inner 50% quartiles) of forest biomass stocks per unit area, with outliers of $>90\%$. World region aggregates of biomass-stock densities on other wooded land range between 15% and 28% of the values for forests, with a world average of 23%. In order to consider non-woody components, which are of larger importance for other wooded land compared to forests, as well as to produce a conservative estimate, we assumed that biomass stocks per unit area on other wooded land were 50% of the corresponding values for forests at the national level. For herbaceous vegetation units (artificial grassland on potential forest sites, cropland and natural grassland without trees), we assumed that biomass stocks were equal to the annual amount of net primary production¹⁸. For permanent cropland, we added 3 kgC m^{-2} for tree-bearing systems and 1.5 kgC m^{-2} for shrub-bearing systems to account for woody above- and belowground compartments, in line with estimates in the literature (see Supplementary Table 3). In the absence of data, and owing to the small extent of this land-use type, biomass stocks on infrastructure areas were calculated as one sixth of potential biomass stocks. This assumes one-third of infrastructure to be covered by 50% vegetation with trees and 50% artificial grassland (the latter was assigned no additional biomass, as the potential biomass stocks already provide a progressive estimate). Effects of land degradation on natural grassland (with and without trees) were modelled on the basis of losses in net primary productivity derived from ref. 43.

Actual biomass stock maps 3 and 4. Actual biomass stock maps 3 and 4 were based on refs 6 and 7, respectively, in combination with ref. 8; see Extended Data Fig. 3c, d. Two remote-sensing-based maps were created by combining independent remote-sensing products for tree vegetation (including foliage) and expanding them to account for belowground and herbaceous compartments where

necessary. At the global scale, five distinct regions can be discerned with regards to the availability of global remote-sensing-based products. For the northern boreal and temperate forests one product is available^{8,44}. A large part of the tropical zone is covered by two datasets^{6,7}. These two datasets show pronounced differences, among each other as well as in comparison with *in situ* data^{9,10}. A smaller fraction of the tropical zone, including a large part of Australia, South America and South Africa is covered by only one of the remote-sensing datasets⁶, whereas a region in China is covered by two datasets^{6,8}. For some regions (the southernmost part of Australia, parts of Oceania), no remote-sensing data are available. In these regions, map 1 was used in the compilation of map 3 and 4. Map 3 was constructed by complementing forest biomass stock data for the temperate and boreal zones⁸ with data on net primary productivity¹⁸ in order to account for herbaceous vegetation, applying a forest–non-forest mask derived from the GLC2000 land cover map³⁴. The resulting map for the northern forests was combined with the biomass stock map for the tropical zone⁶. The latter was also extended with data on net primary productivity¹⁸ to account for the herbaceous fractions. For map 4, we replaced values for woody vegetation from map 3 with data from ref. 7, where available.

Actual biomass stock maps 5 and 6. Grid-cell-based minima and maxima of the remote-sensing maps; see Extended Data Fig. 3e, f. While maps 3 and 4 serve as a best-guess available from remote-sensing products, these two maps were based on a statistical approach, calculating the grid-cell-based minima and maxima of various remote-sensing input data, enabling an assessment of the absolute upper and lower boundaries, breaking up the auto-correlated nature of remote-sensing-derived maps. Maps 3 and 4 were used as input. Furthermore, a modulation was calculated for the area covered only by the map of ref. 8. This map uses a forest mask derived from GLC2000³⁴. In order to reflect the uncertainty of this land cover map, we used an alternative forest mask to calculate new values at the grid level. We projected the grid-based biomass stock density (biomass per unit area) values from ref. 8 to the MODIS fractional tree cover dataset⁴⁰. Additionally, alternative maps for net primary productivity were used to complement these biomass stock maps for woody vegetation, derived by a vegetation model⁴⁵, a numerical model⁴⁶ and from remote-sensing estimates⁴⁷. Map 5 was calculated as the cell-based minima, map 6 as the cell-based maxima of these input layers.

Actual biomass stock map 7. A seventh map was taken from the literature⁴⁸; see Extended Data Fig. 3g.

No robust empirical information is available that would allow resolution of the discrepancies between the two datasets on the basis of consistent, spatially explicit land-use information (maps 1 and 2). The difference between these two estimates was 79 PgC. Both assessments are inventory-based, but in ref. 16 long-term measurements of network plots for the tropical regions were used to compensate for data gaps, whereas FRA reports national data that are often based on remote sensing. The contribution of global remote-sensing data (benchmark maps) to resolve this discrepancy is still limited. The two available high-resolution datasets covering the tropics^{6,7} show pronounced differences, between each other and in comparison with *in situ* data^{9,10}. The estimate from ref. 16 is situated between these two estimates, whereas the estimate from the FRA is situated below the minimum. However, a study based on alternative site data¹¹ corrected both maps downwards, close to the grid-based minimum of both accounts, better matching the FRA-based assessment.

Potential biomass stock maps. Potential vegetation refers to a hypothetical state of vegetation, which would prevail without human activities but under current climate conditions⁴⁹. We compiled five maps following an ecozone approach, allocating typical carbon densities of zonal vegetation to state-of-the-art ecozone maps for current climate conditions^{37–39}, with current coastlines and current permanent ice cover. The carbon-density values refer to landscape-level averages and take effects of age distribution and natural disturbance into account. We used high-resolution data from the ESA GlobCover 2009 Project⁵⁰ to exclude small water bodies and small-scale bare areas, with the exception of ecosystems where carbon-stock values already take bare areas into account, for example, steppes and thorn savannahs. Small-scale variability caused by, for example, the spatial variability of edaphic conditions or water availability (azonal vegetation) was neglected. No information is available that allows us to determine whether this omission, or sampling biases in the input data, introduces an upward or downward bias in the maps. Input data could be biased towards high values if sampling favoured undisturbed, old-grown stands, or towards lower values, if the data were derived from human-disturbed vegetation in the absence of natural vegetation remnants for certain ecosystem types. The comparison with other estimates shows that our data are well in line with the literature (Extended Data Fig. 1) and suggest that such biases have a minor role. Furthermore, approximations of upper and lower estimates for potential vegetation were calculated to determine realistic ranges of global biomass stocks.

Potential biomass stock maps 1 and 2. IPCC-based maps, FRA-adjusted or adjusted to ref. 16; see Extended Data Fig. 4a, b. Two maps were constructed to consistently match the actual biomass stock maps 1 and 2. They build from

best-available estimates on potential, landscape-averaged biomass-stock densities for zonal vegetation, mainly from IPCC values⁵¹, with the exception of boreal forests. For boreal forests, owing to large uncertainties^{42,52,53}, the maximum values of biome-wide actual biomass stocks per unit area between 1990 and 2007¹⁶ were used to derive a conservative estimate. Map 1 was subsequently adjusted at the grid level so that potential biomass stock values below actual biomass stock levels matched the actual biomass stocks in the FRA-based map. For map 2, this adjustment was done with the map based on ref. 16.

Potential biomass stock maps 3 and 4. Maps 3 and 4 were based on classic ecological data: cell-based minima and maxima; see Extended Data Fig. 4c, d. Two further maps were calculated by using biomass stock density values^{3,38,54} for natural, zonal vegetation, from synthesis efforts of site-specific data, for example, from the International Biological Programme⁵⁵. Similar to maps 1 and 2, these values were allocated to the three biome maps^{37–39}, and the cell-based minima (map 3) and maxima (map 4) of all three maps were calculated.

Potential biomass stock map 5. A remote-sensing-based map; see Extended Data Fig. 4e. A fifth map was derived from the remote-sensing maps 3 and 4 on actual biomass stocks. For all 1,303 ecozones that result from the intersection of the three biomes maps^{37–39} mentioned above (see Extended Data Fig. 5e), the 95 percentile biomass stock values of all 30 arc second grid cells (1×1 km at the equator) within one ecozone, excluding agricultural lands, derived from the GLC2000³⁴, was calculated. For ecozones covered by more than one remote-sensing map, we used the arithmetic mean. This approximation builds on the assumption that in each ecozone, areas of natural vegetation units remain that are representative for the potential biomass-stock densities of the respective ecozone and that the values take natural disturbance into account (owing to the grain size of the input maps and selection procedure). This is confirmed by a cross-check that revealed that the 95 percentile is on average 51% lower than the maximum values found in each ecozone. Using maximum values, the global biomass would be 1.56 times larger than the one estimated here. An upper bias in this map could emerge from the neglect of naturally unfavourable sites within an ecozone (owing to, for example, low water availability or soil fertility); a lower bias could emerge if in an ecozone only disturbed vegetation units prevail, or most of the favourable sites are converted.

Potential biomass stock map 6. An independent sixth map was taken from the literature⁵⁶; see Extended Data Fig. 4f.

Calculation of the land-use-induced difference in potential-actual biomass stocks. In order to assess the range of the effect of land use on biomass stocks, 42 potential-actual biomass-stock difference maps were calculated by combining the seven actual biomass-stock maps with the six potential biomass-stock maps. In all cases, we adjusted the maps where necessary, so that the actual biomass stocks would not surpass the potential biomass stocks. Increases in actual over-potential biomass stocks could be caused, for instance, by fire prevention. However, the magnitude of this effect is highly uncertain at larger spatial scales, because fire prevention often leads to less frequent, but more damaging fires with larger biomass loads that could compensate for carbon gains^{57,58} on longer time scales. On unused land (for example, wilderness), no land-use induced biomass-stock reduction was assumed. Unproductive and water areas were excluded from the assessment. Differences in the spatial thematic resolution of potential and actual biomass-stock maps warrant a caveat when interpreting the fine-scale results of the biomass-stock difference.

Attribution to land management and land-cover conversions. For two of the actual biomass stock maps, we could isolate and quantify the impact of individual land-use types, that is, the maps based on consistent, detailed land-use information (actual biomass stock maps 1 and 2). From these maps, land-cover conversion impacts were calculated as the sum of potential-actual biomass-stock differences due to cropland, artificial grassland (that is, grassland on potential forest sites) and infrastructure. The biomass-stock differences of all other land-use types were accounted for as the impact of land management (Extended Data Fig. 2). Forest management was considered to dominate land-management effects in forests, and land-management practices on other used lands were considered as grazing. This approach represents a proxy only. A sharp and unambiguous separation between land-cover conversion and land management would require information on past land uses, which currently is not available, as well as arbitrary decisions on thresholds of change. Examples to illustrate these intricacies are: the biomass stock change on a parcel of land that was cleared from pristine forests to cropland in the past and, after cropland abandonment, is used as forest plantation, would be accounted for as land management, while it would—at least to a certain degree—also represent land-cover conversion if historic uses were to be considered. Similarly, if a forest clear-cut area is used for grazing during the re-growth phase, the biomass-stock difference would be attributed to land-cover conversion, whereas it might also represent land management. If, due to land use, a forest is changed in terms of its species composition, crown closure, stem height and so

on, but still remains within key forest parameters (for example, >10% tree cover, stem height >5 m), it is eventually an arbitrary decision whether this change is a land-cover conversion or land management. Additionally, the effects of forest management versus grazing cannot fully be disentangled, because of practices, such as forest grazing and wood extraction for fuel in natural grasslands. Given these practical and theoretical ambiguities, we argue that the simple allocation scheme adopted here is a useful proxy based on transparent considerations, making best use of the available datasets. For preparation of Figs 1c and 2b, we calculated the contributions of land management and conversions separately for the maps based on the data from FRA and ref. 16. The minima of the contribution of each land-use type were used for the attribution. The difference in the sum of all minima to 100% was labelled as ‘ambiguous’, as it is attributed to land management in the map based on FRA¹⁵ and land-cover conversion in the map based on ref. 16, or vice-versa (see Extended Data Table 1).

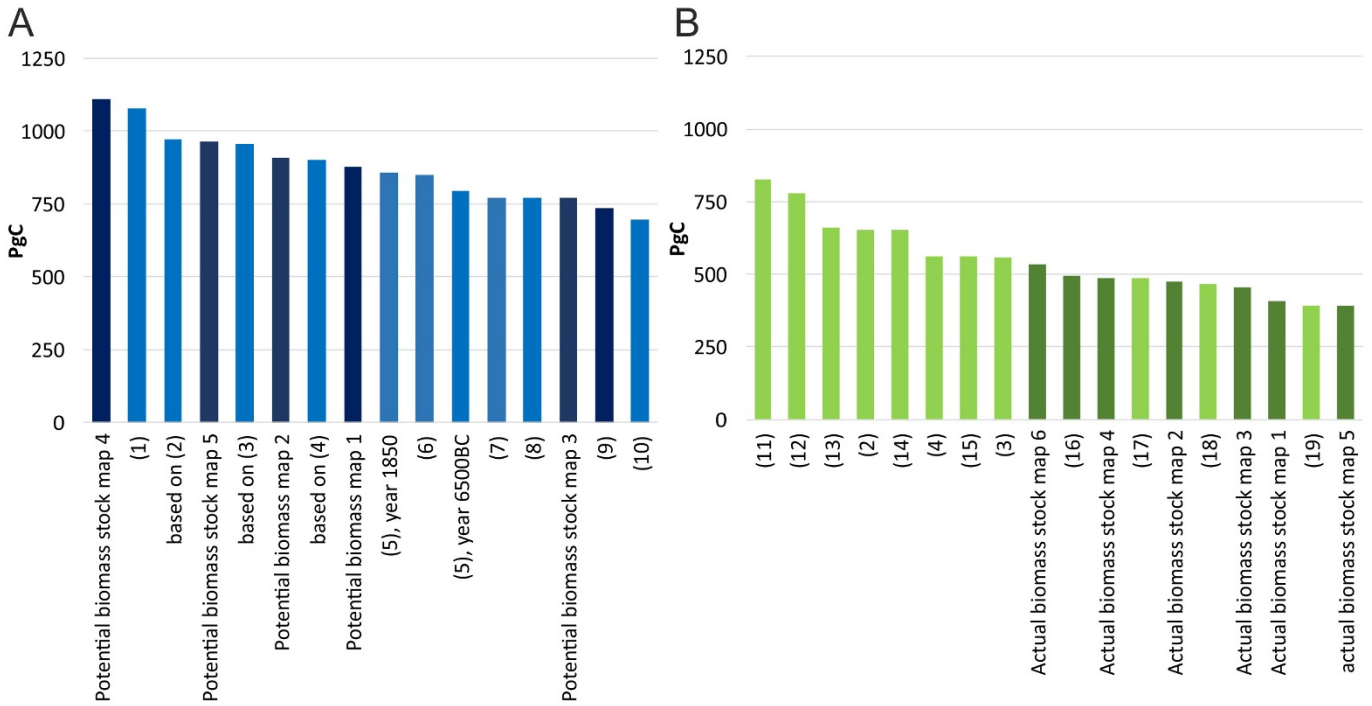
Calculation of the detection limits on the basis of the actual biomass-stock maps. The spatially explicit detection limit for stock changes in actual biomass was estimated from the variation between the seven actual biomass estimates. This assumes that the uncertainty is driven by differences in approaches rather than measurement errors within a single approach and that the seven estimates of the actual biomass stocks are equally likely and, therefore, the main source of uncertainty. For each grid cell we mimicked a stocktaking at present (t) and after 10 years ($t + 10$) by randomly selecting two biomass stocks from the uncertainty between approaches for that cell. Subsequently, the detected annual change in biomass stock was calculated. A distribution of 1,000 detected annual changes was obtained through resampling. Given that the annual changes were calculated by sampling the same distribution at t and $t + 10$, there were no underlying changes in biomass stock. The inner 95% of the detected stock changes within each grid cell were assumed to be insignificant. The 5% stock changes that were found to be significant despite the biomass stock being constant between t and $t + 10$, were used as an estimate for the detection limit in that grid cell. Given present-day uncertainties, a real stock change should thus exceed the detection limit to be correctly classified as a change. At present, evidence is missing to consider one approach as being more precise and accurate than the other approaches^{9,10,59}. Nevertheless, if future advances would enable selecting a single best approach, the uncertainty and detection limit would decrease and in turn enhance the capacity for verification of changes in biomass stocks.

Code availability. Esri ArcGIS and MATLAB codes used in the compilation and analysis of results are available upon request from the corresponding author.

Data availability. The data sources for actual and potential biomass-stock estimates are listed above. Source Data for Figs 1b, c, 2a, b, 3a, b and Extended Data Fig. 1 are provided with the online version of the paper. Final results, data and maps are available at <http://www.uni-klu.ac.at/socec>. Underlying data, for example, data from other sources, which support findings of this study, are available from the corresponding author upon request.

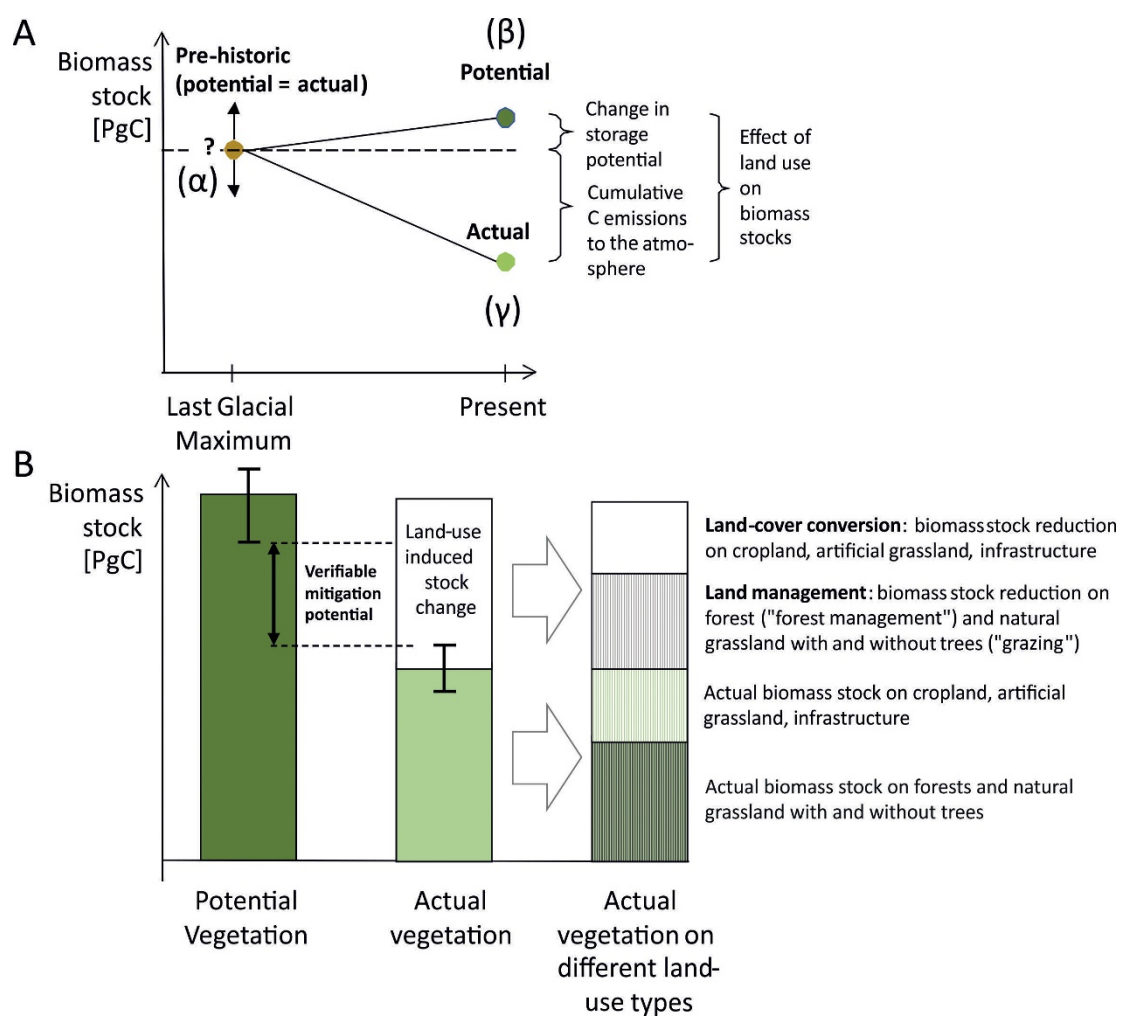
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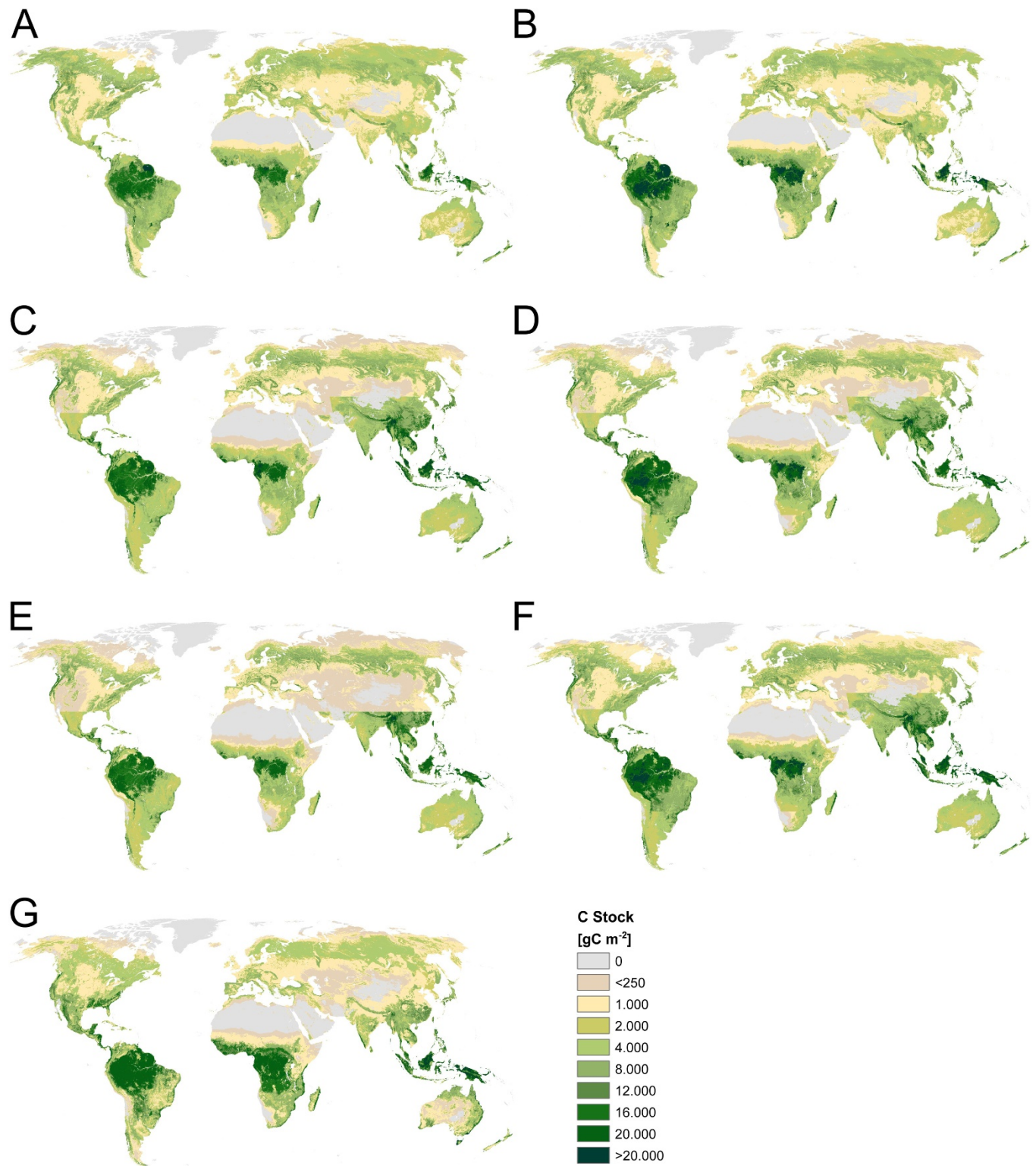
Extended Data Figure 1 | Estimates of the potential and actual biomass stocks from the literature and this study. a, Potential biomass stocks. **b,** Actual biomass stocks. Datasets from the following studies were used:

(1)⁶⁹, (2)³, (3)⁷⁰, (4)⁵⁴, (5)²⁰, (6)⁷¹, (7)⁷², (8)⁷³, (9)⁵⁶, (10)⁷⁴, (11)⁷⁵, (12)⁷⁶, (13)⁷⁷, (14)⁷⁸, (15)⁷⁹, (16)⁴⁸, (17)⁸⁰, (18)⁸¹ (19)⁷². The darker shaded columns are those used in this study (for details see text).



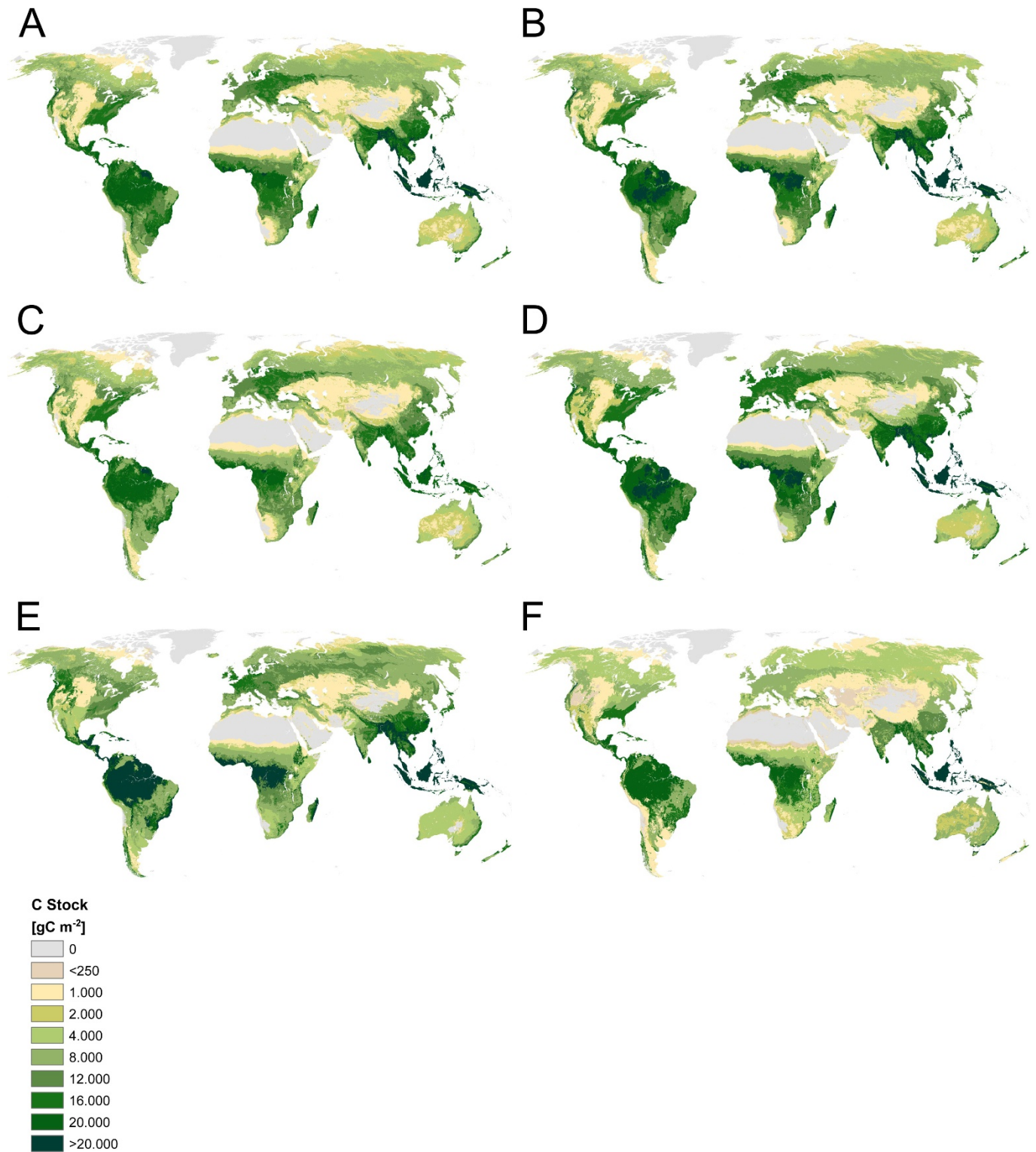
Extended Data Figure 2 | Conceptual and methodological design of the study. **a**, The relation of prehistoric (α), potential (β) and actual (γ) biomass stocks. Potential vegetation refers to the vegetation that would prevail in the absence of land use but with current environmental conditions. As both actual and potential vegetation refer to the same environmental conditions, their difference must not be interpreted as a stock change between two points in time. As a consequence, the comparison of potential and actual biomass stocks does not refer to the cumulative net balance of all fluxes from and to the biomass compartment (for example, induced by land-use and environmental changes). Rather,

it isolates and quantifies the effect of land use on biomass stocks. The effect of land use consists of two components, that is, cumulative land-use emissions and land-use-induced reductions in carbon sequestration that would result from environmental changes. For more information and discussion, see Supplementary Information. **b**, Conceptual attribution of the difference between potential and actual biomass stocks to land conversion and land management. Error bars reflect the divergence among datasets for the respective vegetation types and indicate the determination of verification volumes.



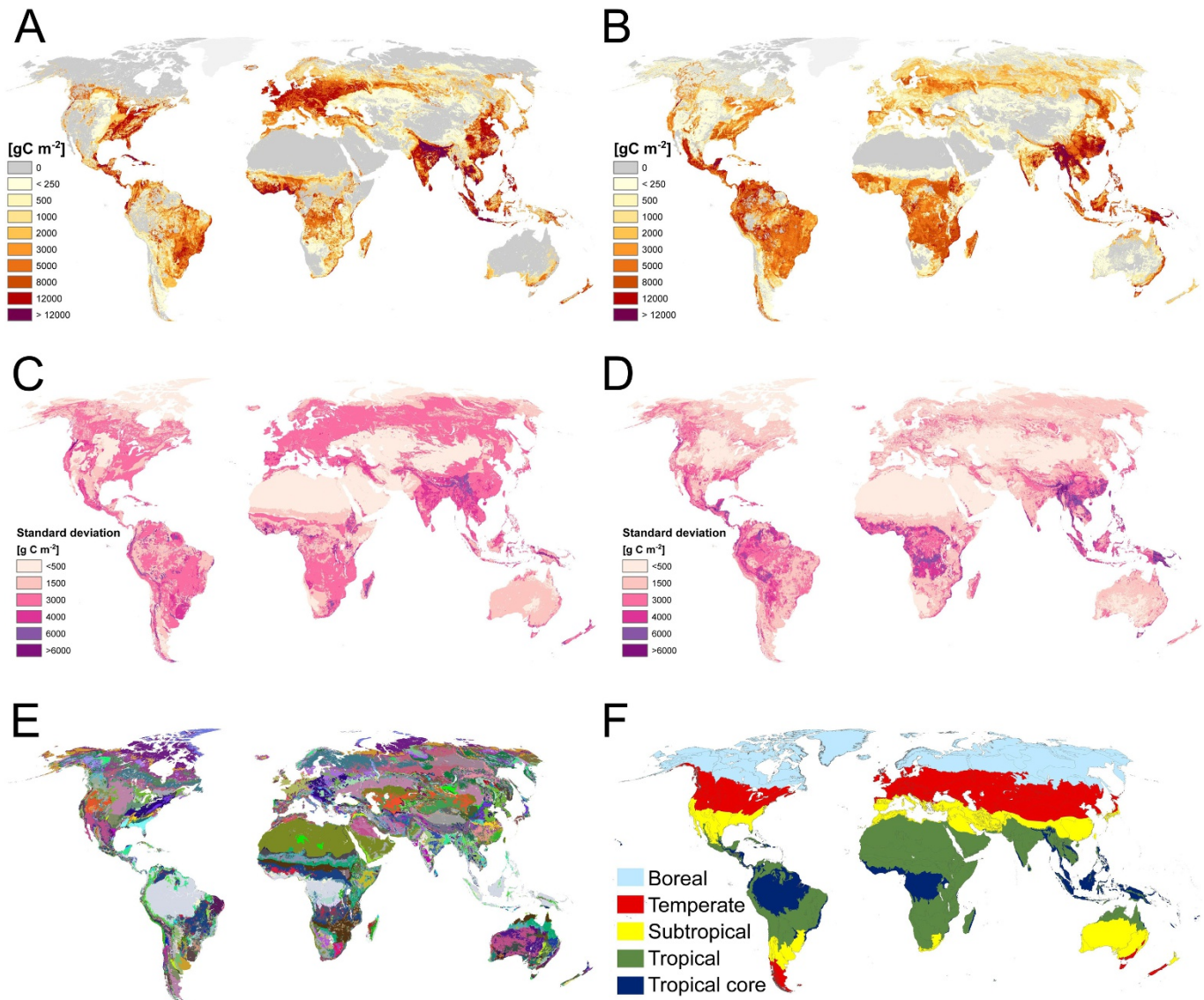
Extended Data Figure 3 | Actual biomass stock maps used in the study. **a**, FRA-based map. **b–d**, Maps based on refs 16 (**b**), 6 and 8 (**c**), and 7 and 8 (**d**). **e**, Remote-sensing-derived minimum. **f**, Remote-sensing-derived

maximum. **g**, Map from ref. 48. The same mask for unproductive areas has been applied to all maps. For details and sources of maps in **a–f**, see Methods.



Extended Data Figure 4 | Potential biomass stock maps used in the study. **a**, IPCC-based, FRA-adjusted map. **b**, IPCC-based map adjusted using data from ref. 16. **c**, Cell-based minima of classic data. **d**, Cell-based

maxima of classic data. **e**, Remote-sensing-derived map. **f**, Map from ref. 56. The same mask for unproductive areas has been applied to all maps. For details and sources for maps in **a–e**, see Methods.



Extended Data Figure 5 | Land-use-induced difference in potential and actual biomass stocks, uncertainty of input data and vegetation units used in the study. a, Impact of land-cover conversion. b, Impact of land management. a, b, Maps are based on the FRA-based actual biomass-stock map and the corresponding, IPCC-based FRA-adjusted potential carbon-stock map. c, Standard deviation of potential biomass-stock maps ($n = 6$).

d, Standard deviation of actual biomass-stock maps ($n = 7$). e, Intersect of all three^{37–39} biome maps used in the ecozone approaches and for the construction of the remote-sensing-based potential biomass-stock map. f, FAO ecozones³⁷ used for the aggregation of results. The ‘tropical core’ consists of humid rainforests. The tropical zones contain moist deciduous forests, dry forests, tropical shrubs, savannahs and hot deserts.

Extended Data Table 1 | Biomass stocks per type of land use

	Area [Mkm ²]	Potential Biomass Stocks		Actual Biomass Stocks		Difference [%]	Contribution to difference [%]
		[PgC]	[kgC m ⁻²]	[PgC]	[kgC m ⁻²]		
Total	130.4	876-906	6.7-6.9	407-476	3.1-3.6	48-54%	100%
<i>Infrastructure</i>	<i>1.4</i>	<i>12</i>	<i>8.6-8.7</i>	<i>1</i>	<i>0.7</i>	<i>92-93%</i>	<i>2-3%</i>
<i>Cropland</i>	<i>15.2</i>	<i>139-141</i>	<i>9.2-9.3</i>	<i>10</i>	<i>0.6</i>	<i>93%</i>	<i>28-31%</i>
<i>Grassland and grazing land</i>	<i>54.3</i>	<i>374-379</i>	<i>6.9-7.0</i>	<i>119-121</i>	<i>2.2</i>	<i>69-70%</i>	<i>54-60%</i>
<i>Forests</i>	<i>40.7</i>	<i>443-460</i>	<i>10.9-11.5</i>	<i>297-368</i>	<i>7.3-9.0</i>	<i>22-33%</i>	<i>23-31%</i>
<i>Unused non-forest land</i>	<i>26.2</i>	<i>16-17</i>	<i>0.6</i>	<i>16-17</i>	<i>0.6</i>	<i>0%</i>	<i>0%</i>
Land cover change (LCC)							
Cropland	15.2	139-141	9.2-9.3	10	0.6	93%	28-31%
Artificial grasslands	11.3	114-116	10.1-10.3	7	0.6	94%	23-25%
Infrastructure	1.4	12	8.6-8.7	1	0.7	92-93%	2-3%
Land management (LM): forest management							
Used forests							
tropical	22.3	311-327	14.0-14.7	192-251	8.6-11.3	23-38%	18-25%
temperate	5.4	51	9.3-9.4	33-35	6.1-6.4	32-34%	4%
boreal	7.0	40-41	5.7-5.8	30-32	4.2-4.6	21-25%	2%
<i>Subtotal forest management</i>	<i>34.7</i>	<i>401-419</i>	<i>11.6-12.1</i>	<i>255-318</i>	<i>7.3-9.2</i>	<i>24-36%</i>	<i>23-31%</i>
Land management (LM): grazing							
Other wooded land, grasslands-tree mosaics							
tropical	14.6	109-110	7.5	47	3.2	57%	13-15%
temperate	4.0	11	2.8-2.9	5-6	1.2-1.4	50-58%	1-2%
boreal	2.9	10	3.4-3.5	5	1.5-1.7	51-56%	1%
Natural grassland w/o trees	14.2	21	1.5	19	1.3	11-13%	0-1%
<i>Subtotal grazing land</i>	<i>35.7</i>	<i>151-153</i>	<i>4.2-4.3</i>	<i>75-76</i>	<i>2.1</i>	<i>50-51%</i>	<i>16-18%</i>
No biomass stock change							
Wilderness, productive, w/o trees	9.7	16-17	1.6-1.7	16-17	1.6-1.7	0%	0%
Unused forests	6.0	42-50	7.0-8.3	42-50	7.0-8.3	0%	0%
Unproductive area	16.5	-	-	-	-	0%	0%
Land cover change (LCC)	27.8	265-269	9.5-9.7	17.1	0.6	94%	53-58%
Land management (LM)	56.2	553-572	7.9-8.1	312-374	4.7-5.6	31-40%	42-47%

Ranges indicate the difference between the estimates based on FRA and on ref. 16. Mkm², million km².

Extended Data Table 2 | Compilation of published estimates of emissions associated with anthropogenic land-cover change and land management until present (industrial and pre-industrial)

Reference	Land management activities considered	Cumulative emissions
Total cumulative emissions from land use		
DeFries et al., 1999 ⁶¹	--	182-199
Strassmann et al., 2008 ⁶²	--	233
Olofsson and Hickler, 2008 ⁶³	Crop harvest	194-262
Pongratz et al., 2009 ⁶⁰	--	171
Kaplan et al., 2010 ²⁰ , Hyde 3.1 based*	--	137-189
Kaplan et al., 2010 ²⁰ , KK10 based*	Land-use intensity, shifting cultivation	325-357
Stocker et al., 2014 ⁶⁴	Wood and crop harvest, tillage, shifting cultivation	243
<i>This study, FRA- and Pan-based</i>	<i>Top-down, all activities</i>	<i>431-469</i>
<i>This study, inner quartiles of 42 estimates</i>	<i>Top-down, all activities</i>	<i>375-525</i>

Note that most model-based results include fluxes from soils and wood products. Datasets are from refs 20, 60–64.

*Pre-industrial emissions only.

Extended Data Table 3 | Comparison of the difference between potential and actual biomass stocks to components of the global carbon balance, including land-use change (LUC) emissions and net terrestrial biosphere sink

	i) cumulative, before 1800	ii) cumulative, since 1800	iii) Cumulative (i + ii)	This Study (potential-actual biomass stock difference)
(1) LUC emissions	353 PgC (310 -395); calculated from (2) and (3)	140 PgC (100-180, Sabine et al. ⁶⁸) [IPCC ⁴ : 100-260 PgC]	493 PgC (410 - 575) [IPCC ⁴ : 410-655 PgC]	447 PgC (375 - 525)
(2) Terrestrial biosphere sink	-270 PgC (Peat, e.g. Carcaillet et al. ⁶⁵ , Kleinen et al. ⁶⁶ , Yu et al. ⁶⁷)	-101 PgC (-61 - -141; Sabine et al. ⁶⁸)	-371 PgC (-331 - -411)	
(3) Net terrestrial balance (1)+(2)	83 PgC 40 – 125 (Kaplan et al. ²⁰)	39 PgC (11-67; Sabine et al. ⁶⁸)	122 PgC (51-192)	

The difference in biomass stock of 447 PgC (375–525) is well in line with estimates of total (before and since 1800) cumulative emissions from LUC. For details and discussion, see Supplementary Information. Datasets are from refs 4, 20, 65–68.

Extended Data Table 4 | Hypothetical absorption potentials of carbon stock restorations and indicative years until saturation at a current emission level of 9 PgC yr⁻¹

Restoration of	FRA-based	Pan-based	Years*	
	[PgC]	[PgC]	[yr]	[yr]
All C-stocks to 100% of potential	469	431	52	48
Cropland to 100% potential	129	131	14	15
Artificial pastures to 100% of potential	107	109	12	12
Cropland & artificial pastures to 30% of potential	60	61	7	7
Boreal forests to 100% of potential	10	9	1	1
Temperate forests to 100% of potential	17	16	2	2
Tropical forests to 100% of potential	119	76	13	8
All forests to 100% of potential	147	101	16	11
Boreal forests to 90% of potential	6	4	1	0
Temperate forests to 90% of potential	12	11	1	1
Tropical forests to 90% of potential	88	44	10	5
All forests to 90% of potential	106	59	12	7
Boreal forests to 80% of potential	2	0	0	0
Temperate forests to 80% of potential	7	6	1	1
Tropical forests to 80% of potential	57	11	6	1
All forests to 80% of potential	66	17	7	2
Other wooded land and savannas to 100% of potential	73	75	8	8
Other wooded land and savannas to 80% of potential	47	49	5	5

Note that a restoration to 100% of the potential probably entails a cessation of the respective land use, due to the intrinsic relations of harvest and carbon stocks²⁵.

*Years until saturation at current carbon emissions of 9 PgC yr⁻¹.

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▶ Experimental design

1. Sample size

Describe how sample size was determined.

No statistical methods used to predetermine sample size. All relevant data were used, datasets were chosen based on their coverage (i.e. only maps covering large parts of the globe were included) and their plausibility. Methods section, para 1 and 2 contains info on the selection of analyzed maps.

2. Data exclusions

Describe any data exclusions.

No data excluded from the analysis,

3. Replication

Describe whether the experimental findings were reliably reproduced.

not applicable

4. Randomization

Describe how samples/organisms/participants were allocated into experimental groups.

not applicable

5. Blinding

Describe whether the investigators were blinded to group allocation during data collection and/or analysis.

not applicable

Note: all studies involving animals and/or human research participants must disclose whether blinding and randomization were used.

6. Statistical parameters

For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or in the Methods section if additional space is needed).

- | | |
|-------------------------------------|---|
| n/a | Confirmed |
| <input type="checkbox"/> | <input checked="" type="checkbox"/> The <u>exact sample size</u> (n) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.) |
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| <input checked="" type="checkbox"/> | <input type="checkbox"/> A statement indicating how many times each experiment was replicated |
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| <input checked="" type="checkbox"/> | <input type="checkbox"/> The test results (e.g. P values) given as exact values whenever possible and with confidence intervals noted |
| <input type="checkbox"/> | <input checked="" type="checkbox"/> A clear description of statistics including <u>central tendency</u> (e.g. median, mean) and <u>variation</u> (e.g. standard deviation, interquartile range) |
| <input type="checkbox"/> | <input checked="" type="checkbox"/> Clearly defined error bars |

See the web collection on [statistics for biologists](#) for further resources and guidance.

► Software

Policy information about [availability of computer code](#)

7. Software

Describe the software used to analyze the data in this study.

Microsoft Excel 2013, Esri ArcGis 10.2, Matlab R2013a

For manuscripts utilizing custom algorithms or software that are central to the paper but not yet described in the published literature, software must be made available to editors and reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). *Nature Methods* [guidance for providing algorithms and software for publication](#) provides further information on this topic.

► Materials and reagents

Policy information about [availability of materials](#)

8. Materials availability

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a for-profit company.

No restrictions

9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).

not applicable

10. Eukaryotic cell lines

a. State the source of each eukaryotic cell line used.

not applicable

b. Describe the method of cell line authentication used.

not applicable

c. Report whether the cell lines were tested for mycoplasma contamination.

not applicable

d. If any of the cell lines used are listed in the database of commonly misidentified cell lines maintained by [ICLAC](#), provide a scientific rationale for their use.

not applicable

► Animals and human research participants

Policy information about [studies involving animals](#); when reporting animal research, follow the [ARRIVE guidelines](#)

11. Description of research animals

Provide details on animals and/or animal-derived materials used in the study.

not applicable

Policy information about [studies involving human research participants](#)

12. Description of human research participants

Describe the covariate-relevant population characteristics of the human research participants.

not applicable